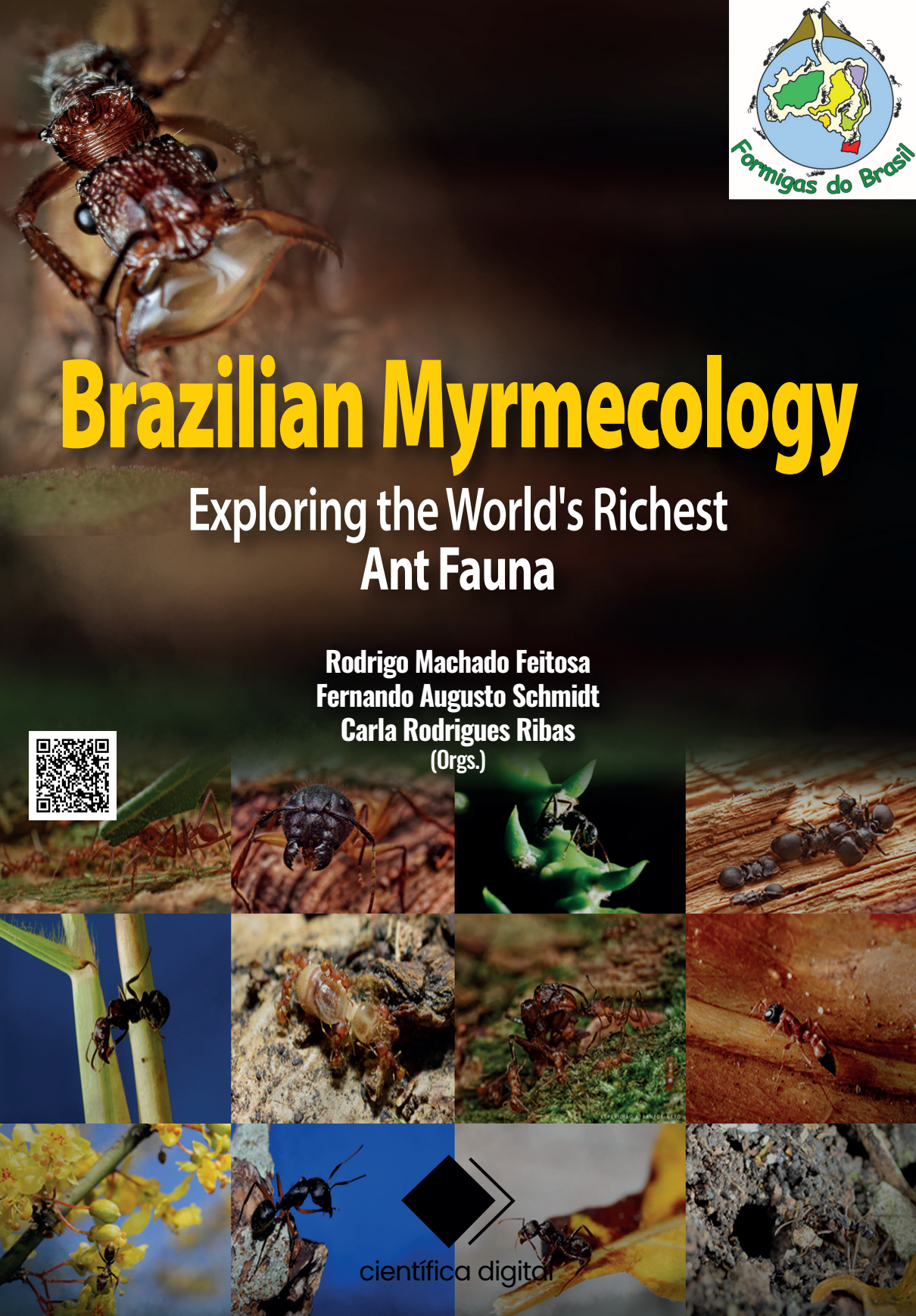


# Brazilian Myrmecology

## Exploring the World's Richest Ant Fauna

Rodrigo Machado Feitosa
Fernando Augusto Schmidt
Carla Rodrigues Ribas
(Orgs.)

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Índice para catálogo sistemático:
I. Ciências biológicas

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# Exploring the World's Richest Ant Fauna

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# PREFACE

A new scientific work is always exciting for readers interested in the field. Such is the case with *Brazilian Myrmecology: Exploring the world's richest ant fauna*, which presents itself as a treasure for Brazilian myrmecologists and for all those wishing to venture into this wonderful and fascinating world of ants.

This volume comprises 24 chapters written by professionals in the field and by students preparing to work in myrmecology. It covers a wide range of topics related to taxonomy, bioecology, and ethology of these insects, as well as a brief history of myrmecology in Brazil. On this latter subject, I feel both proud and nostalgic for having been part of this journey in our country.

I share with readers here my feelings of countless cherished memories from the time when the "Encontro de Mirmecologia" always took place in the state of São Paulo, and when the female presence was still very limited. There were only a few of us women who actively participated in the work, lectures, short courses, etc., such as Professors Elena Diehl, Maria José Hebling, Ana Harada, myself, and later Dr Ana Eugênia Campos. With the event expanding to other states, I feel that myrmecology truly grew in Brazil. The "Encontro" became a Symposium, first held in Viçosa, Minas Gerais, in 1988, organised by us at the Federal University of Viçosa (UFV), and later in Campo Grande, Mato Grosso do Sul. In 1993, the International Symposium on Pest Ants took place in Belo Horizonte, Minas Gerais, also organised by us at UFV, where the book *As Formigas Cortadeiras* ("The Leaf-Cutting Ants"), edited by me, was launched.

Needless to say, the Myrmecology Symposia have only grown over time and have become major events, even attracting a considerable international audience. I am grateful to have witnessed this progress.

The female presence has steadily increased over the years, and I have the impression that today we are very close to equalling the number of men in the field. To them, I can only express gratitude for the encouragement and good experiences. This is one of the reasons for the success of myrmecology in Brazil: unity has brought progress.

I shall not go on at length, as an engaging reading awaits the reader in this great and indispensable volume for all those who wish to engage with this fascinating branch of science.

**Dra. Terezinha Maria Castro Della Lucia**
Professora Titular Emérita do Departamento de Biologia Animal
Universidade Federal de Viçosa

# EDITORIAL

## BRAZILIAN MYRMECOLOGY: EXPLORING THE WORLD'S RICHEST ANT FAUNA

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It does not matter if you are sweeping your backyard, enjoying a drink at a beachside bar, or hiking in the mountains. It will not take long before an ant walks past you. Except for the Earth's poles, ants are found in abundance in virtually every terrestrial environment. In fact, it is estimated that there are 20 quadrillion (20,000,000,000,000,000) ants in the world—that is, about 2.5 million ants for every person on the planet. These ants are distributed among roughly 14,500 species (BOLTON, 2025), although the real number very likely exceeds 20,000, highlighting just how much remains to be explored in terms of the diversity of this group.

Being such a conspicuous, abundant, and diverse group, ants are obviously fundamental creatures in any ecosystem. They engage in a wide range of ecological interactions with countless organisms, from bacteria to trees, and occupy different trophic levels, with some species at the base of the food chain and others considered highly efficient predators (PARKER; KRONAUER, 2021; DEJEAN *et al.*, 2025). Unsurprisingly, ants have received growing attention as a model for studying biodiversity across different dimensions and scales. They are also the focus of considerable research due to their economic and sanitary importance, with some species regarded as agricultural pests and others as potential carriers of disease-causing microorganisms in hospital environments (DELLA-LÚCIA, 2011; CINTRA-SOCOLOWSKI; BUENO, 2017).

Given the prevalence and importance of ants on a global scale, Myrmecology is the branch of Zoology with the largest number of researchers devoted to a single insect family (Formicidae), with hundreds of scientists working in numerous institutions around the world (LUCKY *et al.*, 2020). With approximately 500 researchers, both established and in training, distributed across about 70 laboratories in different regions of the country (FEITOSA *et al.*, 2022), the Brazilian myrmecological community is a global reference in the study of the "little creatures that run the world," as the great myrmecologist Edward O. Wilson referred to ants.

As impressive as the strength of Brazilian Myrmecology are the numbers associated with the diversity of ants inhabiting the country. Approximately 1,700 species distributed in 117 genera are found in Brazil's wide range of natural and urban environments (FEITOSA; DIAS, 2024). However, we know these numbers are widely underestimated, since vast natural areas of the country have never been myrmecologically surveyed (SCHMIDT *et al.*, 2022), and an immense number of species deposited in the country's largest myrmecological collections still lack nominal identification or even formal description (FEITOSA *et al.*, 2023).

As challenging as it may be to deal with the greatest ant diversity in the world, this very condition makes Brazil stand out for the quantity and relevance of its scientific production in Myrmecology, with its research groups annually publishing a representative share of the global output of articles and books on a wide range of subjects, from taxonomy, diversity, physiology, and behavior, to the ecological role, economic importance, and medical and sanitary significance of ants (SCHMIDT *et al.*, 2022), besides their relationship with humans (COSTA-NETO *et al.*, 2005; 2006; NOVATO *et al.*, 2020; BARRET; PENA, 2023).

Nevertheless, the numbers mentioned above represent a temporal snapshot of Brazil's myrmecological production and do not consider important initiatives associated with, for example, training courses, events, outreach activities, ethnobiological projects, and movements of inclusion and belonging. In this sense, in 2012, we launched the *Formigas do Brasil* initiative, with the primary goal of contributing to the training of new generations of myrmecologists and advancing research in the many fields where Brazilian ants are studied. Thus, our initiative is structured around three main lines of action: i) teaching, ii) researching, and iii) dissemination.

Within the teaching line, we have offered a recurring course on ant systematics and ecology, held in different Brazilian biomes at each edition. To date, the course has been conducted in five of the six Brazilian biomes (Figure 1). Across these editions, 199 participants have attended, and 172 ant specialists have contributed as instructors.

In the research line, a collaborative network of more than 40 ant researchers has developed the largest data set on ant diversity studies carried out in Brazil. This dataset has so far supported the publication of five synthesis papers addressing: the profile of ant diversity studies (SCHMIDT *et al.*, 2022); the taxonomic profile of the ant fauna reported in these studies (FEITOSA *et al.*, 2022); the tools used by the Brazilian myrmecological community to validate taxonomic identification of ants (FEITOSA *et al.*, 2023); the response of ant diversity to seasonality (QUEIROZ *et al.*, 2023); and the effects of land-use change in Brazilian ant assemblages (WILKER *et al.*, 2024).

For science communication, we maintain a website (formigasdobrasil.com) where visitors can learn more about the initiative and access the material of all course editions. We also engage with the community through social media, particularly Instagram (@formigasdobrasil), which has become the main channel for communication with the Brazilian myrmecological community, and also on Facebook (@Formigas do Brasil). Finally, since the beginning of our initiative, we have planned the publication of this book as a comprehensive resource for Brazilian myrmecology. "Brazilian Myrmecology: Exploring the world's richest ant fauna" offers a representative compilation of systematic reviews and narrative accounts that reflect the state of the art across diverse research areas and initiatives focused on Brazilian ants.

In the 24 chapters of this book, 144 authors from 48 institutions representing all regions of the country and some foreign ones, present a historical overview that ranges from the accounts of the first naturalists who ventured in search of Brazilian ants in the 19th century to the most recent advances in different fields of myrmecological research. In addition to being a highly relevant scientific contribution for those interested in Brazilian ants, this book is also a preservation of memory and a tribute to all the individuals who made, and continue to make, Brazil the "Ant Capital of the World."


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**Figure 1.** *Curso Formigas do Brasil* – Ants of Brazil Course, across seven editions. A) Pilot edition 1 (2012) – *Universidade Federal de Lavras,* Lavras, MG. B) Pilot edition 2 (2013) – *Universidade Federal de Minas Gerais*, Belo Horizonte, MG. C) *Cerrado* edition (2014) – *Universidade Federal de Uberlândia,* Uberlândia, MG. D) Amazon edition (2016) – *Universidade Federal do Acre,* Rio Branco, AC. E) *Mata Atlântica* edition (2018) – *Instituto Nacional da Mata Atlântica,* Santa Tereza, ES. F) *Caatinga* edition (2022) – *Universidade Estadual do Ceará,* Crateús/Pacoti, CE. G) *Pantanal* edition (2024) – *Universidade Federal do Mato Grosso do Sul,* Corumbá/Campo Grande, MS. H) *Pampa* edition (2026) – Somewhere in Rio Grande do Sul.

**Source.** Authors' archives(2025).

Finally, we are most grateful to the people who submitted manuscripts and to the 46 referees (see Scientific committee) who reviewed the chapters

that made up the book. Thanks to everyone supportive of the Formigas do Brasil initiative.

*Sonho que se sonha só*
*É só um sonho que se sonha só*
*Mas sonho que se sonha junto é realidade*
**Raul Seixas**

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# TABLE OF CONTENTS


## Roots and Trajectories of Brazilian Myrmecology

Chapter 01 ..... 18

**ECHOES OF A LEGACY: FRIAR KEMPF AND THE DAWN OF MYRMECOLOGY IN BRAZIL**

Livia P. Prado; Rodrigo M. Feitosa

Chapter 02 ..... 28

**BRAZILIAN MYRMECOLOGY – A BRIEF HISTORICAL REVIEW**

Livia P. Prado; Rodrigo M. Feitosa

Chapter 03 ..... 52

**LONG STORY SHORT: AN OVERVIEW OF ANT TAXONOMY AND ANT TAXONOMISTS IN BRAZIL**

Mônica A. Ulysséa; Itanna O. Fernandes; Gabriela P. Camacho

## Behavior, Physiology, and Applied Perspectives

Chapter 04 ..... 76

**THE STATE OF THE ART IN ANT BEHAVIOR RESEARCH IN BRAZIL**

Ronara S. Ferreira; Daniel H. Tavares; Diana M. Urcuqui; Matheus Bastos-Chaves; Ana Maria C. Ferreira; Thalles R. B. Muniz; Gabriela B. C. Nascimento

Chapter 05 ..... 100

**UNVEILING THE LIVES OF ANTS: A CALL TO OBSERVE THEIR FASCINATING NATURAL WORLD**

Mônica A. Ulysséa; Marianne Azevedo-Silva; Félix B. Rosumek; Gabriela F. Jacintho; Esperidião A. Santos-Neto ; Hilário P. de Lima; Igor N. de Souza; Raquel L. C. de Lima

Chapter 06 ..... 123

**DIET AND FORAGING BEHAVIOUR IN BRAZILIAN PONERINAE ANTS: A COMPREHENSIVE SYSTEMATIC REVIEW**

Maria Eduarda Lima Vieira

Chapter 07 ..... 149

**CUTICULAR HYDROCARBONS IN BRAZILIAN ANTS: A SYSTEMATIC REVIEW**

Poliana G. Santos; Jean Carlos S. Lima; Michele C. Paula-Silva; Kamylla B. Michelutti; Elane G. Santos; Vinicius E. S. Oliveira; Dayana A. S. Cunha; Claudia A. L. Cardoso; Sidnei E. Lima-Junior; William F. Antonialli-Junior

Chapter 08 ..... 171

**ADVANCES IN UNDERSTANDING THE MICROBIOTA OF ANTS IN BRAZIL: REVIEW AND FUTURE PERSPECTIVES**

Alexandra Gianaris; Felipe P. Rocha; Ygor V. F. Pinheiro; Odair C. Bueno; Manuela O. Ramalho; Cintia Martins

**Ecology**

Chapter 09 ..... 204

**TRENDS AND GAPS IN THE STUDY OF ANTS IN ECOLOGICAL RESTORATION IN BRAZIL**

Diego V. Anjos; Chaim J. Lasmar; Lino A. Zuanon; Ruthe E. O. S. Leão; Vitor M. Costa-Silva; Raquel L. Carvalho

Chapter 10 ..... 226

**THE DIVERSITY AND ECOLOGY OF ANT GARDENS IN THE BRAZILIAN RAINFOREST: A COMPREHENSIVE REVIEW OF A COMPLEX ANT-PLANT MUTUALISM**

Ricardo E. Vicente; Laura C. Leal

Chapter 11 ..... 246

**CARRION-VISITING ANTS IN BRAZIL: A 26-YEAR SYSTEMATIC REVIEW**

Bianca R. Nogueira; Amanda A. Oliveira; Alexandre A. F. Souza; Poliana G. Santos; Tatiane A. D. Silva; Odair C. Bueno; Claudio J. Von Zuben

Chapter 12 ..... 271

**WHO ARE THE ANTS INTERACTING WITH PLANTS BEARING EXTRAFLORAL NECTARIES IN BRAZIL?**

Amanda V. Silva; Gustavo Marques; Henrique Saporito; Anselmo Nogueira; Sebastian Sendoya; Laura C. Leal

Chapter 13 ..... 295

**ANTS AS FLAGSHIP SPECIES: WHICH ONES AND WHY? A STUDY CASE WITH BRAZILIAN ANTS**

Eder C. B. França; Corina A. Barrera; Jarbas M. Queiroz

**Ant Diversity**

Chapter 14 ..... 319

**BRAZILIAN AMAZONIA MYRMECOFAUNA IN THE CONTEXT OF BIODIVERSITY RESEARCH**

Livia P. Prado; Joudellys Andrade-Silva; Otávio G. M. Silva; Tereza C. Giannini; César A. C. Favacho; Rogério R. Silva

Chapter 15 ..... 345

**THE ANT FAUNA OF THE CERRADO: DIVERSITY, ECOLOGICAL DRIVERS, AND HUMAN PRESSURES IN A GLOBAL BIODIVERSITY HOTSPOT**

Heraldo L. Vasconcelos; Karen C. Neves; Icaro Wilker; Antônio C. M. Queiroz; Carla R. Ribas; Rodrigo M. Feitosa

Chapter 16 ..... 371

**ENDEMISM AND VULNERABILITY OF ANTS IN THE PHYTOPHYSIOGNOMIES OF THE BRAZILIAN ATLANTIC FOREST**

Nathalia S. Silva; Débora C. O. Gonçalves; Claudia T. Wazema; David Aciole-Barbosa; Lívia P. Prado; Joudellys Andrade-Silva; Tae T. Fernandes; Rogério R. Silva; Maria S. C. Morini

Chapter 17 ..... 395

**GLOBAL CHANGES AND THE FUTURE OF THE CAATINGA DRY FOREST: LESSONS FROM ANTS**

Inara R. Leal; Xavier Arnan; Diego Centeno-Alvarado; Talita Câmara; Gabriela F. Pachêco; Mikael A. Castro; Francisca R. Oliveira; Adrielle Leal; Cícero L. S. Alencar; Bruna I. S. Pompéia; Douglas T. M. Neves; Juliana T. Silva; Pedro E. Santos-Neto; Gabriela B. Arcoverde; Isabelle L. Holanda Silva; Haymeé N. Alencar; Jonatas L. Gomes-da-Silva; Byanca N. T. Cavalcante; Ana Beatriz C. Corrêa; Katherine Bombi-Haedo; Daniel Vasconcelos; Felipe F. S. Siqueira; Clarissa Knoechelmann; Fernanda M. P. Oliveira

Chapter 18 ..... 422

**PANTANAL ANTS: ESTABLISHING A DATA SET OF ANT COMMUNITIES FROM THE BRAZILIAN WETLAND**

Suelen S. Carvalho; Vivian A. F. Nacagava; Camila Aoki; Paulo R. Souza; Jean C. S. Lima; Cândida Anitta P. Rodrigues; Ricardo E. Vicente

Chapter 19 ..... 443

**ANTS OF THE BRAZILIAN PAMPA: INSIGHTS INTO DIVERSITY, DISTRIBUTION AND CONSERVATION**

Gabriel G. Barbosa; Daniel A. Carvalho; Carolina V. C. Silva; William Dröse; Sebastian F. Sendoya; Luciana R. Podgaiski

Chapter 20 ..... 465

**THE WESTERN FRONTIER OF BRAZILIAN ANT DIVERSITY: CONTRIBUTIONS OF *REDE BIA* TO KNOWLEDGE ON ANT DIVERSITY IN THE SOUTHWESTERN AMAZON**

Fernando A. Schmidt; Marília M. S. Costa; Luane K. Fontenele; Dhâmyla B. S. Dutra ; Otávio G. M. Silva ; Victor H. Nagatani ; Esperidião A. Santos-Neto ; Rodrigo M. Feitosa

Chapter 21 ..... 479

**ANTS FROM THE STATE OF PARAÍBA: PAST, PRESENT AND FUTURE**

Anderson Dantas; Raissa Vitoria; Igor N. de Souza; Aline Lourenço; Alexandre Vasconcellos; Marília Costa

## People and Ants

Chapter 22 ..... 497

**WOMEN'S JOURNEY THROUGH MYRMECOLOGY: AN INSPIRING STORY**

Ana Carolina A. Neundorf; Laura Laino; Daniela Cubillos; Jaqueline A. M. Paes; Maria Eduarda Indalêncio; Paloma L. Andrade; Simone Simioni; Tainara T. Jory; Vitória Brunetta

Chapter 23 ..... 531

**A QUICK BREAK FROM FIELDWORK TO TALK ABOUT BRAZILIAN ANTS - AN EXPERIENTIAL ACCOUNT**

Chaim J. Lasmar; Mariana A. Rabelo; Agnis C. Souza; Antônio C. M. Queiroz; Carla R. Ribas; Clarissa Rosa; Cynthia V. Oliveira; Elisa Mousinho; Icaro Wilker; Jonas Aguiar; Marcos Mendes; Marina A. Angotti; Mayara M. G. Imata; Rafael C. R. Souza; Rafael G. Cuissi ; Sabrina Farsura

Chapter 24 ..... 544

**KEEPING ANTS IN THE ANTHILL: SEVEN EDITIONS OF THE *FORMIGAS DO BRASIL* COURSE**

Natalia Ladino

**INDEX** ..... 559

# Roots and Trajectories of Brazilian Myrmecology

# 01

# ECHOES OF A LEGACY: FRIAR KEMPF AND THE DAWN OF MYRMECOLOGY IN BRAZIL

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Friar Walter W. Kempf (1920–1976) (Figure 1) was one of the most prominent taxonomists and myrmecologists worldwide, having described more than 200 ant taxa and published over 100 scientific papers. He passed away prematurely at the age of 56 while preparing to attend the 'XV International Congress of Entomology' in Washington, D.C., USA. At the same time, William L. Overal arrived in Brazil to take up the position of entomologist at the Museu Paraense Emílio Goeldi (MPEG) in Belém, Pará, Brazil. His arrival marked the resumption of entomological research activities at MPEG, after years affected by institutional crises and challenges in scientific research in the Amazonia.

Before his arrival in Brazil, Overal had already been in correspondence with several Brazilian researchers, including Friar Kempf. However, the day of his arrival in Brazil was also, regrettably, marked by the passing of Friar Kempf. Some time later, in a gesture that symbolically brought their paths together, Overal received from Domiciano Pereira de Souza Dias, scientist, photographer and professor (now retired) at the Universidade de Brasília, a small selection of Friar Kempf's library materials. Among these, works on the ant fauna of Amazonia were of particular significance, including the article *Levantamento das formigas da mata amazônica, nos arredores de Belém do Pará, Brasil* (Kempf, 1970), a by-product of the International Year of Biology (1966–1967).

Nearly five decades later, while revisiting the library with Overal (Figure 2), already in retirement, and sorting through its materials, we struck "gold": an unpublished manuscript by Friar Kempf, preserved in three versions, two preliminary and one apparently final. Our analysis indicates that the text was never published. It begins with observations on the ant fauna of the state of São Paulo, but across the versions it expands into a broader reflection on the history of myrmecological studies in Brazil (Figure 3). Whether Friar Kempf conceived it as a publication, as a lecture draft, or for educational purposes remains unclear. However, the existence of multiple, progressively refined versions in both content and formatting, strongly suggests that Friar Kempf intended it for wider circulation.


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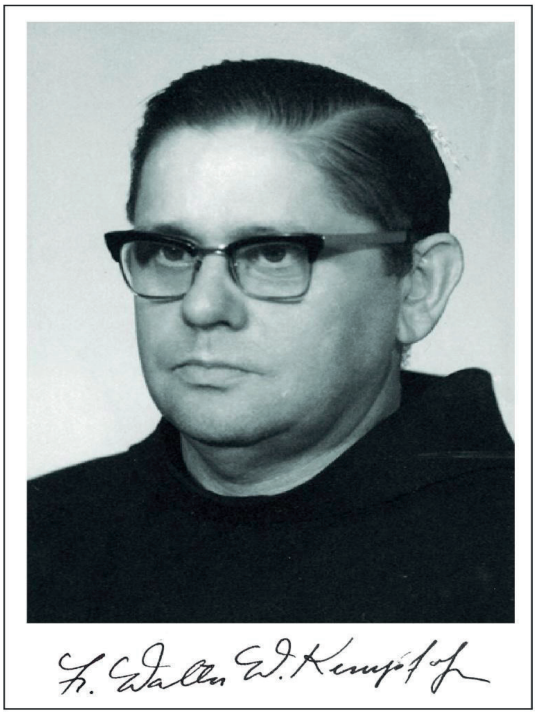
**Figure 1:** portrait of walter w. kempf (photographer unknown); with his signature taken from a dedication to friar thomaz borgmeier in an article.



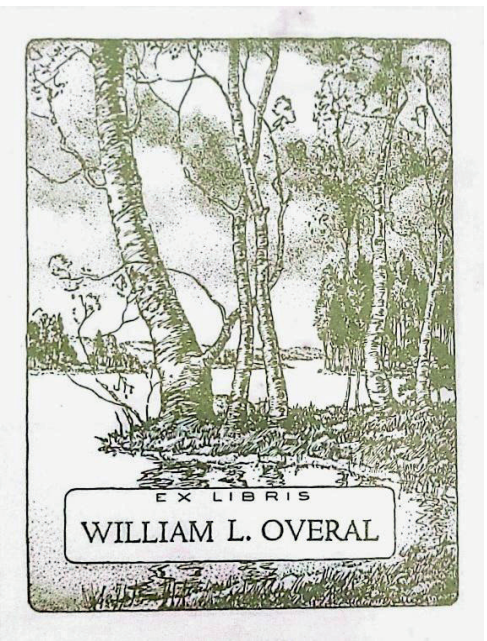
In tribute to Friar Kempf, Cardinal Paulo Evaristo Arns (1978) recalled a phrase he often repeated, summarizing his scientific ethos (freely translated): "*I must get used to speaking and writing using only nouns; adjectives distract*". The unpublished text reflected this principle: it is concise, direct, and each section contributes precisely to the understanding of the history of myrmecology in Brazil. The relevance of the text is also evident in its contemporary significance. Friar Kempf acknowledges the value of pre-Linnaean records and traditional knowledge, such as vernacular names, integrating them with the scientific framework of his time. He concludes by stressing the need to decentralize the production of knowledge about Brazil's fauna and underscores the importance of creating and maintaining scientific collections across the country.

All myrmecologists working in Brazil are, to varying degrees, heirs to the legacy of Friar Kempf (Prado *et al.*, 2021). The recovery of this text allows a revisit of the early days of myrmecology in the country from the perspective of a

researcher who was instrumental in building and consolidating its foundations. The publication of this material within a book, the result of a major initiative that once again projects Brazilian myrmecology onto the world stage, coincided in a particularly special way with the discovery of this text, a symbolic coincidence that will be recorded in history. Making the text available today not only helps preserve Kempf's legacy for future generations but also sheds light on the broader history of myrmecology in Brazil.

This discovery is also an opportunity to publicly express gratitude to Professor William L. Overal, recently retired as a senior researcher at the Museu Paraense Emílio Goeldi. Overal has contributed to the study of Amazonian fauna from multiple perspectives to the training of generations of researchers, and to the preservation of the memory of science in Brazil. His name appears on numerous ant specimen labels in the MPEG collection and in many publications documenting the fauna of one of the most biodiverse regions on Earth. Once again, he contributed by providing key information, carefully translating this manuscript according to the recommendations he had received from his friend Nelson Papavero, and generously sharing both knowledge and materials.

**Figure 2:** Ex-libris from the library of Dr. William L. Overal.



# ESSAY ON THE HISTORY OF THE EXPLORATION OF ANTS IN BRAZIL

**Walter Wolfgang Kempf (1920-1976) †**
(Translated from the Portuguese by William Leslie Overal)

There are over a thousand species of ants in Brazil. However, the systematic survey and study of this rich fauna is relatively recent. Information dating back to the pre-Linean period, i.e. before 1758, is scarce and imprecise. For example, Marcgrave (1648) lists two or three species, of which only one, the *saúva*, can be recognized with any certainty.

Equally poor in this respect are the results of the first century of binomial nomenclature. Lineu, in the tenth edition of his *Systema Naturae*, recognized 17 species of ants, seven of which actually occur in Brazil, but these were described using material from the Guianas, which at the time provided the overwhelming majority of new species from the Neotropical Region.

In the first monograph on ants, the *Histoire Naturelle des Fourmis,* written by Latreille in 1802, there is a direct reference to Brazil only in the case of one species. This is the well-known black *sará-sará* with red legs, now known as *Camponotus (Myrmothrix) rufipes*, described as early as 1775 by Fabricius, and very common in southern Brazil.

With the advent of the 19th century, the era of the great voyages of scientific exploration of Brazil began, carried out by the "classic" naturalists such as Spix, Martius, Maximilian de Wied Neuwied, St. Hilaire, Eschwege, Pohl, and others. The reference to ants in the works of these travelers is merely incidental. Small, unsightly animals were generally not collected. As a result, few specimens reached European taxonomists and few species were described at that time. Among the first collectors of our ants were the Englishman William Swainson, who visited various locations along the coast from Pernambuco to Rio between 1817 and 1818, John Miers, who set up and headed the first minting workshop in Rio between 1831 and 1838, and above all the traveler W. Burchell, who visited a large part of Brazil and collected, among other things, the first ant officially recorded as coming from São Paulo, *Eciton burchelli*, a native of Santos, described by Westwood.

All these achievements were only fragmentary, of little significance. The honor of having devoted more interest to our ants, of having collected them in large numbers and systematically, belongs among many others to the famous English naturalist H. W. Bates, who for eleven years, from 1848 to 1959, traveled along the Amazon River and its tributaries. Among the immense zoological collection amassed by this zealous researcher was a good number of new species of ants, and he made the first major contribution to our myrmecography, with the description of around 100 species. It is only to be regretted that the copious and extremely interesting material fell into the hands of a taxonomist with very little talent, Frederick Smith, who elaborated on the material in various publications, above all in the sixth volume of the British Museum's Hymenoptera catalog, and managed to produce a great deal of confusion which to this day challenges the curiosity of those who want to know what species Bates collected.

Peter Wilhelm Lund, the famous explorer of Lagoa Santa, also made a myrmecological contribution in 1831 with his letter to M. Audouin about the habits of some ants in Brazil. Written in French, this letter caused quite a stir and was immediately translated into German and English. The letter, which takes up 25 printed pages in the original publication, contains biological observations, some of which are erroneous and inaccurate, and new names for species that unfortunately have not been well characterized.

Around 1880, Lothar Hetschko collected ants in what is now the state of Santa Catarina and in Contestado, in the south of Paraná and in the Palmas region. He was an expert collector of precise and refined collecting methods that have not been surpassed to this day. The numerous ants ended up in the hands of the "Ameisen-Mayr" in Vienna, the competent Dr. Gustav Mayr, one of the best ant taxonomists to date. Mayr published a work on this material in 1887, entitled *Suedamerikanische Formiciden*, which is still the basis for the study of Brazilian ants, especially in the southern region.

The great flowering of systematic science in the last half of the 19th century led to an intensification of collecting. A. Schulz collected in Pará, where Emilio Goeldi also became interested in ants. The latter also collected in Rio and São Paulo. In Ceará we find the first native Brazilian to take an interest in ants, Mr. Diaz da Rocha, who put together a good collection, studied by A. Frei. E. Ule, a botanist of great stature, was also interested in the ants that nest in Amazonian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plants. In the south of Brazil, we have Dr. Moeller, nephew of the great Fritz Mueller, who studied the *quenquéns* and other related ants in Blumenau, and Germain. We could go on and on with this list, but as these are fragmentary contributions, we have chosen to end it.

When Mayr laid the foundations of myrmecological systematics in Brazil, and the sage men of myrmecology, Carlo Emery and Auguste Forel, emerged in Europe, the eminent German naturalist Hermann von Ihering moved to Brazil. He settled in Rio Grande do Sul and began studying the ants of that region. The systematic elaboration was the responsibility of the competent Emery (1887), who also supervised the biological and zoogeographical work that Ihering personally wrote. This work, published under the title *Die Ameisen von Rio Grande do Sul*, appeared in 1894, when its author had already become Director of the *Museu Paulista* (since 1892).

The figure of Ihering is of great importance in Brazilian myrmecology, firstly because he transplanted the study of ants to the country, secondly because when he moved to São Paulo, he began to explore the myrmecofauna of this state, which is now the best known in Brazil, and thirdly because he was able to pass on his interest to his intellectual followers and heirs, Hermann Luederwaldt and Friar Thomas Borgmeier.

At the head of the Museum, von Ihering organized large collections in São Paulo and neighboring states, adding to the museum's holdings. Among the collectors were the two Garbe men, father and son, Schwebel, and João L. Lima. As he had done in Rio Grande do Sul, he sent the ants to Emery for determination and description. In 1906, however, Emery suffered a paraplegic attack, which left him paralyzed on one side, and while he was recovering from the bout, he gave the material to his colleague and friend Forel.

This was a rather unfortunate circumstance, because by that time, despite his recognized competence, Forel had embarked on a mass production of new species, subspecies, and varieties through quick and superficial descriptions, taking little care to systematically assimilate them. Luckily, von Ihering kept half the specimens of all the series, so that the *Museu Paulista* was left, if not with the holotypes, at least with authentic material of the species described by Forel.

Administrative posts and other interests gradually took Hermann von Ihering away from myrmecological activities, which were soon taken over by

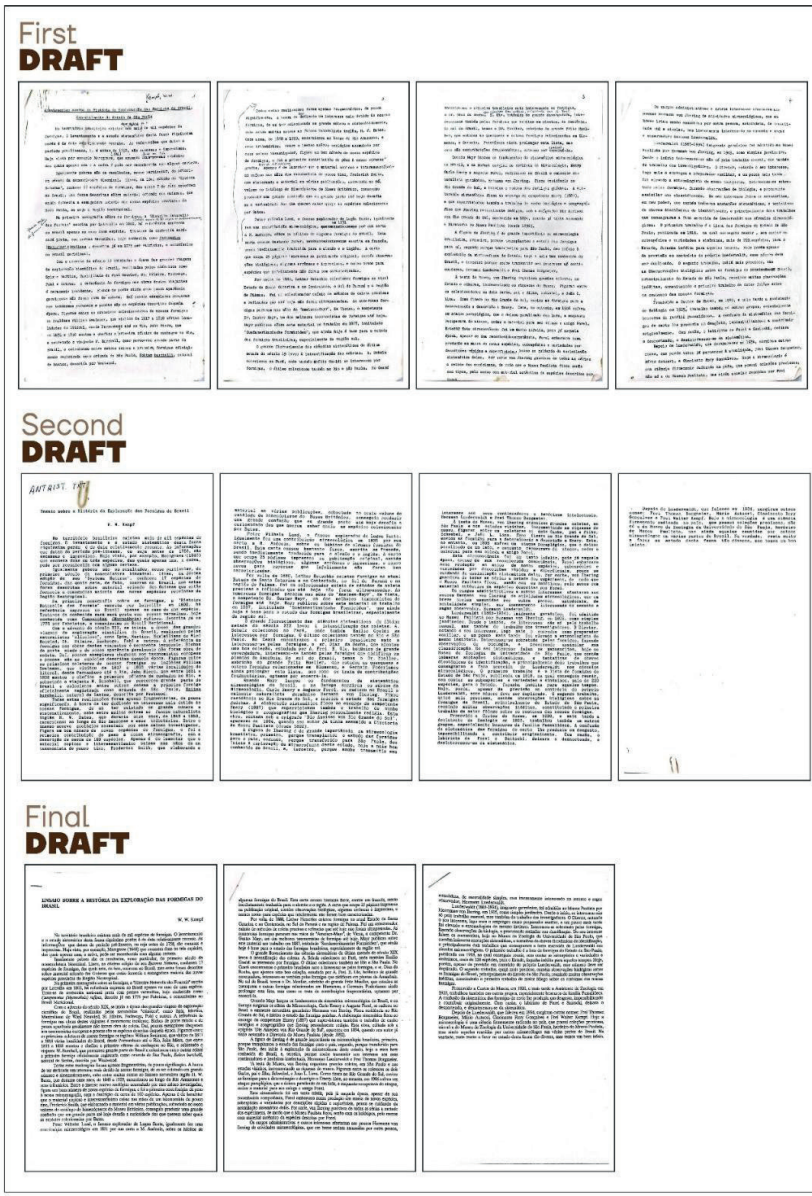
another person, self-taught, unsophisticated, but immensely interested in the subject and a shrewd observer, Hermann Luederwaldt.

Luederwaldt (1865-1934), a German immigrant, was admitted to the *Museu Paulista* by Hermann von Ihering in 1905 as a simple gardener. From the start, he was interested not only in manual labor, but also in the work of researchers. The Director, noticing his interest, soon employed him as an assistant preparator, and a little later he was promoted to entomologist at the same institute. He was particularly interested in ants, making biological observations and trying to assimilate their classification. His interest is reflected in the manuscripts, now in the Zoology Museum of the University of São Paulo, which contain numerous systematic notes and attempts at dichotomous identification keys, and above all two works that have earned Luederwaldt well-deserved fame in myrmecological circles. The first work is the list of ants of the state of São Paulo, published in 1918, in which he managed to gather, not counting subspecies and varieties and synonyms, more than 220 species for the state, an unprecedented feat for those times. Today, however, despite Luederwaldt's own prediction to the contrary, that number should be doubled. The second work, perhaps more valuable, contains biological observations on the ants of Brazil, especially in the state of São Paulo, bringing together many unpublished observations, constituting the first major work on the ecology of our ants.

Promoted by the museum in 1920, and later to Assistant in Zoology in 1925, he also worked on other groups, especially beetles of the Passalidae family. The confusion over the systematics of ants certainly caused him anguish, making it impossible for him to contribute originally. The labyrinth of Forel and Santschi had left him bewildered, and he became disinterested in systematics.

After Luederwaldt, who died in 1934, other names emerged: Friar Thomaz Borgmeier, Mário Autuori, Cincinnato Rory Gonçalves, and Friar Walter Kempf. Today Myrmecology is a science firmly established in the country, which has precious collections, not only that of the Zoology Museum of the University of São Paulo, heir to the *Paulista* Museum, but also those gathered by other myrmecologists in various parts of Brazil. In fact, there is still much to be done in the study of this diverse fauna, but we have made a good start.

**Figure 3.** The three versions of Walter W. Kempf's document, recently rediscovered at the Museu Paraense Emílio Goeldi.



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# 02

# BRAZILIAN MYRMECOLOGY – A BRIEF HISTORICAL REVIEW

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*"O total das formigas conhecidas no mundo inteiro e no período actual foi calculado pelo Prof. H. Ludwig, — no anno de 1886, em 1200 especies [...]. E por um recente trabalho do Prof. Dr. A. Forel (1893) vejo que elle avalia hoje em dia o total já em 2000 especies (e 150 generos). Tomando, por base a primeira indicação, o Brazil participaria com bastante mais de um terço do total, e guiando-nos pela segunda avaliação (Forel) obteriamos a proporção de 9:40, ou um pouco menos que a quarta parte. Seja como for, é intuitivo, que a riqueza faunistica d'este paiz mais uma vez se manifesta em relação á família dos Formicides".*
Pará, 1 de janeiro de 1895.
Dr. Emilio A. Goeldi.

10.37885/250920245

# ABSTRACT

Given their abundance in nature and cultural significance, it is not surprising that ants have influenced historical events and engaged the interest of researchers over time. Despite the challenges facing Entomology, Myrmecology has solidified itself as a prominent field in scientific research, particularly in Brazil. Recognized for its immense biodiversity, the country has become a reference center for ant studies, reflecting the growing interest of researchers who, over the years, have dedicated their careers to this field, which is important both nationally and for global scientific advancement. This chapter explores some of the central events, initiatives, and legacies that shaped the development of Myrmecology in Brazil. Based on the collaboration of various professionals and historical sources, we present an overview of the field's trajectory in the country. The chapter is organized around broad themes that highlight the integration of Myrmecology into Brazilian science, the institutional and collaborative efforts that supported its development, the establishment of research groups and training programs, and the initiatives that consolidated its position in both academic and applied contexts. While inevitably constrained by the scarcity of dedicated historical studies in Myrmecology, this chapter reflects on the field's development in Brazil. By emphasizing the value of historical perspectives, we aim to enrich scientific inquiry, encourage future research and strengthen the understanding of ants.

**Keywords:** Ants; biodiversity; entomology; history of science; scientific research.

## INTRODUCTION

The history of science serves many purposes: it not only helps us understand scientific content and methods within the context of contemporary practice but also enriches scientific knowledge where modern science may remain limited (Chang, 2017). It fosters critical thinking, revives forgotten or overlooked knowledge, acknowledges achievements, and underscores the importance of ethical standards (Casadevall; Fang, 2015). While the history of science is often portrayed through stories of heroic scientists, tragic figures, accidental discoveries, or eccentric experiments, sometimes simplifying the complexities of the scientific process, beyond these myths lies a deeper importance. Understanding the evolution of our current knowledge is important, as it not only enhances our comprehension of scientific concepts but also strengthens the foundation of science by providing a more rigorous justification for results and situating them within their historical context (Chang, 2017).

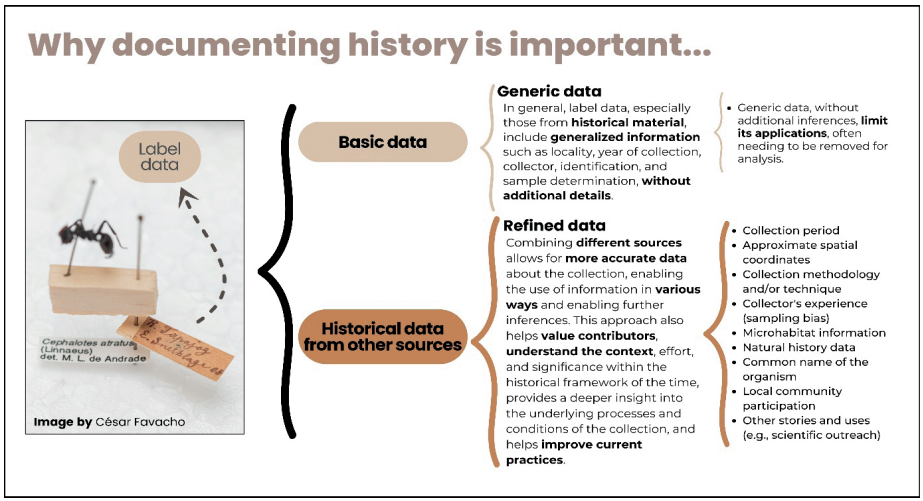
Documenting scientific processes and consulting historical data should be standard practices among scientists, as they advance knowledge and enhance science's role within society. However, this step is often undervalued, treated superficially, and lacks formal protocols in many institutions (Sanjad; Costa, 2021). In Myrmecology, as in many fields, historical documentation is still limited. While there are libraries, memory centers, and individual efforts, these initiatives remain in their early stages. Additionally, few specialists focus on this area, and historical training is not a major component of undergraduate or graduate programs, unlike in fields such as law, economics, and social sciences, where the historical background is indispensable for a deeper understanding of the field (Casadevall; Fang, 2015).

In this chapter, we present a brief history of Brazilian Myrmecology, though we do not aim to cover the entire history of the field in Brazil, as our knowledge remains limited in light of the complexity of this journey. However, through the collaboration of various professionals and the consultation of different sources, we make an initial, although limited, attempt to tell this story. Our intention is not only to provide an overview of the expansion of the field but also to inspire new investigations and reflections that broaden this knowledge. The chapter is structured into five main sections, each addressing a different aspect of Brazilian

Myrmecology's history and development. In the first, we explore the introduction of Myrmecology into Brazil's scientific agenda, emphasizing the role of expeditions, collections, and Taxonomy in the field's development. Next, we discuss the consolidation of Myrmecology through key events, journals, and scientific societies. In the third section, we examine the formation of research groups, the role of graduate programs, and the establishment of courses focused on the study of ants. We also assess the significance of large projects and initiatives dedicated to Myrmecological research in Brazil. Finally, in the last section, we provide a current overview of Myrmecology in the country, addressing its perspectives from both scientific research and historical study viewpoints.

For this chapter, we adopt the concept of knowledge networks, which refers to how individuals, institutions, and scientific communities collaborate to produce, transmit, and validate knowledge over time. These networks can be formal or informal and encompass the dissemination of ideas, techniques, practices, and the trajectories of scientific objects/organisms (Secord, 2004). To this end, we consulted source literature, gathered information from various researchers who actively participated in the development of the discipline and experienced many of the events described (see the acknowledgments section), and examined museum registers, field notebooks, and historical files. Our findings also rely on the collaboration of the archives of the *Serviço de Arquivo e Memória do Museu Paraense Emílio Goeldi* (SEARM/MPEG), *Fundo Museu Paraense Emílio Goeldi – Gestão Emília Snethlage/Arquivo Guilherme de La Penha/Museu Paraense Emílio Goeldi/MCTI*, Belém, Pará, Brazil, and the Library, Hymenoptera Lab, *Centro de Memória* of the *Museu de Zoologia da Universidade de São Paulo* (MZUSP) and the personal library of Professor William L. Overal. Additionally, we utilized data deposited in myrmecological collections, which, aside from offering opportunities for biodiversity studies, allow for investigating the various uses attributed to these collections over time and the knowledge generated through their interpretation (Figure 1). These data are fundamental for recording the trajectory of each specimen and for understanding the processes underlying the construction of biological knowledge (Sanjad; Costa, 2021).

**Figure 1 -** Example of how historical knowledge and complementary sources can enhance data use. The image shows a *Cephalotes atratus* worker collected by Emilie Snethlage during a legendary expedition to the Tapajós River region in 1908 (MPEG). For more details about this expedition, see Snethlage, 2002 [1910]. Research on the scientist's career has helped link valuable scientific and historical information to the collected samples.




## THE ANTS

A remarkable treatise on ants, *Ants: Their Structure, Development, and Behavior*, written by William Morton Wheeler in 1910, states:

> *"Ants are to be found everywhere, from the arctic regions to the tropics, from timberline on the loftiest mountains to the shifting sands of the dunes and seashores, and from the dampest forest to the driest deserts".*

Even those who have never had the pleasure of reading this book have likely referenced something similar in a paper, project, or talk about ants. After all, ants are present in nearly all environments and inspire many aspects of human culture. Their impact reaches from agriculture, with ants being the pioneers of this practice for tens of millions of years, long before humans (Schultz *et al.*, 2024), to indigenous rituals and cuisine, as mentioned by von Ihering (1940). In folklore, there are numerous fascinating stories of popular knowledge collected by Lenko & Papavero (1979), including, for example, the 44 common names exclusively recorded for fungus-growing ants. Additionally, these insects have been widely

mentioned by naturalists, politicians, and religious figures throughout history (Lenko; Papavero, 1979). And we have only referred to accounts of fungus-growing ants so far.

Given their abundance in nature and importance in culture, it is not surprising that ants have influenced historical events and captured the interest of various researchers over time. Despite the gaps and barriers in Entomology (Cardoso *et al.*, 2011), Myrmecology has built a solid space in scientific research. Brazil, a country that hosts one of the most diverse biotas in the world, is affectionately recognized as the "Capital das Formigas" (the Ant Capital), a term coined by Edward O. Wilson during the *XXIII Simpósio de Mirmecologia: An International Ant Meeting*, held in Curitiba, Paraná, in 2017. In fact, Brazil plays a pivotal role in the international Myrmecology scenario due to its unparalleled ant diversity, thriving research community, and contributions to evolutionary biology, Ecology, and applied sciences. From there, we turn our attention to understanding the events, initiatives, and stories that led researchers from all regions of Brazil to dedicate their careers to Myrmecology.

## MYRMECOLOGY IN BRAZIL – FOUNDATIONS

The early development of myrmecology reflected the society of its time. It was led mainly by male scientists with access to financial resources and intellectual circles. Others, though fewer, pursued research despite limited opportunities. The field's history also includes clergy who balanced religious and scientific responsibilities, war refugees, and a few women who worked as volunteers, supported their husbands' research, or had to make considerable sacrifices to obtain formal research positions. This group, comprising researchers, naturalists, technicians, collectors, curators, students and interns, established Myrmecology in Brazil.

Although records of ants in Brazil date back to the 16th century, appearing in the letters and treatises of Father Anchieta and Gabriel Soares de Souza (LENKO and PAPAVERO, 1979), it is likely that numerous Indigenous references to these insects exist, though they remain largely undocumented in the scientific literature (WHEELER, 1907). In the development of Myrmecology in Brazil, three key pillars stand out: expeditions, which drove the discovery of new species

and expanded sampling areas; Taxonomy, which organized and systematized this knowledge; and collections, which played a fundamental role in preserving specimens and disseminating biodiversity information.

Within a taxonomic context, the first ant species recorded in Brazil were described in *Systema Naturae* (1758), the seminal work of zoological Taxonomy by Carolus Linnaeus, regarded as the father of modern Taxonomy. Among the 55 ant taxa he described, seven are now recognized as occurring in Brazil (*Atta cephalotes*, *Atta sexdens*, *Cephalotes atratus*, *Dolichoderus bidens*, *Monomorium pharaonis*, *Odontomachus haematodus*, and *Neoponera foetida*). Although Linnaeus broadly attributed these species to America Meridionali (South America), and they are indeed widely distributed in Brazil, it is now known that the specimens he studied were collected in Suriname during expeditions led by the Swedish naturalist Daniel Rolander from 1753 to 1956 (PAPAVERO, 1971; BACCARO *et al.*, 2015). However, even before Rolander's collections, several expeditions had already taken place in Brazil, including those specifically focused on collecting insects such as ants. These scientific journeys were documented in works by authors such as Papavero (1971) and Vanzolini (2004), among others. Yet, records of ants from this period appear only sporadically in broader studies of Brazil's regional fauna. To date, no comprehensive list consolidates data on the ant species collected during these early explorations, limiting our understanding of the historical development of Myrmecology in Brazil.

Moving into the period when Myrmecology was becoming established as a scientific field both in Brazil and globally, with researchers around the world dedicating themselves to the study of ants as a primary focus, two institutions stood out and continue to play a central role in ant research in Brazil: the *Museu Paraense Emílio Goeldi* (MPEG) and the *Museu de Zoologia da Universidade de São Paulo* (MZUSP). Founded in 1866, the MPEG, despite its challenging and resilient early history (LEITE, 1993; FAULHABER and TOLEDO, 2001), played a key role in advancing Myrmecology, operating comprehensively for the standards of its time. The museum staff supported collecting expeditions conducted by foreign researchers, organized collection efforts to obtain specimens in the Brazilian Amazon, though not limited to this region, and sent these specimens to international specialists for identification and description. In addition, the MPEG maintained a scientific journal from its inception (as will be detailed later),

which was fundamental in disseminating early Myrmecological contributions. Two names stand out in this process as central figures in the global scientific landscape of the time: Emílio Goeldi and Emilie Snethlage, who served not only as researchers and collectors but also as directors of the museum. The Stanford Expedition to Brazil, which took place in 1911 and resulted in William W. Mann's doctoral thesis and a publication (MANN, 1916), is an example of an expedition supported by the MPEG under Emilie Snethlage's leadership. The first checklist of ants from Brazil, published by Forel (1895), was made possible thanks to the shipment of specimens to the author by the MPEG. Notably, this work, titled "A Fauna das Formigas do Brazil", was published in Portuguese and in a Brazilian journal (then *Boletim do Museu Paraense*) at the request of Emílio Goeldi and in alignment with the journal's editorial policy. For these reasons, it is common to find ant species with specific epithets such as "goeldii", in reference to Emílio Goeldi, and "emiliae", in honor of Emilie Snethlage, particularly among species described between the late 19th and early 20th centuries (Prado *et al.*, 2020). However, much of the material sent to foreign institutions was never returned to Brazil, including type specimens. Throughout its turbulent history following the decline of the rubber boom in the Amazon, the MPEG suffered significant losses, not only to foreign interests but also due to individuals who took advantage of various circumstances and pretexts (LA PENHA, 1982). As a result, most of the historical myrmecological collection of the MPEG is no longer housed within the institution.

The MZUSP, on the other hand, originated as the Zoology section of the *Museu Paulista*, founded in 1834. Later, in 1939, it became part of the *Departamento de Zoologia da Secretaria da Agricultura do Estado de São Paulo*, until its definitive integration into the University of São Paulo in 1969 (Vanzolini, 1994). Although the first records of ants correspond to material collected by Hermann von Lüderwaldt and Hermann von Ihering in the early 20th century, the history of the collection expanded with the incorporation of several collections and the deposit of material from different origins with a Neotropical scope, along with continuous curatorial work. This work was initially carried out by curator Karol Lenko and intern Aristides Rocha, who dedicated themselves to curatorship, collection, and material exchange. However, perhaps the most important milestone was the incorporation of the ant collections and libraries of the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entomologists and friars Thomas Borgmeier and Walter W. Kempf, acquired by MZUSP from the Franciscan Order in 1977, with financial support from the *Conselho Nacional de Desenvolvimento Científico e Tecnológico* (CNPq) and the *Fundação de Apoio à Pesquisa do Estado de São Paulo* (FAPESP). This event, followed by the curatorial and taxonomic leadership of Carlos Roberto Ferreira Brandão, consolidated MZUSP's collection as one of the most relevant in the world, continuously revealing new species and scientific findings (PRADO *et al.*, 2021). With continuous curatorial work and stability in research funding, something historically achieved only by the state of São Paulo within Brazilian standards, the MZUSP ant collection is recognized as one of the most representative in the Neotropical region, both in the number of types and species and in geographical coverage.

In recent decades, the growing interest in myrmecological studies in Brazil has led to the development of several ant-focused collections or the transformation of previously established collections, which have since become key reference centers for taxonomic, ecological, and evolutionary research. Today, these collections play complementary and strategic roles in advancing knowledge on ant biodiversity in the country. Among some notable examples is the *Coleção de Formicidae do Centro de Pesquisas do Cacau* (CPDC), created in 1990, which is oriented toward ecological and taxonomic studies and holds a particularly rich assemblage of samples from various agricultural systems and natural areas in southern Bahia state (DELABIE *et al.*, 2020). Similarly, the *Coleção Entomológica Adolph Hempel* (IBSP/IB) is recognized for the specimens of great historical importance deposited therein since 1920, predominantly originating from cultivated areas (IDE *et al.*, 2005; OLIVEIRA *et al.*, 2020). The *Coleção Entomológica do Laboratório de Coleoptera da Universidade Federal de Viçosa* (CELC – UFV), which began to appear more frequently in the literature starting in 2019, incorporated the collection of LABECOL (*Laboratório de Ecologia de Comunidades da UFV*), which has existed since the 1990s. Currently, in addition to conducting studies on extant taxa, CELC stands out for its contributions to fossil ant research and for its leadership in the sharing, digitization, and high-resolution imaging of myrmecological material on the AntWeb.org platform. The *Coleção Entomológica Padre Jesus Santiago Moure* (DZUP), in turn, has become an important center for training ant taxonomists since 2013 and

serves as a reference for the identification and sorting of material from various regions of Brazil (Andrade; Feitosa, 2020). An emerging example is the *Coleção de Referência Silvia Sayuri Suguituru* (LAMAT) (founded in 2000), at the *Universidade de Mogi das Cruzes*, which is dedicated to the detailed documentation of the ant fauna of the Upper Tietê River. This collection employs integrative approaches compatible with various disciplines and has contributed to the development of public policies related to regional biodiversity (Souza-Campana *et al.,* 2020). In the Amazonia region, the Instituto Nacional de Pesquisas da Amazônia (INPA), whose ant collection holds specimens since the beginning of the 1920 decade, has a long-standing tradition in ecological research and, more recently, in taxonomic investigations, positioning itself as a key center for biodiversity monitoring (Fernandes; Oliveira, 2020). The MPEG currently conducts projects focused on the development of extensive biodiversity databases, the enhancement of collaborative research networks, and field expeditions focusing on remote Amazonian areas as well as regions undergoing land-use change and management. The MZUSP, in addition to housing one of the most representative ant collections in the world, has taken a leading role in the so-called 'museomics' era, with emphasis on the use of ancient and historical DNA extracted from museum specimens, contributing to advances in systematics and phylogenomics. The trajectory and relevance of most of these collections in the development of Brazilian Myrmecology are documented in the special issue of the *Boletim do Museu Paraense Emílio Goeldi – Ciências Naturais*, entitled "*A Mirmecologia Brasileira no Século XXI*" (2020), which provides a comprehensive overview of the evolution of the field in the country.

## OTHER INFLUENCES ON THE DISSEMINATION OF MYRMECOLOGY IN BRAZIL

Far beyond expeditions, the establishment of collections, and the publication of works focused on the description and organization of Brazil's biodiversity, several other factors have influenced and continue to shape the trajectory of Myrmecology in the country. While the impact of each of these elements across Brazil's political regions remains insufficiently understood, it is clear that the more inclusive these initiatives are, the greater their influence on strengthening


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the discipline. Scientific practices, after all, are not limited to the production of knowledge alone, but also involve communication, application, and institutionalization, shaped by diverse dynamics, standards of conduct, and interactions within the scientific community that ultimately lead to concrete outcomes (Silveira *et al.*, 2015).

Another fascinating aspect is to explore the history of the earliest scientific events in Myrmecology and how they have evolved over time. Understanding the development of these gatherings in their various dimensions can reveal key elements that help explain the directions the field has taken. Part of this progress is due, though not exclusively, to the active engagement of myrmecologists working in diverse contexts. These initiatives have driven scientific advancement, improved biological collections, secured research funding, promoted the dissemination of knowledge, fostered collaborative networks, expanded the reach of studies, supported technological development, enabled information sharing, and refined technical protocols, making the field more democratic and accessible. In this context, we highlight some of these elements that have contributed to the development and expansion of Myrmecology in Brazil. We present selected examples that, in different ways, reflect the evolving structure, institutional engagement, and collaborative nature of the field over time.

### *Brazilian Journals*

Scientific journals historically published in Brazil have played a fundamental role in strengthening research in the country, especially throughout the 20th century. With different formats, goals, and editorial policies, each journal had its relevance shaped by the historical and scientific context of its time. Since the late 19th and early 20th centuries, publications such as *Boletim do Museu Paraense Emílio Goeldi*, *Archivos do Museu Nacional do Rio de Janeiro, Arquivos do Instituto Biológico* and *Naturalia* among others, that underwent reformulations and name changes over time, contributed to the dissemination of scientific knowledge on the biodiversity, especially in the Neotropical region. Some of these journals stood out, for instance, by adopting editorial policies focused on publishing in Portuguese, which made knowledge more accessible to local audiences, valued national scientific production, and confronted the prejudices prevailing in a time

when science was still consolidating in the country. However, the irregularity of publications, often caused by financial limitations, with gaps of over a decade between issues (e.g., Leite 1993), led to the emergence of new journals dedicated to specific fields such as Entomology (Garmus, 2012).

An important milestone was the creation of the *Revista de Entomologia*, founded in 1931 by Friar Borgmeier. Motivated by the difficulty of quickly publishing his research results, Friar Borgmeier took on the roles of editor and publisher, ensuring a more efficient editorial flow. Unique in its field at the time, the journal reached subscribers in 21 countries and published articles in seven languages. A total of 22 volumes were published until 1951, when the journal was discontinued. In 1958, the publication was revived under the name *Studia Entomologica*, remaining active until 1976, with issues coordinated by Friars Borgmeier and Kempf. *Studia Entomologica* became a landmark in Brazilian and international Entomology, particularly in the areas of taxonomy and insect diversity. Its high editorial quality, the excellence of its published articles, and its openness to international collaboration made it one of the most respected journals in the world at the time (personal communication with Nelson Papavero and Dione Seripierri, 2022). A notable example was the Catalogue of the Ants of the Neotropical Region, published by Kempf in 1972. Until then, the most recent catalogs had been published by Emery in the 1920s (e.g., Emery, 1925). Kempf's catalog was the first comprehensive one for the Neotropical region. Taxonomic catalogs remain essential tools, but in a world without the internet, their importance was even more evident. As Kempf (1972) stated (freely translated):

> "*Zoological catalogs need no justification regarding their usefulness and timeliness. They are repositories of quick and organized information about the number, nomenclature, distribution, and classification of known organisms within certain groups. Therefore, they represent a remarkable aid to many fields of biological research.*"

A particularly interesting feature of these pioneering journals was the presence of sections dedicated to brief communications, in which researchers could express opinions, announce discoveries, pay tribute, or present critiques on scientific issues. These more informal and dialogic spaces enriched the scientific debate of the time, although they have disappeared from most current

publications. Today, several journals continue to play a relevant role in disseminating myrmecological research in Brazil, many of them with myrmecologists serving on their editorial boards. Some examples include: *Revista Brasileira de Entomologia*, *Acta Amazonica*, *Sociobiology*, *Papéis Avulsos de Zoologia*, *Entomological Communications*, among others. Despite their importance, these journals still face persistent challenges regarding visibility and investment, both nationally and internationally.

### *Scientific Events*

Scientific events are diverse instruments for the dissemination of knowledge, enabling multiple forms of communication and exchange. In Brazil, a variety of events have traditionally been held that include the participation of myrmecologists, ranging from broad conferences to more specialized meetings. Examples include the *Congresso Brasileiro de Zoologia*, the *Congresso Brasileiro de Entomologia*, and the meetings and workshops organized by the *Brazilian Section of the International Union for the Study of Social Insects* (IUSSI-SecBras).

However, the most emblematic event for the global myrmecological community is undoubtedly the *Simpósio de Mirmecologia*. The event was born as a small meeting in 1980 with the *I Encontro de Mirmecologia do Estado de São Paulo*, organized by the *Departamento de Biologia* at the *Instituto de Biociências* of the *Universidade Estadual Paulista* (UNESP), Rio Claro *campus*. Over the years, the meeting expanded both in scope and audience, and in its 16th edition held in Florianópolis (Santa Catarina) in 2003, it was officially renamed *Simpósio de Mirmecologia*. In 2011, during the 20th edition in Petrópolis (Rio de Janeiro), the event emphasized the participation of the Latin American community under the title *20º Simpósio de Mirmecologia / 1º Encuentro de Mirmecologistas de las Américas*. The current format was consolidated in the 21st edition held in Fortaleza (Ceará) in 2013, adopting the name S*impósio de Mirmecologia: An International Ant Meeting*, and has since been hosted in different regions of Brazil. Today, the event is informally referred to as *Ant Meeting* by the international community and as *Mirmeco* by the broader community.

Throughout its history, *Mirmeco* has adopted a variety of formats, from informal gatherings focused on sharing experiences and providing training

through workshops and courses, to its current model, which is broader and more inclusive. Today, the event is held biennially and includes plenary sessions, round tables, oral and poster presentations, cultural activities, and science outreach initiatives. It has become the largest meeting of myrmecologists in the world, bringing together around 300 specialists from Brazil and various other countries. By rotating its location throughout different cities in the country, the current format has played a key role in decentralizing Myrmecology in Brazil, allowing for broader local engagement and promoting more diverse regional experiences. This dynamic has helped strengthen local research networks, expand access to knowledge, and encourage the inclusion of researchers from historically underrepresented areas. As a result, it has become the largest meeting of myrmecologists in the world, featuring strong international participation while continuing to highlight and disseminate ant research conducted in Brazil.

***Courses and Academic Training in Science***

In a broader context, but with the active participation of myrmecologists as both instructors and students, several initiatives have contributed to the training of multiple generations of specialists. In the field of *Cursos Especiais de Sistemática Zoológica* promoted by CNPq were fundamental in guiding numerous generations of researchers in the study and application of modern systematic theories. Held throughout the 1980s at various universities and regions across Brazil, these courses played a central role in the training of experts in zoological systematics (Klassa; Santos, 2012), significantly contributing to establishing Brazil as one of the most productive countries in this field worldwide (Rafael *et al.*, 2009). Among these initiatives, several insect collection training courses were organized by institutions, laboratories, and research groups (Figure 2A). In the field of Ecology, intensive field courses stand out, especially in regions with major knowledge gaps. An example is the course *Ecologia da Floresta Amazônica*, part of the *Projeto Dinâmica Biológica de Fragmentos Florestai*s (PDBFF), which has had nearly 30 editions and has been mainly integrated into INPA's graduate programs. Another example is the field course *Ecologia e Conservação da Caatinga*, linked to the graduate programs in *Biologia Vegetal and Biologia Animal* at the *Universidade Federal de Pernambuco* (UFPE), and the *Ecologia*


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*de Campo* course/class offered by the Graduate Program in Ecology at the *Universidade Estadual de Campinas* (UNICAMP), initiated in 1976. These courses offer immersive experiences in scientific practice, covering everything from field observations of biological phenomena to the formulation of research questions, method selection, experimental design, data analysis, and discussion of results. Thematic undergraduate courses have also made progress. One of the most traditional is the *Curso de Verão em Entomologia*, organized since 2003 by students and faculty from the Graduate Program in Entomology at the *Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto da Universidade de São Paulo*. Currently, similar initiatives are being carried out across all regions of Brazil.

In the specific context of Myrmecology, the pioneering work of Donat Agosti and Jacques Delabie stands out. They were responsible for introducing the Winkler extractor methodology in Brazil. Initially tested in cacao plantations and local forests in Bahia, the technique was consolidated during the ALL Workshop (*Leaf-Litter Ants*), held in Ilhéus in 1996 (Figure 2B). This meeting led to the development of the book *Ants: Standard Methods for Measuring and Monitoring Biodiversity*, published in 2000 by Agosti *et al.*, and widely used since then. The publication established Winkler extractors as the standard method for studying leaf-litter ant diversity. In 1997, Agosti, in collaboration with Delabie, Jim Carpenter, Sofia Campiolo, and other researchers, organized a field course in Uruçuca (Bahia) aimed at presenting field and laboratory methodologies for the study of ants to Brazilian students (Figure 2). Considered the first course of its kind in South America, this event marked a turning point for Myrmecology in the region, fostering the dissemination of one of the main sampling techniques still in use today (Delabie, 2018). More recently, the course *Sistemática e Biologia de Formigas*, coordinated by Rodrigo Feitosa at UFPR, has played an important role in introducing graduate students to the study of ants. The course provides taxonomic updates, a broad overview of various research contexts, and encourages the inclusion of ants in scientific projects. It has been offered in different formats (in-person, online, and hybrid) and several regions of the country and is currently taught at UFPR. Another remarkable effort is the course *Formigas do Brasil*, launched in 2012 (Figure 2C). Held biennially, it has covered several Brazilian biomes with support from universities across the country. Organized by Fernando Schmidt (UFAC), Carla Ribas (UFLA), and Rodrigo Feitosa (UFPR),

the course offers a comprehensive approach to various areas of Myrmecology through lectures, fieldwork, and activities focused on ant sample identification and sorting.

**Figure 2 -** Some images of field activities. A. Dr. William Overal conducting a field collection training for students, technicians, and interns at MPEG, who are also some of the collectors named on the labels of the MPEG ant collection. B. Participants of the ALL Workshop in front of the Cocoa Research Center (CEPEC/CEPLAC), Ilhéus, Brazil. C. Participants of the Formigas do Brasil course – Pantanal edition.

***Network-based initiatives***

In a broader context, network-based initiatives stand out. Despite numerous challenges, Brazil has followed a promising path in fostering scientific collaboration focused on biodiversity. Several research programs have promoted the development of collaborative networks, primarily supported by *CNPq* and the *Fundações Estaduais de Amparo à Pesquisa (FAPs)*, but also through international contributions, private resources, and sectoral funds. Among the most notable examples are the *Programa de Pesquisa em Biodiversidade (PPBio)*, the *Programa de Pesquisas Ecológicas de Longa Duração (PELD)*, the *Institutos Nacionais de Ciência e Tecnologia (INCTs)*, the *Iniciativa Amazônia +10*, and *Biota-FAPESP*. As new funding calls are launched, these networks have increasingly integrated emerging demands, helping science in Brazil become more responsive to society and its needs. These programs have not only strengthened scientific infrastructure but have also played a key role in training new generations of researchers. They have served as a foundation for undergraduate research, master's, and doctoral projects. Moreover, the most structured data and materials produced by these initiatives have been incorporated into scientific collections and have supported ecological studies, biodiversity monitoring


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efforts, and taxonomic research. More recently, thematic networks have been established to address specific questions about certain biological groups, such as ants. One example is the work carried out by the *Formigas do Brasil* group, responsible for a series of scientific publications (Schimidt *et al.*, 2022; Feitosa *et al.*, 2023; Wilker *et al.*, 2024), with collaboration by researchers from various regions of the country and by students affiliated with the initiative's leadership. Another highlight is the *Atlantic Ants* project, led by *Rogério R. Silva*, which resulted in the development of a datapaper on Atlantic Forest ants (Silva *et al.*, 2022), currently one of the most robust databases for these ants, comprising around 150,000 records. These include validated published and unpublished data, along with records from scientific collections. This network is an example of an open and democratic initiative, allowing anyone to share data and be included in the publication, thus promoting the collective use of information. The database was made publicly available, encouraging its use by other researchers and enabling impactful research, especially in regions with limited resources and infrastructure.

### *Scientific Societies*

Scientific societies play a crucial role in advancing knowledge about biodiversity by fostering collaboration, disseminating research, and promoting best practices in conservation and taxonomy. These organizations bring together researchers, educators, and policymakers, facilitating the exchange of ideas and data across disciplines. Through conferences, journals, and working groups, they help standardize methodologies, ensuring that biodiversity studies are comparable and reproducible. By supporting early-career scientists and funding fieldwork, societies also drive innovation in ecological and taxonomic research.

Moreover, scientific societies advocate for evidence-based conservation policies, translating complex research into actionable recommendations for governments and NGOs. They often lead initiatives to document endangered species, monitor ecosystem health, and combat biodiversity loss. This is also the case with Myrmecology. Founded in 1937, the *Sociedade Brasileira de Entomologia* (Brazilian Society of Entomology - SBE) is the oldest entomological association in Brazil, being one of the first to be founded in Latin America. Throughout its nearly 90 years of existence, SBE has had some of the most prominent names

in Entomology worldwide on its directive body, including Friar Kempf, arguably the most important name in Brazilian ant taxonomy. SBE's mission is to promote basic and applied scientific research in the different areas of Entomology, contributing to the advancement of knowledge about the diversity, evolution, ecological, economic, and sanitary importance of insects. These objectives are also promoted by supporting the training of young Brazilian entomologists through grant notices and the organization of scientific events focused on Entomology. In addition, since 1954, SBE has been the manager of the "*Revista Brasileira de Entomologia*: A Journal of Insect Diversity and Evolution", the most traditional entomological journal in Latin America, where several contributions on ant taxonomy and diversity are published to the current day.

Still, regarding the support to Brazilian Myrmecology, societies like the *Sociedade Entomológica do Brasil* (SEB) and the Brazilian section of the International Union for the Study of Social Insects (IUSSI) have been instrumental in shaping biodiversity science in Brazil and beyond, promoting both local and global research networks. SEB and IUSSI-Brazil are also of extreme importance for the dissemination of knowledge on Brazilian ants by publishing several studies in their respective entomological journals, *Neotropical Entomology* and *Insectes Sociaux*. Ultimately, these organizations amplify the impact of individual researchers, creating a collective force that accelerates discoveries and informs sustainable practices. Their work is essential for understanding Brazilian ant diversity and preserving it for future generations.

## THE ANTS OF BRAZIL TODAY

With ongoing advancements and emerging opportunities, research groups and graduate programs have become increasingly consolidated, many of which are responsible for key initiatives driving the growth of Myrmecology in Brazil. These programs demonstrate that science is being built through increasingly collaborative efforts, bringing together technicians, field assistants, undergraduate and graduate students, postdoctoral researchers, fellows, and other dedicated contributors. These individuals often move between laboratories across Brazil, field expeditions, and academic networks, connecting diverse contexts of knowledge production and sustaining the momentum of research.


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Today, laboratories dedicated to the study of ants, or incorporating ant research as a core focus, are present in all regions of the country. As the field continues to strengthen, initiatives have also begun to emerge in more remote areas, far from major research centers. These efforts not only support regional scientific development but also help fill long-standing gaps in knowledge about Brazilian ant diversity. Another defining characteristic of Brazilian Myrmecology is the integration of different scientific disciplines, particularly the interplay between Ecology and Taxonomy. This synergy has expanded both the scope and impact of the research, promoting broader approaches to biodiversity studies.

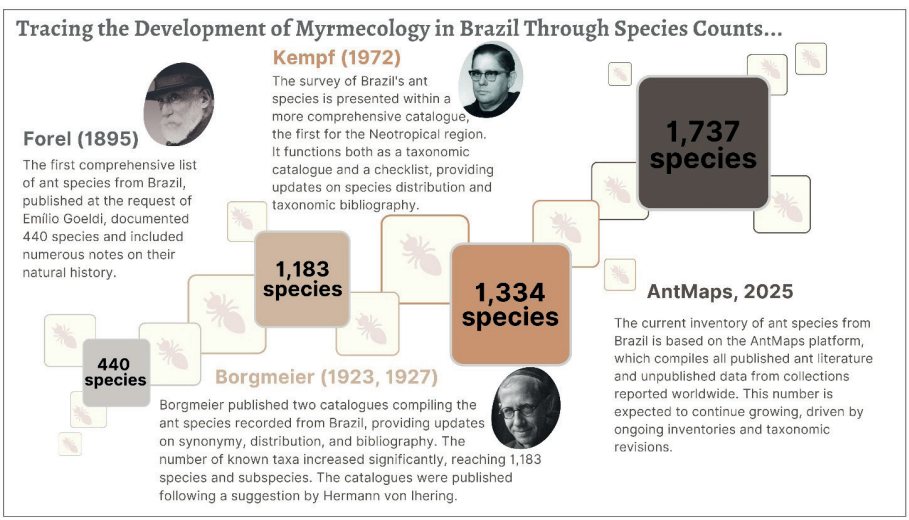
The establishment of dedicated ant research laboratories in Brazil transformed Myrmecology from a primarily taxonomic discipline into a dynamic field integrating Ecology, behavior, conservation, and control. As aforementioned, before the 1980s, Myrmecology in Brazil was mostly descriptive, with taxonomists mainly documenting species diversity. Institutions like Universidade Estadual Paulista "Julio de Mesquista Filho", Universidade Federal do Acre, Universidade Federal de Viçosa, UNICAMP, Universidade Federal de Uberlândia, UFPE, and INPA (among many others across Brazil), along with their researchers, have been instrumental in positioning Brazil as a global leader in ant studies. Additionally, there is a growing, though still emerging, trend toward expanding scientific outputs beyond academia to inform public policy and engage broader audiences. Together, these developments reflect the vitality of Brazilian Myrmecology and its potential to foster social and environmental transformation, both within and beyond academic spheres.

### *The Ants of Brazil: Centuries of Discoveries, Diversity & Dedication*

When Forel published the first list of ant species from Brazil in 1895, comprising around 440 species and subspecies (checklist and supplement), Myrmecology was still emerging as a scientific field on the globe. His work marked the beginning of the systematic documentation of Brazil's ant diversity, at a time when few researchers were exclusively dedicated to this group. A few decades later, with myrmecologists already active in the country, Borgmeier compiled two key catalogs (1923, 1927), expanding the number of known species and subspecies to 1,183 (checklist and supplement). This period was

fundamental for the consolidation of a national scientific community focused on ants and for the growing recognition of the richness of the fauna, both in terms of diversity and geographic distribution. Species descriptions increasingly came to be framed within more rigorous taxonomic revisions, incorporating discussions on synonymy and intraspecific morphological variation. By the 1970s, ant taxonomy in Brazil had reached a new level. The catalog published by Kempf in 1972 reflected this advancement, listing 1,334 species and subspecies and consolidating decades of taxonomic work. This landmark publication became a key reference and helped drive further studies on Neotropical ant fauna. As of 2025, Brazil harbors the greatest known ant diversity on the planet, with 1,737 recorded species and subspecies (AntMaps.org; Janicki *et al.*, 2016), a number that continues to grow thanks to ongoing efforts in collection, description, revision, and data integration. Generations of researchers have contributed to expanding our understanding of this biodiversity, approaching it from multiple perspectives, ranging from Ecology to Biotechnology, and strengthening the interface between science and society through science communication and citizen science initiatives (Figure 3).

**Figure 3 -** Growth in the number of ant species and subspecies recorded from Brazil over time, based on major taxonomic milestones: Forel (1895), Borgmeier (1923, 1927), Kempf (1972), and AntMaps (2025). These compilations reflect the expansion of myrmecological knowledge in the country, driven by continued efforts in species description, taxonomic revision, and biodiversity inventories.



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# 03

# LONG STORY SHORT: AN OVERVIEW OF ANT TAXONOMY AND ANT TAXONOMISTS IN BRAZIL

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# ABSTRACT

Brazil, the largest country in South America, boasts the greatest diversity of ants in the Americas and ranks among the most species-rich countries globally. It has long been recognized as a key hub for myrmecology, driven by its remarkable biodiversity and a rich history of research in ant ecology and taxonomy. However, mapping ant species and developing a comprehensive understanding of them remains a significant challenge. Here, we present an overview of the state of the art in ant taxonomy and the work of ant taxonomists in Brazil. Early taxonomic studies in the country were initiated by European naturalists. Over the years, Brazilian research institutes and universities have expanded their infrastructure, bringing in new professionals, broadening graduate programs, and pushing the boundaries of ant research, including taxonomy. The nationalization of scientific production, combined with increasing collaboration among researchers, has shifted the field from individual, single-author taxonomic descriptions to team-based approaches. The establishment of the *Brazilian Ants Course & Consortium* and the growing expertise in ant taxonomy underscore Brazil's status as a global leader in myrmecological research. Taxonomists primarily rely on voucher specimens stored in museums, universities, and laboratory collections to expand our understanding of biodiversity despite ongoing challenges. The growth of scientific output, the training of new taxonomists, and the advancement of analytical techniques have positioned Brazil's myrmecological community to effectively tackle complex taxonomic and evolutionary questions.

**Keywords:** Formicidae; entomology; biodiversity; alpha taxonomy.

## INTRODUCTION

Brazil has been recognized as a cradle for ant taxonomy and myrmecology in general, due to its great biodiversity and long history of research on systematics. During this history, ant taxonomy has seen many different stages. At first, species were described by European naturalists who visited the country or received material sent by local researchers and naturalists. Gradually, research institutes and universities implemented broader research initiatives, hired new professionals and expanded their graduate programs, encompassing new frontiers in taxonomy, ecology, systematics, evolution, phylogenetics, genetics, biogeography, ethology, and conservation, using ants as model organisms. The consolidation of Brazilian Myrmecology and its achievements are exemplified by the *Symposium of Myrmecology*, a prominent international meeting, and the *Brazilian Ants Consortium*, composed of around 40 scientists with varied expertise. In this chapter, we present the state of the art of Myrmecology in Brazil, with a focus on taxonomy. First, we trace the history of ant taxonomy in Brazil, highlighting the remarkable legacies of its various key figures, from the early stages to the present—considering active Ph.D. researchers on ant taxonomy in the country who have already described at least one new ant species. Finally, we discuss future perspectives for ant taxonomy in Brazil. All genera and species names cited in the chapter are listed by author and year in the supplementary material (Table S1), along with all corresponding taxonomic references (Table S2).

## THE EARLY DAYS OF BRAZILIAN ANT TAXONOMY

From the mid-eighteenth century to the late nineteenth century, a succession of European naturalists and entomologists made significant contributions to the knowledge of Brazilian ant diversity, often expanding the known distributions of Neotropical species to include Brazil or formally describing species from the country. The first such contribution came from Swedish naturalist Carolus Linnaeus, who in 1758, included species occurring in Brazil in his *Systema Naturae* (*e.g.*, *Atta cephalotes*, *A. sexdens*, *Cephalotes atratus*, *Dolichoderus bidens*, *Odontomachus haematodus*). Although his work was primarily based on specimens from Suriname collected by his student Daniel Rolander

(1722–1793) (BACCARO *et al.*, 2015), several of these taxa are known to occur in Brazil, including *Neoponera foetida*, which is restricted to the Amazon region.

Almost 20 years later, in 1775, Danish entomologist Johann Christian Fabricius (1745–1808) described the first ant species explicitly attributed to Brazil: *Formica attelaboides* and *F. rufipes*. Unfortunately, these descriptions lack precise locality data or information about the collectors, leaving only the country as a general reference. Towards the close of the eighteenth century and into the early nineteenth century, French naturalists Guillaume-Antoine Olivier (1756–1814) and Pierre André Latreille (1762–1833) also contributed to the characterization of Brazilian ant fauna. Working largely with material from French Guiana, they described species whose ranges extend into Brazil, such as *Formica vagans* and *F. crassinoda*. Latreille, in particular, named the first species based on a Brazilian specimen—*Formica spinicollis*—collected from Rio Negro by German naturalist and explorer Friedrich Heinrich Alexander von Humboldt (1769–1859) during his travels in equinoctial America.

The second half of the nineteenth century saw important British contributions, most notably from Frederick Smith (1805–1879) of the British Museum. In the 1850s, Smith described numerous species collected in the Amazon by English naturalist Henry Walter Bates (1825–1892) during his expedition from 1848 to 1852. While many of these were only broadly assigned to Brazil, others had more precise localities, such as Pará, Santarém, Villa Nova on the Amazons, and the Tapajós river. In 1858, Smith's catalogue of Formicidae went beyond listing species, incorporating new descriptions from Bates' material, such as *Formica solitaria* from Ega (=Tefé, Amazonas), *F. arborea* from Ilha do Marajó (Pará), and *Atta fabricator* from Rio de Janeiro. This work also used material collected by English cleric and coleopterist Hamlet Clark (1823–1867) and the naturalist and artist William Swainson (1789–1855), expanding the Brazilian distribution of several species previously known only from other parts of the Neotropics. Around the same time, Austrian entomologist Gustav L. Mayr (1830–1908) began describing Brazilian ants (MAYR, 1862). His first contributions (*e.g.*, *Camponotus westermanni*, *Cryptocerus spinosus*, *Pheidole opaca*) were based on specimens in the "Mus. Caes. Vienn." collection, some from unnamed collectors and others from Westermann and H. Drewsen. However, much of this material, like *Prenolepis fulv*a, came from the Novara frigate's scientific circumnavigation (1857–1859,


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which stopped in Rio de Janeiro and was organized by Austrian naturalist Georg Ritter von Frauenfeld (1807-1873) (BASCH-RITTER, 2008). In 1865, Mayr published a fuller account of the *Novara* ants (*e.g.*, *Apterostigma pilosum*, *Sericomyrmex opacus*) and went on to describe additional Brazilian species from material in the *Zoologischen Museum* in Halle and from collections made by James William Helenus Trail (1851–1919) in the Amazon. These specimens provided key records from localities including Lagoa Santa (Minas Gerais), Paraná, and the Amazon River basin (*e.g.*, *Camponotus clypeatus*, *Prionopelta punctulata*, *Crematogaster brasiliensis*, respectively).

In 1879, Swiss myrmecologist Auguste-Henri Forel (1848–1931) began working on Brazilian material, describing new species from São Paulo and Rio de Janeiro, such as *Camponotus naegelii*, and extending the known ranges of others into Brazil. Based on specimens collected by H. Naegeli or Joseph, and deposited in the collections of Swiss entomologist Henri Louis Frédéric de Saussure (1829–1905) and at the *Musée de Munich*, Forel recorded species from Bahia, Caravelas[1], Rio de Janeiro, and Taubaté (São Paulo).

All of these scientists contributed to documenting the global ant fauna, a pursuit shaped in its early stages by imperial expansion, political power, and the cultural prestige of natural history collections (ALBERTI, 2002). In this period, major Brazilian museums were founded as part of broader scientific and cultural development efforts. The *Museu Imperial* (MI), created in Rio de Janeiro in 1818 by King D. João VI, later became the *Museu Nacional do Rio de Janeiro* (MNRJ). The *Museu Paraense Emílio Goeldi* (MPEG), established in 1866 by Brazilian naturalist Domingos Soares Ferreira Penna (1818–1888) (PRADO *et al.*, 2020), grew from the continuous flow of material sent to the MNRJ. In São Paulo, the amalgamation of collections from the Geographic and Geological Commission of the São Paulo province, the private collection of Colonel Joaquim Sertório (?–1905), the Pessanha collection, and the São Paulo Province Museum collection, led to the creation of the *Museu Paulista* (MP) (ULYSSÉA; BRANDÃO; 2020),

[1] The specimens from "Cravellas" may be collected by the German naturalists Georg Heinrich von Langsdorff (1774–1852), Friedrich Sellow (1789–1831), and Georg Wilhelm Freyreiss (1789–1825) during his expeditions in Brazil from 1813 to 1818 (PAPAVERO, 1971).

whose zoological holdings were incorporated into the University of São Paulo in 1969, forming the *Museu de Zoologia da Universidade de São Paulo* (MZSP/USP).

## PIONEERING INITIATIVES IN BRAZIL

The first local efforts to document Brazil's ant fauna were led mainly by male scientists working in a few institutions or conducting independent studies in entomology. Many were German-born and later becoming Brazilian citizens, such as Fritz Müller[2] (1822–1897), Hermann von Ihering (1850–1930), Wilhelm Müller (1857–1940), Lothar Hetschko (18??–19??), Ernst Garbe (1853–1925), Hermann von Lüderwaldt (1858–1938), Alfred Möller (1860–1921), Miguel Witte (1885–1967), and Fritz Plaumann (1902–1994). Others included Swiss-Brazilian Emílio Augusto Goeldi (1859–1917), U.S.-born Brazilians Orville Derby (1851–1915) and Adolph Hempel (1870–1949), Luxembourgish Edouard-Pierre Luja (1875–1953), and Austro-Hungarian-Brazilian Adolpho Ducke (1876–1959). Most emigrated from Europe, then in the turmoil of the Industrial Revolution, during a period when the Brazilian imperial government was encouraging immigration.

Brazilian-born researchers such as Adolpho Lutz (1845–1940), Francisco Dias da Rocha (1869–1960) (CARVALHO, 2013), and Alberto José de Sampaio (1881–1946) also played important roles. These naturalists collected ants during their travels or near their residences, sometimes independently, sometimes under institutional direction. Their work largely involved gathering and sending specimens to foreign experts for identification and description, such as Mayr, Forel, Carlo Emery (1848–1925), William M. Wheeler (1865–1937), Felix Santschi (1872–1940), August Reichensperger (1878–1962), Carlo Menozzi (1892–1943), and Marion R. Smith (1894–1981). The first publications from this phase appeared in 1886, when Mayr described *Eciton hetschkoi* from material sent by Hetschko in Paraná and Santa Catarina, and Forel described *Pheidole guilelmimuelleri* and *Strumigenys fridericimuelleri* from W. Müller's Santa Catarina collections. In 1888,

[2] Fritz Müller published numerous articles on entomology, marine biology, and botany. He is internationally renowned for his discoveries of Müllerian mimicry and Müllerian bodies; the latter being linked to his description of the *Azteca-Cecropia* mutualism. In 1893, Emery described the species *Azteca muelleri* based on the specimens sent by Fritz Müller (BOLTON, 2025).


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Emery of the *Museo Civico di Storia Naturale Giacomo Doria* (MSNG) in Genoa described ants from Rio Grande do Sul collected by Ihering, a traveling naturalist from MNRJ at the time (NOMURA, 2012). Emery dedicated two species to Ihering —*Atta iheringi* (Figure 1A-B) and *Rhopalothrix iheringi*. Emery went on to describe dozens of Neotropical species, primarily from Costa Rica but also from Brazil and other South and Central American countries. Within Brazil, specimens were commonly collected in Rio Grande do Sul by Ihering, Santa Catarina by F. P. Schmalz, Mato Grosso and Rio de Janeiro by Germain, and Pará by A. Schultz, with some lacking collector data.

**Figure 1 -** Lateral view (A) and labels (B) of Atta iheringi type worker.

**Source:** Photos by Will Ericson (A) and Alexandra Westrich (B), from www.antweb.org (ANTWEB, 2025).

Articles by Reichensperger, W. Wheeler, Santschi, Menozzi, and M. Smith likewise contain numerous examples of Brazilian ant species described from specimens sent abroad for identification and formal description. This practice, characteristic of the early efforts to uncover the Brazilian ant fauna, occurred alongside the first species lists compiled by resident naturalists[3], and gradually gave way to the expansion of local taxonomy and the training of Brazilian specialists.

[3] In 1895, Forel published the first compendium of Brazilian ants at the request of Goeldi, listing 440 species. At that time, this number represented 22% of the known global ant fauna. This initial checklist of Brazilian ants did not include the 84 species recorded by Ihering in 1894 for the state of Rio Grande do Sul. The second Brazilian state to compile a list of its ant fauna was Ceará, with 76 species listed by Forel in 1908 at the request of Dias da Rocha—who likely wrote the article's preface and estimated approximately 700 ant species known in Brazil at the time. São Paulo was the third state documenting its myrmecofauna, with 315 species listed by Lüderwaldt in 1918. In his article's preface, Lüderwaldt highlighted the significant progress in ant studies, with the number of known ant species rising from 2,000 worldwide in 1886 to 5,031 by 1910.

## ANT TAXONOMY IN BRAZIL

Forel was probably the most prolific taxonomist in the early phase of Brazilian ant studies. Between 1893 and 1915, he described dozens of species from material sent by Dias da Rocha, Goeldi, Lutz, and especially Ihering, then director of the *Museu Paulista* (MP). Although six species were named after Ihering by Forel, most specimens were actually collected by MP staff, including Garbe and Lüderwaldt, as well as park rangers Ernesto Schwebel and Mathias Wacket from Cajuru Park (now Alto da Serra de Paranapiacaba Biological Reserve) (BOCCHI; PATACA, 2022), with Ihering contributing to a lesser extent (ULYSSÉA *et al.*, 2025). These collections came mainly from São Paulo, but also from Acre, Espírito Santo, Minas Gerais, Rio de Janeiro, Rio Grande do Sul, and Santa Catarina. Lutz, a physician and epidemiologist of the *Instituto Bacteriológico* (now *Instituto Adolfo Lutz*), contributed with specimens from São Paulo and was honored by Forel, while Goeldi, working at the MI (now MNRJ) and later the MPEG, supplied material from Rio de Janeiro and the Amazon region, also earning species epithets in his name. Exchanges of specimens between institutions (MP, MI/MNRJ, MPEG, *Museu Dias da Rocha*), specialists, and amateur naturalists were frequent (FRANCO; DRUMMOND, 2005).

In 1918, Lüderwaldt became the first scientist based in Brazil to describe local ant species, from specimens collected in São Paulo and Minas Gerais, though some of his attributions were later disputed. Four species he credited to other myrmecologists—*Crematogaster crassipes* to Mayr, *C. montezumia fumata* to Forel, *Sericomyrmex squamosus* to Smith, and *Odontomachus haematoda minuta* to Emery—are actually *nomina nuda*, and one is a misapplied name of *O. haematodes pubescens minutus* (BOLTON, 2025). In the same work, Lüderwaldt described *Camponotus rufipes cajurensis*—previously mentioned by Forel (1911: 310) as a variety—and three valid new species: *Acanthoponera dolo schwebeli*, *Anochetus altisquamis fumata*, and *Pachycondyla metanotalis*. In 1920, he added *Eciton hamatum mattogrossensis* from Mato Grosso, collected by Garbe.


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**Borgmeier-Kempf period**

The development of a consistent body of work on Brazilian ants within the country is closely tied to the efforts of Thomas Borgmeier and Walter Kempf, both of whom made remarkable contributions to Neotropical ant taxonomy during a period of limited resources. Not surprisingly, each was honored with species (4/7), subspecies (1/1), and genera (*Borgmeierita*/*Kempfidris*) bearing their names.

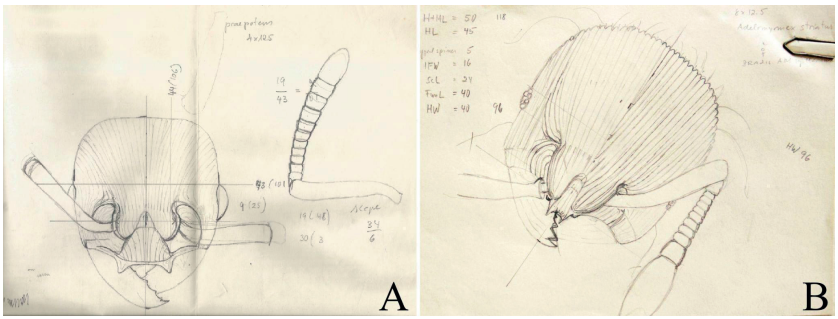
Borgmeier, mentored by Priest Hermann Schmitz and influenced by Jesuit Austrian entomologist Erich Wasmann (1859–1931), initially specialized on phorids (GARMUS, 2011) but, with the support of Ihering, who donated his entire myrmecological library to him, committed himself to ant studies. Over his career, he worked at the MNRJ, *Instituto de Biologia* (IB), and the entomology section of the Rio de Janeiro Botanical Garden, publishing 45 papers between 1920 and 1959. He described 161 taxa and ergatoid forms, revised genera, and made important contributions to species' natural history (e.g., *Acropyga pickeli, Odontomachus affinis*), with a particular focus on army ants worldwide (Table S2: Borgmeier, 1930, 1933a, b, 1936, 1948, 1950, 1953, 1954, 1955, 1956, 1957, 1958) (KEMPF, 1972b). Many of his studies were published in the *Revista de Entomologia*, which he founded in 1931 (BACCARO *et al.*, 2015).

In 1944, Borgmeier recognized the potential of theology student Kempf and encouraged him to pursue a career in myrmecology. After earning a bachelor's degree in Natural Sciences and a Ph.D. in Entomology in the United States (1947-1951) (PRADO *et al.*, 2021), Kempf returned to Brazil, where he taught at the Franciscan Seminary in Agudos, and at the School of Philosophy, Sciences and Languages in Bauru, both in São Paulo, and later at the University of Brasília. In the late 1950s, Borgmeier transferred his collection and library to Kempf (KEMPF, 1959b). Together, they co-founded the journal *Studia Entomologica*, with Kempf as its editor until his death in 1976. Kempf described 157 taxa and published 95 papers[4], producing taxonomic revisions, identification keys, and well-illustrated (Figure 2A-B) synopses for numerous tribes and genera (*e.g.*,

[4] Kempf also contributed to the ethnology of indigenous people in Brazil, specifically the "Mundurucus" and "Jê", publishing five papers (LANE, 1978).

*Acanthognathus*, *Anochetus*, Basicerotini, Cephalotini, *Cyphomyrmex*, Dacetini, *Dinoponera*, *Gigantiops*, *Heteroponera*, *Hylomyrma*, *Monacis*, *Mycetarotes*, *Mycocepurus*, *Oxyepoecus*, *Pseudomyrmex*, *Rogeria*, *Strumigenys*, and *Thaumatomyrmex*), as well as species lists for regions across the Neotropics (KEMPF, 1959a, 1960a, 1961b, 1970, 1972a).

**Figure 2 -** Kempf's drafts for *Hylomyrma praepotens* (**A**) and *Adelomyrmex striatus*[5] (**B**).




**Source:** MZSP Hymenoptera lab archives, photos by Mônica A. Ulysséa (A) and Diego M. Matielo (B).

Borgmeier and Kempf also exchanged material with Lenko, curator of the former *Museu Paulista* Ant Collection, then housed at the Department of Zoology of the Secretariat of Agriculture, Industry and Commerce of São Paulo (DZSP, 1960 to 1969). During this period, Lenko collaborated with MPEG, published five ant-related papers, described *Gnamptogenys kempfi*, documented teratology in *Paracryptocerus pusillus*, recorded the rare *Stegomyrmex manni* in a bird gut, and co-authored studies with Kempf on *Gigantiops destructor* (Table S1-S2: Lenko, 1964a, b, 1966; Kempf & Lenko 1968).

A contemporary of the friars, Cincinnato Rory Gonçalves (1909–1985), an agricultural engineer at the *Instituto de Biologia* of the Rural Federal University of Rio de Janeiro (IBUS/UFRRJ), specialized in leafcutter ants *Acromyrmex* and *Atta*, key agricultural pests. Gonçalves published 16 papers on their biology, ecology, and taxonomy,, describing eight species and addressing the phylogeny

[5] Fernández (2003) named and described this species based on two specimens designated as types by Kempf, who discovered this new species and labelled them as *Adelomyrmex striatus*, but never formally described it.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of *Atta* in his final work (GONÇALVES, 1986). After his death, UFRRJ named its Integrated Pest Management Center in his honor.

Collectively, Borgmeier, Kempf, and Cincinnato established the foundation for modern Brazilian ant taxonomy, shifting focus from purely medical entomology and agricultural pests concerns toward a broader understanding of the country's myrmecofauna, while still recognizing the economic impact of pests such as leaf-cutters, epitomized by Yves Saint-Hilaire's remark: "If Brazil doesn't get rid of the *Saúva*, the *Saúva* will get rid of Brazil."

**Traditional ant taxonomy research centers in Brazil**

From the late 1970s to the 1990s, Brazilian myrmecology entered a phase of multidisciplinary growth, combining taxonomy, systematics, ecology, natural history, and conservation. This new generation of scientists advanced knowledge of Neotropical ants, built and curated major collections, and mentored students who now sustain and expand the field.

One of those major collections resides at the ***Museu de Zoologia da Universidade de São Paulo*** (MZSP). After the transfer of the DZSP collections to University of São Paulo (USP) in 1969, the acquisition of the Borgmeier-Kempf collection in 1977 provided a foundation for systematic research at the MZSP (ULYSSÉA; BRANDÃO, 2020). Hired in 1981, Carlos Roberto Ferreira Brandão expanded the MZSP Ant Collection to over 380,000 pinned specimens (CHIMENTI *et al.*, 2020), produced eight catalogs of type material (KLINGENBERG; BRANDÃO, 2009; SCOTT-SANTOS *et al.*, 2008; BRANDÃO *et al.*, 2010; ESTEVES; PRADO; BRANDÃO 2011; ULYSSÉA; BRANDÃO, 2013; PRADO; BRANDÃO, 2013; ULYSSÉA *et al.*, 2015, 2017), and described 71 taxa (*e.g.*, *Adelomyrmex longinodus*, *Cyatta abscondita*, *Gnamptogenys vriesi*), including notable revisions of *Megalomyrmex*, *Blepharidatta*, *Trachymyrmex*, and *Mycetagroicus*. His work spanned living and fossil ants (*e.g.*, †*Cariridris bipetiolata*, †*Technomyrmex caritatis*), fostering ongoing debates on the oldest Formicidae in the fossil record (GRIMALDI *et al.*, 1997; RASNITSYN, 2002; OSTEN, 2007; WARD; BRADY, 2003), species rarity and the importance of habitat-specific collection methods (BRANDÃO *et al.*, 2008).

More recently, Gabriela Procópio Camacho joined the Hymenoptera curatorship, implementing a new discipline in genomic studies from museum material. By the latest account, the collection holds type specimens for 641 valid species/subspecies, 216 obsolete combinations, 211 synonymized species, and 16 unavailable names (ULYSSÉA *et al.*, 2025). Camacho has described three *Gnamptogenys* species and has been mentoring graduate students in taxonomy, while also working on the incorporation of the fossil collection of Maria Aparecida Vulcano (1921–2018), which comprises approximately 3,000 paleoentomological records from the Crato Formation of the Araripe Basin, northeastern Brazil. In the first paper resulting from the examination of these fossils, the oldest ant specimen known to science was described—†*Vulcanidris cratensis*, a 113-million-year-old hell ant that once lived in northeastern Brazil.

Another important center is the ***Comissão Executiva do Plano da Lavoura Cacaueira*** (CEPLAC). Since 1986, French-Brazilian Jacques Hubert Charles Delabie has led ant research at CEPLAC's Cocoa Research Centre (CEPEC) in Bahia, developing the CPDC Ant Collection (DELABIE, 2007b, 2020). His work integrates taxonomy, ecology, natural history, cytogenetics, and conservation, with emphasis on poneromorph ants, invasive species (*e.g.*, *Hypoponera punctatissima*, *Tetramorium lucayanum*, *Wasmannia auropunctata*), and agricultural systems (DELABIE, 1993; DELABIE; MARIANO; NASCIMENTO, 1998; FOWLER *et al.*, 2002; DELABIE *et al.*, 2007; DELABIE *et al.*, 2015). He co-authored the description of 30 taxa, including two genera—*Asphinctanilloides* and *Diaphoromyrma*—and 28 species, trained dozens of students, and built a strong collaborative network. Now one of the five largest ant collections in Brazil, CPDC contains 299 type specimens of 63 taxa (DELABIE *et al.*, 2020).

The ***Entomological Collection Ângelo Moreira da Costa Lima*** (CELC) is led by Antônio Mayhé-Nunes, a former mentee of Cincinnato at MNRJ, who has specialized in fungus-growing ants, mostly *Mycetagroicus*, *Mycetarotes*, and *Trachymyrmex*, describing 14 taxa across these three genera. The Cincinnato Ant Collection was incorporated into CECL (MAYHÉ-NUNES, 2007), which has since grown through specimens collected by Mayhé-Nunes and his mentees, holding 160 type specimens of 21 species/subspecies ants (MAYHÉ-NUNES; VEIGA-FERREIRA; RACCA FILHO, 2001).


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At the ***Museu Paraense Emílio Goeldi*** (MPEG) since 1996, Ana Yoshi Harada began her career at the ***Instituto Nacional de Pesquisas da Amazônia*** (INPA), where she focused on expanding the INPA Ant Collection (FERNANDES; OLIVEIRA, 2020). She has contributed to ant ecology (BENSON; HARADA, 1988), inventories (SANTOS *et al.*, 2012; HARADA, 2016), *Azteca alfari* natural history, and taxonomy, focusing on under-sampled Amazonian regions and mentoring students on diverse genera. Harada described *Monacis inpai*—likely the first ant type specimen in INPA collection, as no Formicidae or even Hymenoptera were cited in the 1983 article on invertebrate types (RAFAEL; PENNY; HARADA, 1983). In 2017, she reported *Camponotus brettesi* in Brazil for the first time, extending its known range southward to the mangroves of Bragança, Pará.

Since 2013, Rogério Rosa da Silva has led ecological research at the Laboratory of Ant Morphology and Functional Ecology (AntMor), addressing broad ecological questions using morphometric data and big datasets. His work focuses on ant functional ecology (ALMEIDA *et al.*, 2023; ANDRADE-SILVA *et al.*, 2022; CARVALHO *et al.*, 2023; SILVA; BRANDÃO, 2014; SILVA *et al.*, 2022); however, he also designs fieldwork to significantly expand the MPEG Ant Collection and support systematic research. Silva led the description of three taxa: *Leptanilloides atlantica* and the monotypic genus *Tropidomyrmex* with *T. elianae*, and has also been mentoring graduate research projects in ant taxonomy and training students in collecting techniques, curatorial practices, and species identification.

Maria Santina de Castro Morini (Mogi das Cruzes University) frequently collaborates with Silva on research projects and publications. Alongside Feitosa and Silvia Sayuri Suguituru, they co-authored an excellent science outreach book on ant biodiversity in the Alto Tietê region (SUGUITURU *et al.*, 2015). More recently, Silva and his mentees founded SCIANTS.org, an initiative promoting scientific knowledge and awareness of Amazonian ant diversity.

Rodrigo dos Santos Machado Feitosa has transformed the Zoology Department Collection at the Federal University of Paraná into a major ant research hub. The department houses the country's second-largest entomological collection, named after its founder—***Priest Jesus Santiago Moure Entomological Collection*** (DZUP), but the DZUP Ant Collection's exponential expansion aligns with Feitosa's efforts in fieldwork focused on undersampled habitats in Paraná and material exchange (ANDRADE; FEITOSA, 2020). The

collection also received a significant donation from CEPLAC, consisting of ant specimens representing 906 species from around the world, and incorporated the Jorge L. M. Diniz Ant Collection.

Fostering a collaborative research environment, he has co-authored the description of over 50 taxa, including 16 as lead author (see *Ectatomma*, *Lachynomyrmex*, *Sphinctomyrmex*, *Stegomyrmex*) and 25 in collaboration with his mentees, who are currently working on additional 50 taxa (Table S3).

Later on, Colombian-born and Venezuelan at heart, John Edwin Lattke Bravo enriched the DZUP Ant Collection with ethanol-preserved specimens from all biogeographical regions, collected during his professional stints in the United States, Spain, Germany, and Venezuela (ANDRADE; FEITOSA, 2020). Lattke has described an impressive total of 189 ant taxa, both fossil and extant species, within the genera *Apterostigma*, *Bariamyrma*, †*Dilobops*, *Gnamptogenys*, †*Haidomyrmex*, *Leptogenys*, *Platythyrea*, *Protalaridris*, and *Strumigenys*. At UFPR, he and his mentees described the genus *Igaponera* and 12 new species (Table S3). Together, Feitosa and Lattke have mentored a new generation of taxonomists now working in prominent institutions countrywide.

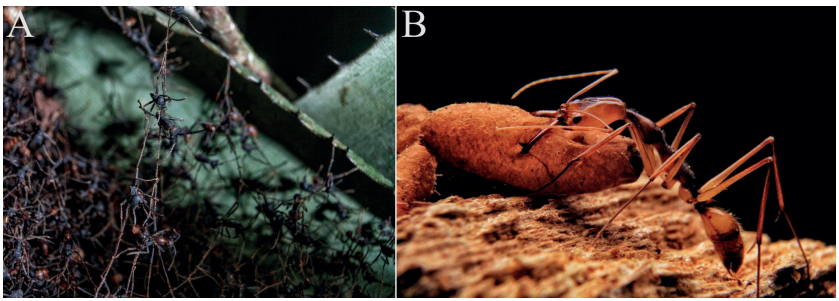
**Expanded horizons for Ant Taxonomy in Brazil**

Building on the work of earlier researchers, a new generation of ant taxonomists in Brazil has expanded research hubs nationwide and forged strong collaborations. These efforts provide top-level academic training for mentees while allowing them to explore cutting-edge technologies in ant taxonomy, such as phylogenomics, μ-CT, 3D geometric morphometrics, biogeography, phyloecology, and palaeoentomology—all grounded in solid curatorial practices.

Since 2013, new laboratories have emerged, such as Benoît Jahyny's group at Federal University of the Vale do São Francisco (UNIVASF), focusing on ants and other arthropods of the *Caatinga* and São Francisco River sand dunes. His work spans natural history, taxonomy, eusociality, and behavior (JAHYNY *et al.*, 2008, 2015), and he has co-described *Thaumatomyrmex fraxini* and *Eurhopalothrix oxente* with his students. At the Federal University of Viçosa (UFV), Júlio Cezar Mário Chaul emerged as a new voice in Brazilian ant taxonomy, specializing in the genus *Strumigenys*. He has described 18 taxa, including fossils in the genera

†*Camelosphecia*, †*Gerontoformica*, †*Pheidole*, and †*Zigrasimecia*, and two extant species of *Mycetomoellerius* with his mentee. At INPA, Itanna O. Fernandes—trained under Márcio Luiz de Oliveira and Jacques Delabie—specializes in the *Pachycondyla foetida* complex and trap-jaw ants, leading a global phylogeny of *Anochetus* and *Odontomachus* (FERNANDES *et al.*, 2021). She has described several species (*e.g.*, *Cryptopone pauli*, *Proceratium amazonicum*, *Simopelta anomma*), supervised taxonomic revisions, and continues advancing INPA's Ant Collection. Lívia P. do Prado, currently at MPEG, trained at MZSP and MPEG specializing in Myrmicinae genera. She has described species such as *Megalomyrmex peetersi* and contributed to inventories (PRADO *et al.*, 2019; ALBUQUERQUE *et al.*, 2021), curatorial work, *Megalomyrmex ayri* natural history (PRADO *et al.*, 2022), and science outreach. She co-founded the aforementioned platform SCIANTS.org. Mônica A. Ulysséa, now at UFPR and a mentee of Brandão and Silva, has described 14 *Hylomyrma* species and discovered that intercastes are quite common in this genus. Her findings highlight *Hylomyrma* as a promising model for studying ant caste development and evolution (ULYSSÉA; BRANDÃO, 2021; ULYSSÉA; FARDER-GOMES; PRADO, 2024). She also worked extensively in the curation of the MZSP Ant Collection. Natalia M. Ladino, a Colombian myrmecologist and now professor at the Federal University of Pelotas (UFPel), revised *Prionopelta* and described four new species, in addition to studies on subterranean and melanic ants (LADINO *et al.*, 2024; LADINO; FEITOSA, 2024). Esperidião A. dos Santos-Neto, a mentee of Delabie, focuses on *Strumigenys*, describing new species (*S. xoko* and *S. itannae*) and documenting exotic introductions (*S. rogeri*), while combining meticulous fieldwork with striking macro photography (Figure 3A-B). He has also contributed significantly to the curation of the CPDC Ant Collection (DELABIE *et al.*, 2020). Frederico S. R. Marcineiro, now adjunct professor at Federal University of Santa Catarina (UFSC), is dedicated to the study of Ponerinae ants. He has described two new species with his mentor, Lattke—*Pachycondyla beneditoi* and *Gnamptogenys rugimala*—and co-described the genus *Igaponera*. His Ph.D. dissertation addressed the *Pachycondyla harpax* complex, identifying eight new species within it. Collectively, these researchers have strengthened ant taxonomy in Brazil, broadened its geographical and taxonomic scope, and trained the next generation of myrmecologists through fieldwork, collection curation, and integrative approaches.

**Figure 3 -** Photos of *Eciton burchellii* bivouac in bromeliads in Ilhéus (**A**) and *Odontomachus hastatus* carrying pupa after nest disturbance in the Amazon Forest, Manaus (**B**).




**Source:** Esperidião A. dos Santos-Neto (2025).

The consolidation and growth of ant research in Brazil is reflected in the *Symposium of Myrmecology* and the *Brazilian Ants* initiative. The symposium began in 1980 at UNESP – Rio Claro as an annual regional meeting of researchers, professors, and students studying ants. It has since become the world's largest scientific conference focused on ant research, drawing hundreds of contributions from Brazilian and international students and scientists, and fostering global collaborations (BRANDÃO, 2020). In its 2023 edition in Manaus, the event gathered 300 participants and was organized by 29 researchers from eight Brazilian institutions (Bocaina, INPA, MPEG, MZSP, UFAC, UFAM, Unifespa, UNL) and three international ones (Ohio State University, UNAL, Université de Guyane). The program featured eight keynote speakers, 10 roundtables, 97 oral presentations, and 109 posters (SIMPÓSIO DE MIRMECOLOGIA, 2024). Founded in 2012, *Brazilian Ants*, led by Fernando Schmidt, Carla Ribas, and Rodrigo Feitosa, is a national initiative that promotes myrmecology through student training and research collaboration. They organize the biannual *Brazilian Ant Course*, which offers focusing hands-on training in ant sampling, mounting, identification, and key topics in ant natural history, taxonomy, systematics, evolution, and ecology. As part of their broader mission, they also established the *Brazilian Ants Consortium*, which brings together around 40 researchers from across the country. One of the consortium's major efforts was compiling a comprehensive database of 491 ant diversity papers conducted in Brazil between 1970 and 2021. This effort led to several key publications: a profile of ant diversity studies in the country (SCHMIDT *et al.*, 2022), an updated overview of the ants of Brazil

(FEITOSA *et al.*, 2022), and a study on the validation of taxonomic identification in myrmecological research (FEITOSA *et al.*, 2023).

**Future Perspectives**

Brazil has become a global hub for ant taxonomy and myrmecology, supported by its exceptional biodiversity, a strong tradition of systematic research, and recent initiatives like *Brazilian Ants*. The field has evolved from the era of early European naturalists sending Brazilian specimens abroad to a collaborative and increasingly nationalized research environment. While historical descriptions were typically single-authored by European specialists, today's studies often involve multiple authors, institutions, and areas of specializations, with rapid information sharing through preprints, alerts and social media real-time updates. These changes reflect both scientific progress and national policies aiming at preserving genetic heritage and natural resources, while fostering collaboration between Brazilian and foreign scientists.

While molecular taxonomy in Brazil is still developing, many researchers have laid the groundwork through international collaborations. Expanding domestic capacity for advanced analyses remains an urgent priority. Despite these challenges, myrmecological research is growing rapidly, with specialized laboratories at CEPLAC, INPA, MPEG, MZSP, UNIVASF, UFPel, UFPR, and UFV advancing ant diversity and systematics.

The future of ant taxonomy in Brazil will depend on strengthening national and international collaboration networks, improving local molecular infrastructure, and building well-equipped research centers to reduce reliance on foreign facilities. Substantial government support for training, personnel, and research funding will be essential to maintaining Brazil as one of the global leaders in myrmecology.

Brazilian researchers abroad are gaining valuable experience and contributing to the advancement of taxonomy and myrmecology. Their return and collaboration with national teams can accelerate the adoption of innovative methodologies and strengthen domestic research.

Finally, the future of ant taxonomy in Brazil is also closely tied to biodiversity conservation and citizen science. Initiatives such as fauna inventories, ant

monitoring programs, and digital tools—like online databases and identification apps—can democratize knowledge and engage the general public in ant research and conservation. Thus, the key challenge for the future of ant taxonomy in Brazil will be fostering an environment that supports both the training of new specialists and the production of innovative research within the country. Brazil's continued success in myrmecology will rely on combining its historical strengths with collaboration, innovation, and education.

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# Behavior, Physiology, and Applied Perspectives

# 04

# THE STATE OF THE ART IN ANT BEHAVIOR RESEARCH IN BRAZIL

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# ABSTRACT

This chapter provides a synthesis of contemporary research on ant behavior in Brazil over the last decade. We assess the diversity of ant species, research approaches and behavioral aspects studied in Brazil. By integrating an ethological perspective with recent advances in ecology, behavioral ecology, and applied entomology, we explore how ant behavior is modulated by ecological interactions, immediate causes, and developmental plasticity, and discuss its adaptive value and implications for management strategies. Behavioral research on ants in Brazil reveals a great diversity of topics, including foraging, division of labor, social dynamics regulation, communication, intra- and interspecific interactions, highlighting the ecological and social complexity of these eusocial insects. In the supplementary material, we present the socio-academic profile of the researchers in the field, which reveals significant gender imbalance and regional disparities, pointing to a broader need for actions that promote equity in the field. Finally, this chapter should not be viewed as a definitive survey, but rather as a starting point to encourage and inspire continued multidisciplinary collaboration among students, researchers, and professionals committed to understanding the diverse and intricate behavioral world of ants in Brazil.

**Keywords:** Brazilian behavioral myrmecology; behavioral approaches; interspecific interactions; social behavior; socio-academic profiles.

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## INTRODUCTION

The scientific study of animal behavior finds its origins in Darwin's theory of evolution and, more recently as a discipline, with the Nobel Prize in Medicine awarded to three great researchers in Ethology: Karl von Frisch, Konrad Lorenz, and Nikolaas Tinbergen in 1973 (Alcock, 2011). Ethology was, therefore, the first discipline to formalize the study of behavior from the perspective of Darwinian evolutionary theory (Izar, 2018). Since then, this discipline has expanded and diversified, giving rise to multiple related fields and investigative approaches, including Ethology itself, Behavioral Ecology, Neuroecology, Physiological Ecology, Evolutionary Psychology, Neuroscience, and others (Yamamoto & Volpato, 2011).

While Ethology was taking place in Europe, a lesser-known fact within the myrmecological and ethological communities is that, in Brazil, through the contemplation of ant behavior, Brazilian Ethology was independently emerging. It all began in the early 1950s, when a young philosophy student carefully observed a trail of tiny *Nylanderia fulva* ants descending the wall of his bedroom, while his brother, engaged in a conversation with him, smashed some ants with his finger. At that moment, he noticed that the remaining ants expressed what he called an "emotional and panic reaction" with a chaotic dispersal, antennae agitation, and jerking movements falling into the ground. This event would completely change the course of his academic and professional life, but also that of animal behavior research in Brazil (Ribeiro, 2021).

In 1960, already as a professor of Animal Psychology at the University of São Paulo, Walter Hugo de Andrade Cunha devoted his time to the understanding and systematic study of the behavior of *Nylanderia fulva* ants towards their crushed nestmates, and this became the main objective of his career in the following years and the central theme of his doctoral thesis, thus solidifying the foundations of Ethology in Brazil. This episode sparked in him the hypothesis that ants possess a kind of "psychological environment" shaped by individual memory and both their recent and distant experiences (Ribeiro, 2021). His thesis and part of his brilliant work were recently compiled in the inspiring book "EMOTION IN THE CIRCUMSPECT PROCESSION: Ant trails as a way to discovery in Psychology and Ethology" (Cunha, 2020), which we invite all myrmecologists and behavioral researchers to read. From this pioneering milestone and using the

large leaf-cutting ant colony installed in his laboratory at Alameda Glete, Cunha created postgraduate courses in which students were tasked with observing and describing the behavior of *Atta* ants. Thus, the Department of Experimental Psychology at USP began training generations of researchers in the ethological approach of animal behavior through the study of ants (Ribeiro, 2021).

It's important to note that what Professor Walter Cunha initiated was not the observation of behavior itself in Brazil, but rather the foundation of Brazilian Ethology as a scientific discipline. At the same time, or even a few years earlier, Mário Paulo Autuori, an eminent researcher from the Biological Institute was already making significant discoveries on the bioecology of leaf-cutting ants, particularly in studies on colony founding and vertical transmission of the symbiotic fungus, and he was the one who gave Professor Walter his first *Atta* ants (Ribeiro, 2021). Also, Elpídio Amante, Thomas Borgmeier, Wolfgang Kempf, Cincinnato Gonçalves, Virgílio and Francisco Mariconi are among several notable myrmecologists who have contributed to the description and understanding of several aspects of ant behavior in Brazil in its early stages, through their important works on the taxonomy, biology, ecology, and control strategies of ants (Obeidi, D'Agostini & Rebouças, 2014).

Similarly, neither the European ethologists nor their predecessors were the first to observe animal behavior. What they accomplished was the formal establishment of a new field of knowledge, characterized by the development and clarification of specific methods and theoretical concepts to study animal behavior (Ribeiro, 2021). Tinbergen (1963), in his cornerstone paper explaining the aims and methods of Ethology, proposed that a comprehensive understanding of behavior requires answering four key questions or problems. First, the **immediate cause**: *What triggers the behavior at that moment?* This involves examining external stimuli and internal physiological or neural mechanisms. Second, **ontogeny**: *How does the behavior develop over the individual's life?* It considers the indissociable influence of genes, environment, and experience from conception to death (Izar, 2018; Resende, 2019). Third, the question of **phylogeny**: *How did this behavior evolve?* This is addressed through comparative studies across species to trace the evolutionary origins of behavior. Lastly, **adaptive value** investigates: *How does the behavior enhance survival or reproductive success?*


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Understanding its current utility helps infer the selective pressures that shaped it (Bateson & Laland, 2013).

As observed for the study of animal behavior in general, in the subsequent decades, the study of ant behavior in Brazil expanded into various methodologies and approaches, for example Behavioral Ecology and Ecology, which examines, for example, how ant behavior affects their fitness, intra- and interspecific interactions, ant responses to environmental stimuli and resources, and how ants influences ecological processes (Suguituru *et al.*, 2015). Additionally, disciplines such as Applied Entomology and Biological Control, that have incorporated ethological principles to optimize pest management strategies (Vilela *et al.,* 2008). But it goes far beyond, the study of animal behavior, particularly in ants, is, by its very nature, a deeply integrative discipline (Delabie et. al., 2015). Whether through controlled experiments or field-based observations, it requires the convergence of multiple scientific domains, such as biology, chemistry, morphology, physiology, evolution, and ecology (Châline *et al.*, 2015). These diverse areas of knowledge are not simply adjacent; they actively intersect in the formulation of hypotheses and in the interpretation of behavioral phenomena.

Unfortunately, with the present work, we were not able to trace the entire trajectory of ant behavior research in Brazil. Therefore, starting from its historical beginnings, we take a big leap in time and concentrate our efforts on a central question: Where do we stand now, almost eight decades after, in our understanding of ant behavior in Brazil?

To address this gap, this chapter aims to present the state of the art in the study of ant behavior in Brazil in the last decade, by exploring the diverse approaches that characterize this field of research in our country. It embraces animal behavior in its most contemporary and multidisciplinary form. First, we aimed to explore the diversity of ant species, genera and subfamilies studied, the diversity of behavioral aspects analysed, methodologies and approaches used. Although not exhaustive, our selection intended to offer a representative overview of key topics and methodologies. Also, applying an ethological perspective, we present and discuss how each Tinbergen's "why" permeates contemporary investigations. In the supplementary material (https://doi.org/10.5281/zenodo.16815510) we provide the methods used here and we analyse the socio-academic profile of researchers behind these investigations, to understand who

they are, where they come from, and which interests they have on the study of ant behavior. Finally, we tried to stress some urgent perspectives in the study of ant behavior in Brazil and to motivate more students and researchers to join this fascinating field of study.

## DEVELOPMENT

### What have we discovered about the behavior of ants in Brazil over the past ten years?

#### From behavioral records to naturalistic descriptions

The first step in studying behavior is to observe and describe it. Within naturalistic studies, foraging is a central focus. In *Dinoponera lucida*, foragers do not exhibit consistent movement patterns but may use visual cues for orientation. Encounters with conspecifics involve antennation, stinging, and biting when facing heterocolonial individuals, or cooperative acts such as load sharing with nestmates (Zocca *et al.*, 2021). In *Atta capiguara* and *Camponotus crassus* foraging is modulated by seasonality, with differences in travel distance and time between dry and rainy periods (Caldato *et al.*, 2016; Lange *et al.*, 2019). Morphology also plays a role: larger workers of *Acromyrmex crassispinus* and *Acromyrmex subterraneus* forage and are more active at night and carry heavier loads (Nickele *et al.*, 2016).

Food acquisition strategies range from aggressive to opportunistic. *Camponotus renggeri* hunts *Agelaia vicina* wasps (Souza *et al.*, 2022), and *C. crassus* uses formic acid to monopolize extrafloral nectaries and hemipteran honeydew (Lange *et al.*, 2019). Passive strategies also occur, such as the capture of unprotected brood by *Crematogaster* sp. and *Labidus praedator* (Souza *et al.*, 2024). The diet includes uncommon prey, such as scorpions in *Ectatomma planidens* (Dionisio-da-Silva & Araujo Lira, 2019) and carrion. Scavenging behavior has been observed in *Wasmannia* sp. and *Solenopsis saevissima*, which cover vertebrate carcasses to delay decomposition and reduce competition (Maciel *et al.*, 2016; Mendonça, Santos-Prezoto & Prezoto, 2019).

Nesting behavior varies considerably. Ants can occupy pre-established places, such as plant domatia in *Pseudomyrmex concolor* (Pacheco Junior, Anjos & Del-Claro, 2022) or abandoned wasp nests in *C. renggeri* (Souza *et al.*, 2022). Nest site choice may reflect ecological constraints. *Atta sexdens* queens prefer moist, shaded soils for deeper excavation (Sousa *et al.*, 2022). Other nesting behaviors include *Cephalotes pusillus* excavating dead wood (Cristiano *et al.*, 2017), *Eciton rapax* forming arboreal bivouacs in the rainy season (Lima *et al.*, 2020), and *Camponotus senex* nesting at high elevations near bird nests (Souza *et al.*, 2023). Polydomy exemplifies complex colony-level coordination. In *Camponotus leydigi*, tandem running, worker and brood transport and resource sharing connect nests up to 30 meters apart (Soares & Oliveira, 2020).

Fungus-growing ants exhibit diverse behavioral repertoires. When exposed to toxic baits, *A. sexdens* mimics leaf-processing: medium-sized workers handle, lick, and cut the baits, while smaller workers inoculate fragments with hyphae (Silva *et al.*, 2015; Camargo *et al.*, 2017). Pathogens, however, trigger colony-level aversion learning, leading to cleaning, removal of infected material, secretion of antimicrobial compounds, and substrate rejection (Goes *et al.*, 2020). In *Sericomyrmex mayri*, waste management is modulated by temperature, humidity, and distance from dumpsites (Bitar *et al.*, 2020). Queens in small colonies of *Trachymyrmex fuscus* and *A. sexdens* have been observed participating in fungus cultivation and foraging (Araujo *et al.*, 2016; Macedo *et al.*, 2021).

Other behaviors include nest defense and maintenance. *Camponotus leydigi* guards nest entrances through phragmosis (Soares & Oliveira, 2020), and *D. lucida* engages in entrance cleaning after rainfall (Zocca *et al.*, 2021).

**From Ecology and Behavioral Ecology**

Ant behavioral ecology encompasses a spectrum of mutualistic and antagonistic relationships that shape ecological dynamics. Extrafloral nectaries (EFNs) play a key role in ant-plant mutualisms, providing nectar that attracts ants, which in turn protect plants against herbivores. *Camponotus rubritorax* and *Camponotus atriceps* show increased aggression toward herbivores when foraging on plants with nectar rich in sugars (Flores-Flores *et al.*, 2018). Moreover, ant visitation may enhance plant reproductive success, particularly when involving

aggressive species (Leal, Nogueira, & Peixoto, 2023). Plant-emitted chemical cues following herbivore damage can modulate ant behavior. For instance, in *Tachigali myrmecophila*, *P. concolor* increases patrolling on valuable plant parts in response to phytochemical signals (Pacheco Junior & Del-Claro, 2018).

Although ants often serve as plant defenders, they can also act as herbivores. Leaf-cutting ants such as *Atta cephalotes* can modify plant communities through foraging, opening the canopy, increasing light penetration, and thereby altering seedling density and species richness (Corrêa *et al.*, 2016). The impact of such herbivory varies with plant species and the targeted plant parts (Silva *et al.*, 2024).

Ants also contribute to ecosystem services like pollination and seed dispersal. For example, *Camponotus pallescens* pollinates *Ditassa hastata* at night by transporting pollen on its legs during nectar foraging (Domingos-Melo *et al.*, 2022). In seed dispersal, ants facilitate non-random spatial recruitment of seedlings, with larger ants removing diaspores more efficiently, in line with optimal foraging theory (Wilker *et al.*, 2022). Some ants modulate foraging to minimize pollination interference; *Camponotus blandus* prioritizes caterpillar--derived resources over EFNs (Alves-Silva, Bachtold, & Del-Claro, 2018), while others avoid *Passiflora* reproductive structures, preventing pollination disruption (Ferreira, Izzo & Teixido, 2021).

Ants often engage in complex interspecific interactions. In *Cecropia pachystachya*, *Azteca* ants avoid caterpillars with defensive traits, demonstrating behavioral responses to potential threats (Ramos, Freitas, & Francini, 2018). Ants also form symbioses throughout insect life cycles. For example, *Thisbe silvestre* butterflies maintain associations with ants in the Atlantic Forest, underlining their role in insect development (Kaminski, Iserhard, & Freitas, 2016). Conversely, ants may host parasites, such as phorid flies that parasitize *Atta bisphaerica*, with parasitism influenced by morphological traits of both host and parasitoid (Bragança *et al.*, 2021).

Ant ecological roles are shaped by physiological and behavioral plasticity. *Pheidole* species exhibit high locomotor performance and resilience to temperature and humidity, with no apparent trade-offs among subordinate species (Tschá & Pie, 2019). Ant communities also respond to abiotic factors such as precipitation, which influence trophic networks (Anjos *et al.*, 2019). In the Cerrado, early


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resource arrival can ensure exclusive access, highlighting the role of foraging timing (Alves-Silva, Bachtold, & Del-Claro, 2018). Some species maintain dominance even in human-modified environments. Behaviors such as activity under varying solar exposure (Silva *et al.*, 2019) underscore their adaptive capacities.

## From an Ethological Perspective

### Immediate Cause (Mechanism)

Immediate causes (or mechanisms) refer to internal and external processes that directly elicit, regulate, or modulate behavior at a given moment, such as physiological changes, internal states, and social or environmental stimuli (Izar, 2018). Within-colony interactions and communication regulate behaviors, such as rescue attempts in response to the detection of nestmates stridulations in *Odontomachus brunneus* (Junior, Silva & Antonialli-Junior, 2021), task allocation based on age in *A. sexdens* (Lacerda *et al.*, 2020) and *D. lucida* (Vieira *et al.*, 2024b), and reproductive hierarchies (Châline *et al.*, 2015), which are linked to the detection of chemical fertility cues (Yagound *et al.*, 2015).

Interspecific interactions also modulate behavior. Notable examples are social parasitism, as observed with *Acromyrmex fowleri* (Rabeling *et al.*, 2019) and *Acromyrmex ameliae* (Gandra *et al.*, 2021), and interspecific aggression, such as *A. subterraneus* (Pikart *et al.*, 2015) and *Atta* sp. (Valadares, Nascimento & Châline, 2022). Ants may also adjust responses to heterospecific chemical footprints based on species identity (Santos *et al.*, 2024). Mutualisms influence foraging and nest maintenance: leafcutter ants adapt substrate cleaning based on fungal health (Hastenreiter *et al.*, 2015; Barcoto *et al.*, 2017; Goes *et al.*, 2022; Cordeiro *et al.*, 2021), and *Megalomyrmex incisus* usurp fungal gardens from *Mycetophylax conformis* and *Mycetophylax morschi* (Cardoso *et al.*, 2016). Ant–plant mutualisms also reveal defensive responses to herbivory, which vary across plant tissues (Fagundes *et al.*, 2017; Cruz *et al.*, 2018; Pacheco Junior & Del-Claro, 2018).

Ant behavioral responses are also influenced by abiotic factors. Temperature affects recognition via antennation in *O. brunneus* (Junior *et al.*, 2022) and *Odontomachus chelifer* (Silva, Batista & Antonialli-Junior, 2024), and foraging

rates in *Pheidole oxyops* (Assis *et al.*, 2021), *D. lucida* (Curbani *et al.*, 2021) and *Acromyrmex subterraneus molestans* (Ramirez-Olier *et al.*, 2022). Activity levels can be modulated by seasonality (Medeiros *et al.*, 2016) and daily rhythms (Barbosa *et al.*, 2020; Constantino, Valentinuzzi & Helene, 2021; Rodrigues *et al.*, 2023). Other abiotic factors have also been shown to modulate behaviors, such as barometric pressure affecting recruitment and foraging rate in *A. sexdens* (Sujimoto, 2020) and magnetic fields affecting foraging and conspecific interactions (Pereira *et al.*, 2019a, 2021).

Foraging is among the most extensively studied behaviors, but its mechanisms are often overlooked by studies focused on evolutionary questions and processes (Vieira, Chameron & Châline, 2024). Different strategies modulate foraging behavior, ranging from solitary to cooperative, including liquid foraging and hitchhiking (Nickele, Filho & Pie, 2015; Travaglini, Forti & Camargo, 2015; Gomes *et al.*, 2019; Catalani *et al.*, 2022; Hastenreiter *et al.*, 2016, 2018; Caldato *et al.*, 2020). Communication plays a key role in collective foraging, as for example *A. sexdens* uses complex signaling systems via pheromones and antennation (Brugger *et al.*, 2018). Research on decision-making in *A. subterraneus* emphasizes both self-organized and individually driven processes (Almeida *et al.*, 2018).

Nest-building behavior is crucial to colony success. Beetles can facilitate *C. pusillus* nesting (Del-Claro, Anjos & Torezan-Silingardi, 2022), while *A. subterraneus* queens actively forage during colony founding to cultivate fungal gardens (Sales *et al.*, 2021). Studies with *A. subterraneus* have explored the stimuli that trigger nest excavation (Santos *et al.*, 2017) and worker specialization in digging tasks (Santos *et al.*, 2018), highlighting the complexity of division of labor.

**Development (Ontogeny)**

Studies on development of behavior are crucial for understanding how behavior patterns emerge and change over time. In ants, ontogeny influences, for example, division of labor, social recognition and aggressiveness. In *A. sexdens*, age-related polyethism regulates task transitions throughout life (Lacerda *et al.*, 2020), and in *A. crassispinus*, allogrooming performed by specific age groups helps regulate social interactions and reduce disease transmission (Lopes *et al.*, 2017).

Recognition and aggressiveness can be modulated by repeated intraspecific interactions, with reduced aggression linked to learned chemical cues and individual familiarity, as in the "dear enemy" effect (Valadares *et al.*, 2015; Yagound *et al.*, 2017; Pereira *et al.*, 2019b; Zorzal *et al.*, 2021; Lima *et al.*, 2024). Cuticular hydrocarbon profiles can differ between distant colonies in *E. brunneum*, and the learning of these odors can modulate intraspecific aggressive interactions (Pereira *et al.*, 2019b). In *O. bauri,* differences in diet items influences cuticular hydrocarbon profiles, modulating nestmate behavior and antennation time (Santos Junior *et al.*, 2024).

Solitary foragers in *D. quadriceps* avoid conspecific confrontation through ritualized behaviors and odor marking, potentially influenced by prior interaction history and experience (Vieira *et al.*, 2024a). In this species, foraging behavior is also adjusted based on previous successful experiences, leading ants to return to those locations, and they exhibit a learning process for exploration routes when prey capture is unsuccessful (Eloi *et al.*, 2024).

Foraging decision-making is also complex in *P. striata*, during tandem runs, leader–follower communication appears to be influenced by internal, external, and social factors, along with immediate and prior experience (Silva *et al.*, 2021). Spatiotemporal variation among workers of *P. concolor* influences division of labor, demonstrating site fidelity over time, different responses to the same behavioral stimulus and possibly age polyethism (Pacheco Junior & Del-Claro, 2021).

In *A. sexdens* foragers, food resource selection can be influenced by innate or acquired preferences, and the recognition of harmful plant odors is associated with rejection behavior through associative learning (Arêdes *et al.*, 2022). In workers of *A. subterraneus molestans* and *A. subterraneus brunneus*, social chemical cues can be acquired and learned, and workers exhibit preferential brood care towards conspecific larvae (Lopes, Camargo & Forti, 2017).

**Function (Adaptive value)**

Behavioral research on ants in Brazil has improved the understanding of the adaptive value of diverse behaviors among species, particularly how these behaviors contribute to colony survival and reproductive success. Foraging

remains a central theme in Brazilian literature regarding the adaptive value of behavior. Across multiple taxa, behavioral flexibility in food acquisition stands out as a crucial strategy for adapting to environmental variation. For example, *D. quadriceps* exhibits non-aggressive foraging under unstable conditions, indicating context-dependent decision-making avoiding potential injury or death (Azevedo, Medeiros & Araújo, 2021). Strategies include solitary hunting (Azevedo, Medeiros & Araújo, 2021) and cooperative recruitment, such as tandem running in *Pachycondyla harpax* (Glaser *et al.*, 2021), with responses shaped by resource availability, seasonality as observed in leaf-cutting ants (Gandra *et al.*, 2024; Sujimoto *et al.*, 2020), ultimately promoting colony productivity.

Fungus-growing genera like *Atta* and *Acromyrmex* (Myrmicinae) have been extensively studied, especially regarding their symbiotic fungal gardens. Behaviors like leaf processing, grooming, and substrate removal are regulated by caste-specific division of labor and associative learning, helping to prevent contamination by removing potential pathogen sources, reducing microbial loads, and limiting pathogen spread within the nest (Arêdes *et al.*, 2022; Gandra *et al.*, 2016). These behaviors ensure colony sustainability and reflect behavioral plasticity in response to pathogens.

Beyond its hygiene maintenance aspect, social communication and collective coordination, such as tactile contact and chemical signaling, can facilitate task allocation and traffic regulation (Nickele, Pie & Moura, 2018). In *Acromyrmex crassispinus*, workers adjust their use of trail space according to traffic density, reducing navigation errors at bifurcations and enhancing foraging efficiency (Nickele, Pie & Moura, 2018) highlighting their sensitivity to ecological and social cues.

Grooming behaviors are central to social immunity and can hinder chemical control, since workers of leaf-cutting ants distribute antimicrobial agents or contaminants among nestmates, thus affecting the efficacy of insecticides (Mota Filho *et al.*, 2022; Travaglini *et al.*, 2017). The maintenance of fungal gardens by *Acromyrmex molestans* and *A. subterraneus* also exemplifies collective behavior that supports ecological stability (Gandra *et al.*, 2024).

Behavioral differentiation linked to division of labor also extends to defense tasks. Smaller *Atta* workers display more persistent aggression than majors, influencing access to resources and shaping interspecific competition (Valadares, Nascimento & Châline, 2022; Flores-Flores *et al.*, 2018; Glaser *et al.*,


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2021). In addition, diet quality further affects behavioral responses. Studies show that sugar content in food sources stimulates the intensity of defensive responses in *Camponotus atriceps* toward host plants in ant-plant mutualisms (Flores-Flores *et al.*, 2018). Environmental variables also shape food ingestion and trophallaxis, influencing worker survival and colony performance (Moreira *et al.*, 2015).

Lastly, behavioral variation at both individual and colony levels has received increasing attention. In leaf-cutting ants, personality traits can influence collective outcomes, especially fungus productivity and growth rates (Gandra *et al.*, 2024), emphasizing the adaptive significance of behavioral diversity within species.

**Evolutionary History (Phylogeny)**

To our knowledge, no studies published in the last decade have systematically addressed the evolutionary history of specific ant behaviors through a comparative, phylogenetic approach in Brazil. While the field of ant behavioral research has advanced considerably in Brazil, phylogenetic analyses of behavior remain notably limited. Incorporating evolutionary perspectives could provide critical improvements into how behavioral traits arise, persist, or shift across species.

**Behavior-Based Biological Control**

Biological control increasingly draws on behavioral traits, particularly those involved in contaminant spread during foraging *A. sexdens* (Camargo, Forti & Matos, 2017; Travaglini *et al.*, 2017) or through nestmate interactions in both *A. sexdens* and *Acromyrmex* sp. (Camargo *et al.*, 2017; Lopes *et al.*, 2017; Mota Filho *et al.*, 2021, 2022; Catalani *et al.*, 2022; Scudillio *et al.*, 2023). To maximize efficacy, toxic agents must be lethal yet allow horizontal transfer within the colony, thereby preventing mortality from being confined to foragers (Gomes *et al.*, 2016).

Initial studies often begin with behavioral and faunal surveys to guide control efforts, providing critical data on species identity, nesting sites, and foraging strategies (Travaglini, Forti & Camargo, 2015; Lopes *et al.*, 2016, 2017; Brugger *et al.*, 2018; Bouchebti *et al.*, 2019; De Souza Tavares, Delabie & Zanúncio, 2022). In rare instances, formicidal agents are applied via topical exposure

(Stefanell *et al.*, 2020), though more sustainable methods emphasize physical removal or colony relocation.

Most studies aim to eliminate foragers and other colony members (Gomes *et al.*, 2016; Camargo, Forti & Matos, 2017; Catalani *et al.*, 2019; Graebin *et al.*, 2024). Another strategy targets the fungus cultivated by leaf-cutting ants such as *A. sexdens* and *A. subterraneus*, thereby disrupting their primary food source (Sousa, Camargo & Forti, 2017; Forti *et al.*, 2019).

Non-lethal behavioral manipulation also presents a promising strategy. Altering environmental cues or resource distribution can shift or interrupt foraging routes, while some agents act as repellents, redirecting foraging activity or deterring ants from exploiting a treated resource or territory. This approach has demonstrated some success in the control of *Acromyrmex laticeps, Acromyrmex heyeri* and *A. sexdens* (Boff, Giesel & Boff, 2016; Giesel, Boff & Boff, 2016, 2017; Giesel, 2020).

Understanding foraging dynamics is key to behavior-based control. Knowledge of how ants assess food, establish trails, and respond to spatial shifts informs bait deployment in several *Atta* species (Lopes *et al.*, 2016; Bouchebti *et al.*, 2019; Caldato *et al.*, 2020; Travaglini, Stefanelli & Edringrer, 2023). Internal distribution patterns also affect how toxicants circulate across leaf-cutting ant species (Silva *et al.*, 2015; Forti, Andrade & Camargo, 2020; Forti *et al.*, 2019).

Finally, manipulating environmental variables allows for testing behavioral thresholds and colony resilience. Factors like humidity, temperature, or barriers can reveal colony limits and help optimize timing and techniques (Ramirez-Olier *et al.*, 2022; Sousa *et al.*, 2022), offering species-specific, ecologically sound pest control alternatives.

## FINAL CONSIDERATIONS

This chapter outlines the state of the art in ant behavior research in Brazil, marked by a rich diversity of themes, such as foraging, division of labor, regulation of social dynamics, communication, intra- and interspecific interactions, thus highlighting the ecological and social complexity of these eusocial insects. Emerging topics such as behavioral plasticity, personality traits, and collective decision-making reflect growing interest in ants as dynamic, adaptive, social system.


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Studies span ecological, ethological and applied approaches, addressing both proximate mechanisms and adaptive functions. However, phylogenetic studies on the evolution of behavior remain underdeveloped. Moreover, investigations often concentrate on a narrow group of species, notably from the subfamily Myrmicinae and some Ponerinae species. There is a clear need for expanding this scope to other taxa and to behavioral topics still scarcely explored.

The socio-academic analysis provided in the supplementary material (https://doi.org/10.5281/zenodo.16815510) also reveals a great gender imbalance and regional disparities, emphasizing the need for initiatives that promote equity and inclusivity. Additionally, research remains concentrated in Southeastern and Northeastern Brazil, indicating the need to support research efforts in this field across all parts of the country.

In conclusion, this chapter is not intended as an exhaustive or definitive survey. Rather, it should be seen as a starting point that aims to stimulate further interest and collaborative work among students, researchers, and professionals committed to understanding the diverse and intricate behavioral world of ants in Brazil.

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# 05

# UNVEILING THE LIVES OF ANTS: A CALL TO OBSERVE THEIR FASCINATING NATURAL WORLD

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# ABSTRACT

Natural History (NH) involves observing and describing the biological characteristics of organisms within their environments. However, despite its central role in supporting the development of modern ecology, evolutionary biology, and conservation, NH is often mistakenly regarded as unscientific. Additionally, the decline of NH in training, scientific journals, open calls, grant proposals, and textbooks is partly related to the rise of disciplines, such as molecular biology and theoretical ecology, both of which have higher acceptance rates in more impactful journals. This chapter provides an overview of the NH knowledge related to ants in Brazil. Only ~11% of the Brazilian species have published NH data. Furthermore, NH papers represent 25% of those focused on ant diversity, and ~34% of the NH papers and less than 6% of abstracts from the *Simpósio Internacional de Mirmecologia* include the term 'Natural History'. Secondly, acknowledging the undeniable importance of NH as both a starting point and an ultimate reference in any myrmecological research, we present compelling descriptive and integrative NH studies across Brazilian biomes. These approaches have value in stimulating our curiosity, inspiring new questions, addressing taxonomic problems, and advancing theory. We conclude with recommendations for both established and early-career scientists in myrmecology to support and integrate NH into their projects, emphasizing the long-term value of NH data for scientific progress.

**Keywords:** Natural history; biology; species; formicidae; descriptive data.

## INTRODUCTION

There is no single, widely accepted definition of Natural History (NH), which was once a synonym to all natural sciences (TEWKSBURY *et al.*, 2014). Those days are long past, though, and how "healthy" NH is today depends entirely on the definition chosen, ranging from being basically dead to living happily and well as a part of modern ecology. Regardless of the exact formulation, many definitions agree that one central focus of NH is the *observation and description of biological aspects of organisms in their environments* (TEWKSBURY *et al.*, 2014; BARROWS *et al.*, 2016). This does not mean that NH cannot be systematic, include hypothesis-testing or take advantage of modern techniques (TOSA *et al.*, 2021), but that gathering basic observational data is still a legitimate scientific goal, since we are in dire need of it for most organisms.

Unfortunately, NH has experienced a steady decline over the last decades (TEWKSBURY *et al.*, 2014). This includes less representativeness in training (*i.e.*, taxon-specific biology and field courses), scientific journals, grant proposals, and textbooks (TOSA *et al.*, 2021). Part of this phenomenon has been attributed to the rise of other prominent areas, such as molecular biology and theoretical ecology, leading to less focus on observing organisms in their habitats (WILLSON; ARMESTO, 2006). Those newer areas are boosted by higher acceptance rates in more impactful journals and increased funding. Consequently, more and more students and early-career researchers are shifting away from investigating and teaching NH (TEWKSBURY *et al.*, 2014).

In myrmecology, the scenario is not different. Approximately 1,600 ant species/subspecies occur in Brazil, representing about 10% of the global diversity (ANTWEB, 2025). Nevertheless, the biology of the majority of species, locally and globally, remains largely unexplored, due to four main reasons highlighted by Rosumek (2017): taxonomic uncertainty, high species richness, lack of descriptive or observational studies, and prevalent use of morphospecies. Furthermore, the common misconception among many scientists that the NH approach is unscientific worsens this scenario (TOSA *et al.*, 2021).

An exploratory search into databases (Google Scholar, SciELO, Scopus, Web of Science) using the four possible combinations for the keywords 'Formicidae or Ant + Natural History or Biology + Brazil', in both English and

Portuguese, resulted in 82 documents[1]. Additional active search into the Brazilian researchers resume database (Curriculum Lattes) of 20 well-known researchers[2] for their studies on ants in Brazil resulted in 109 new documents. The total dataset included 190 documents, but seven were excluded from the final database (Supplemental Table S1), which encompasses 183 documents and a time range from 1949 to 2024 (Supplemental Table S2). Comparatively, an overview of the Brazilian ant diversity studies between 1970 and 2021 compiled 491 papers (FEITOSA *et al.*, 2022).

A similar approach was used to analyze works on ants' NH presented in one of the most important scientific meetings in myrmecology: the *Simpósio Internacional de Mirmecologia* - an International Ant Meeting, an event always held in Brazil. When looking into the abstracts of the last four events, works related to distinct aspects of ant NH represented from ~40% (in 2015, 2017, and 2019) to ~60% (2023) of all studies (Supplemental Figure S1) - although abstracts that explicitly used the term 'natural history' summed less than 6% in all years. This suggests that the amount of work on ant NH presented at the conference is not necessarily being translated into publications. For example, the amount of published NH studies is 25% of the number of papers on ant diversity, which may reflect a lower rate of journal acceptance of NH studies (TEWKSBURY *et al.*, 2014).

Despite this trend, and in a seemingly contradictory way, the importance of NH among life scientists remains unquestioned (BARROWS *et al.*, 2016). The observation of nature and NH have long been the foundation of major advances in ecology, evolution, and conservation (TRAVIS, 2020). They continue to provide fundamental knowledge of natural systems necessary to set up more comprehensive theories and to validate modeling hypotheses and laboratory experiments (NANGLU *et al.*, 2023).

[1] Including manuscripts (article, short or scientific note/communication), book chapters, honor thesis, master dissertation, doctoral thesis, and talks and abstracts published from scientific meetings.

[2] A. Harada, MPEG; A. J. Mayhé-Nunes, UFRRJ; B. Jahyny, UNIVASF; C. R. F. Brandão, MZ-USP; C. Mariano, UESC; †E. M. de O. Diehl, UNISINOS; †H. G. Fowler, UNESP Rio Claro; H. L. Vasconcelos, UFU; I. Leal, UFPE; J. H. C. Delabie, CEPLAC/UESC; J. Lattke, UFPR; K. Del-Claro, UFU; L. C. Forti, UNESP Botucatu; M. S. C. Morini, UMC; N. G. Châline, IP-USP; O. Bueno, UNESP Rio Claro; P. S. Oliveira, UNICAMP; R. M. Feitosa, UFPR; R. R. da Silva, MPEG; and Y. Quinet, UECE.


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Regardless of the debate surrounding the definition of NH, our exploratory literature survey is composed by studies on: nesting place, behavior, and foundation; nest structure/architecture (internal, external); colony size/demography/composition/densities, distribution, and associated fauna; colony or foraging activity/schedule/behavior; diet; and details of the reproductive caste (mating period, reproductive strategy). Out of the 183 documents, only 61 contain the term NH in at least one section of the document[3], and among the documents that do not contain the term NH (122), the terms 'Biology', 'Biological', or 'Life Cycle' appear mainly in the title of 39 of them (Supplemental Table S3). The majority of the documents describe one or more aspects of NH for a single species (FORTI *et al.*, 2017; PACHECO; ANJOS; DEL-CLARO, 2022; PRADO *et al.*, 2022) or a few species within the same genus (BRANDÃO; SILVA; DINIZ, 2015; JEŠOVNIK, 2017). Conversely, few studies review one or two aspects of the NH for several species, such as mating flight (NASCIMENTO; DELABIE; DELLA-LUCIA, 2011), or trophic resources and period of activity (ROSUMEK, 2017). Furthermore, the dataset gathers NH data on 190 species belonging to 59 genera (Supplemental Table S4). Clearly, many species must be better studied to deepen and broaden understanding of nature and its biological and ecological processes, which indeed warrants enthusiastic encouragement from scientists.

Recently, Tosa *et al.* (2021) proposed that we have entered into the "Next-Generation Natural History". This phase is characterized by technological advances (*i.e.*, UCEs, eDNA, Autonomous Recording Units), open-access data (*i.e.*, GBIF), and community science (*i.e.*, iNaturalist), along with direct observations of the species in their natural environment. Such a renaissance can already be seen in myrmecology, as new ant databases have emerged, including AntCat, AntWeb, and AntWiki (for species cataloging, specimen records, and general information), AntMaps, GABI, and GABI-I (for biogeography and species distribution), GLAD (for functional traits), FORMIS (for ant literature), and the HGD (for Hymenoptera genomic data). Importantly, these databases remain dependent on NH observations, which are endless given that we live in a world

[3] Title, Keywords, Abstract, Introduction, Objective(s), Material & Methods, Results, Discussion, Conclusion.

where most living organisms are still unknown, many are poorly studied, and only a few—such as the leafcutter ants *Atta*[4]—are well documented (WILSON, 2017; POWERS, 2025). In this chapter, we present exciting NH studies of not so well-documented ant species from two different perspectives. First, from a descriptive approach, we highlight how detailed and opportunistic observations can spark curiosity and guide new research questions—here illustrated by *Dinoponera*, *Strumigenys*, and army ants. Secondly, through an integrative approach, we show how NH can both benefit and contribute to molecular, morphological, and ecological data. This is evident in resolving taxonomic problems in *Camponotus* and *Wasmannia*, and in identifying promising models—such as *Hylomyrma*—for testing theories of caste development.

## MOTHER MARY'S PUPPIES: LIFE AND BEHAVIOR OF *DINOPONERA GIGANTEA* — R. L. C. DE LIMA

*Dinoponera gigantea*, found in the tropical forests of Peru and northern Brazil, is an impressive ant species with the largest workers in the world (3–4 cm) (DIAS; LATTKE, 2021). Its nests are built at the bases of trees or on thick lianas, and workers forage individually for fruits, seeds, small live prey, and dead animals (FOURCASSIÉ; OLIVEIRA, 2002). This queenless species relies on a reproductive worker (gamergate), whose status is established through hierarchies formed by agonistic interactions (MONNIN; RATNIEKS; BRANDÃO, 2003). Grooming behavior is also linked to these hierarchies and can help identify the gamergate (LIMA, 2023).

Despite its remarkable traits, *D. gigantea* remains poorly studied in the field, like most ant species. Polydomy was proposed for this species by Fourcassié and Oliveira (2002), but its occurrence is still uncertain. This prompted us to observe *D. gigantea* in its natural habitat, in Bragança, Pará, Brazil, during 2019 and 2020 (LIMA, 2023). Locally, *D. gigantea* is known as *Cachorrinhos-de-Nossa-Senhora* (Mother Mary's Puppies) or *Formigão Preto* (Big Black Ant),

[4] The taxonomic references (author and year) for all genera and species mentioned in the chapter are listed in the supplemental table S5.


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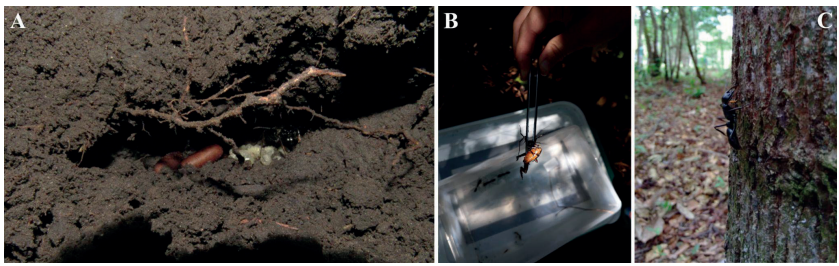
and is often mistaken for *Paraponera clavata*, the bullet ant. Residents report that *D. gigantea* has a painful sting and is commonly found in cassava crops.

Regardless of its large size, their nests are inconspicuous. To find them, we offered apples with honey or sardines in front of foragers or directly into their jaws, then followed them to their nests. To date, 33 nests were found along secondary forest edges and one in primary forest. Most were located at the base of the palm tree *Tucunzeiro* (*Astrocaryum aculeatum* G. Mey.), and had 1 to 4 entrances (1.8–3.8 cm in diameter). Occasionally, independent chambers were found about 1 m from the main nest structure. Nests were typically less than 5 m apart, suggesting overlapping foraging areas.

Foraging typically occurred during milder temperatures—at dawn and late afternoon. Foragers primarily carried seeds and fruit, though we also observed them carrying a live bee and a small frog (Figure 1B). Individual variations in foraging were evident: some workers, possibly more experienced, returned quickly to the nest, while others were more "hesitant", often taking much longer and hiding under, often hiding under dry leaves for extended periods. The ants were docile and did not react aggressively when carefully handled. The workers frequently climbed trees, for unclear reasons (Figure 1C). Dead workers were commonly found along trails, and foragers were observed carrying them away from the nest. *Dinoponera gigantea* was never observed foraging in the rain. Pitfall traps captured 22 workers during the dry season (June–November) and two during the rainy season (December–May), indicating reduced activity; however, no significant differences were found in the numbers of workers, pupae, larvae, or males between the two periods.

**Figure 1 -** *Dinoponera gigantea* brood chamber (**A**), carrying a frog (**B**), and climbing tree (**C**).




**Source:** (A-B) Hilário Póvoas de Lima (2019) and (C) Alexandre Nunes (2020).

Colonies had an average of 50.40 workers (SD = 17.79). Larvae, pupae, eggs, and males were found in deeper chambers (Figure 1A). A probe camera revealed likely *Pheidole* spp. and beetle larvae cohabiting peacefully inside the nests. No agonistic interactions or interspecific competition were observed during fieldwork. Many nests were near those of *P. clavata* nests, and on one occasion, a *D. gigantea* worker entered a bullet ant nest, though it was not seen exiting. *Dinoponera gigantea* also foraged near *Eciton hamatum,* and even when placed on the *Eciton* trail by us, neither species showed aggression.

Our data reveal new aspects of *D. gigantea*'s natural history in an area with no prior records of occurrence. We found limited evidence—relatively high nest density, presence of independent nest chambers, and absence of agonistic interactions—suggesting that *D. gigantea* may form polydomous colonies. However, we did not identify nests sharing resources or examine population genetics. Nonetheless, *D. gigantea* provides a useful model to investigate how dominance hierarchies are established in more complex systems.

## WHAT DO WE KNOW ABOUT BRAZILIAN *STRUMIGENYS*? — G. F. JACINTHO & E. A. DOS SANTOS-NETO

*Strumigenys* is a remarkable group of ants known for its incredible diversity, ranking as the third most speciose ant genus, with over 880 extant species globally distributed (BOLTON, 2025). Of these, 214 species, categorized into 43 groups, inhabit the Neotropics (CHAUL; JACINTHO; SANTOS-NETO, unpublished). Brazil alone includes 106 species in 30 groups, a number that interestingly mirrors the country's area within the Neotropical realm.

In recent decades, the widespread use of Winkler extractors has coincided with a significant rise in the number of *Strumigenys* species recorded in Brazil—from 80 to 106 species since Bolton's global revision in 2000 (SILVA; CHAUL; FEITOSA, 2022). This increase suggests that most *Strumigenys* species inhabit or forage within the leaf litter or upper soil layers. However, is this the complete picture?

To dig this deeper, we conducted a bibliographic survey on the NH of Brazilian *Strumigenys* species. We reviewed original species descriptions, Bolton's global revision (2000), and data from AntWiki, AntWeb, and Google Scholar.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Unsurprisingly, detailed NH information remains scarce. Of the 106 Brazilian species, 85 include data on sampling methods in their descriptions, most of which involve collecting from leaf litter or soil—suggesting that these species likely inhabit or forage in these microhabitats. However, only 37 species have data that go beyond the sampling method. This lack of detailed NH information may lead to an overly narrow understanding of *Strumigenys* species, reinforcing the assumption that most species are restricted to the leaf litter, despite known exceptions.

Recent fieldwork in southern Bahia using less-explored methods—such as the sampling of invertebrates in epiphytes and bromeliads (DAROCHA *et al.*, 2015)—yielded surprising results. Notably, it expanded the known distribution of species in the *schulzi*-group previously unrecorded in Brazil or thought to be restricted to the Amazon, including *Strumigenys castanea* and *S. orchibia* (SANTOS-NETO; CHAUL; DELABIE, 2024). It also led to the discovery of a larger undescribed species resembling the tiny giants in the *precava*- and *mandibularis*-groups, whose queens can exceed 5 mm. These findings indicate that some species prefer arboreal environments and epiphytes for nesting and foraging, while others may favor deeper soil layers (Figure 2A-C; additional images on Supplemental Figure S2). These under-sampled habitats may harbor novel and valuable facts about these tiny ants.

**Figure 2 -** Brazilian *Strumigenys*' habitats. *Strumigenys borgmeieri* nesting on bromeliad (**A**), *S. smithii* foraging on a rotten log (**B**), and *S. subedentata* nesting in the leaf litter (**C**).

**Source:** (A-C) Esperidião A. dos Santos-Neto (2023).

Beyond habitat preferences, even less is known about other aspects of the NH of Brazilian *Strumigenys*—such as predation behavior, diet, and reproduction. Our literature review found only four studies addressing these topics. Two report ergatoid queens in four species (CHAUL; SCHROEDER, 2014; SILVA;

BRANDÃO, 2014); one describes the trap-jaw mechanism in a species likely *Strumigenys rogeri*, an invasive species recently found in Brazil (GRONEMBERG, 1996; SANTOS-NETO *et al.*, 2023); and another compares morphology and behavior in the *thaxteri*-group (LATTKE; SILVA; DELSINNE, 2018).

To encourage broader sampling and stimulate further NH observation of *Strumigenys* species, we provide a database (Supplemental Table S6) that compiles published and personal data. It includes updated species distributions, potential nesting sites—from soil layers to arboreal strata and association with epiphytes—as well as foraging behavior, diet preferences, and other relevant NH data, such as the presence of ergatoid and intercaste.

## SURVIVING ARMY ANT ATTACKS — H. P. DE LIMA & I. N. DE SOUZA

An epic battle unfolds when army ants—armed with stingers and well--developed mandibles—raid other ant species. In the chaos, some prey species flee, others seal their nests, or fight to the death (LIMA, 2022). These attacks can cause devastating losses, sometimes wiping out entire colonies (POWELL; CLARK, 2004). Yet, some colonies manage to survive using little-described defensive strategies (SWARTZ, 1998). Here, we document how ants under army ant attack survived in two Brazilian biomes: Amazon and *Caatinga* (Dry Forest).

**a) Survival camps of *Dolichoderus attelaboides*:** For six days, the defense behavior of *D. attelaboides* during an *Eciton rapax* raid in northeastern Pará, Brazilian Amazon, was recorded (Figure 3A). The *D. attelaboides* nest was located inside the trunk of a small tree. At 7 am, the *E. rapax* approach triggered a rapid evacuation. Some workers fled with immatures toward the canopy (Supplemental Video S1), while others jumped to the ground, occasionally dropping immatures. These were either captured by *E. rapax* or retrieved by nestmates and carried to safety. Escapees formed small groups of four or five, often sheltering together or climbing low bushes. Five minutes later, a new target—a *Camponotus* sp. colony—was attacked by the army ants (Supplemental Video S2). Minutes after the first attack, *E. rapax* climbed vines and branches to


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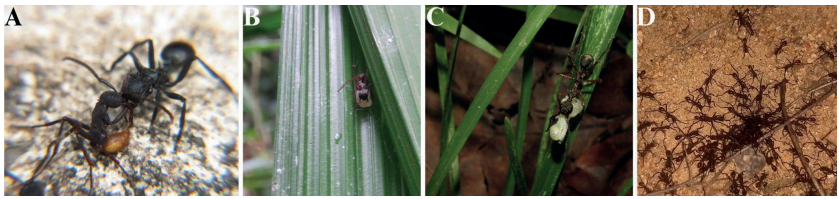
capture *D. attelaboides* immatures placed in the canopy for safety. This second attack was brief; no predator or prey were observed near the nest afterward afterward. By the end of the day, the nest showed no signs of activity. A search of the area revealed several small *D. attelaboides* "survival camps" in small cavities or spaces between leaves, each with stationary workers and at least one visible worker (Figure 3B). Over five days, workers were seen returning to the nest, sometimes carrying immatures (Figure 3C). By the sixth day, the camps were gone, suggesting the colony had reestablished. These camps likely reduced *E. rapax*'s ability to track *D. attelaboides,* aiding escape and nest recovery.

**Figure 3 -** *Eciton rapax* immobilizing *Cephalotes atratus* (**A**); *Dolichoderus attelaboides* carrying immature sheltering behind a leaf (**B**) and returning to its nest (**C**); and *Eciton vagans* invasion into an *Ectatomma edentatum* colony (**D**).




**Source:** (A-C) Hilário Póvoas de Lima (2019), and (D) Igor N. de Souza (2022).

**b) Colony defenses against army ant predation: strategy or panic?**

Two cases of army ant predation and prey defense were observed in Paraíba state, northeastern Brazil, in the *Caatinga*: *Eciton vagans* vs. *Ectatomma edentatum*, and *Neivamyrmex goeldii* vs. *Solenopsis geminata*. In interactions between *E. vagans* and *E. edentatum*, 16 attacks on *Ectatomma* nests were observed, with workers as the main targets. During invasions, *E. vagans* engaged in a "tug of war" as they entered the *Ectatomma* nests (Figure 3D). The narrow nest entrance hindered predator access to brood chambers, while *Ectatomma* workers formed an efficient defensive blockade. Unable to reach the brood, *E. vagans* preyed on the defending workers. Each attack lasted about two hours, killing many *Ectatomma* workers but leaving the brood unharmed, allowing colony survival. The fire ant *S. geminata* responds to army ant raids by effectively "running for the hills". Upon detecting *N. goeldii* foraging near the nest, *Solenopsis* quickly emitted alarm signals that triggered a nest

evacuation: workers and alates climbed nearby plants, carrying eggs, larvae, and pupae, which they stored on leaves—similar to *Dolichoderus* survival camps. The fire ants remained in this refuge for about two hours, returning to the nest with the brood after *N. goeldii* left.

Across biomes, the pressure to survive army ant attacks has shaped diverse anti-predator strategies, best understood through the social-level costs of predation. Survival often depends on preserving key colony members—especially the queen and enough workers to rebuild. Yet, prey success hinders predator success, driving predators to become more efficient. This creates an evolutionary arms race with no clear winners, ultimately balancing both populations in these dynamic predator-prey interactions.

## *WASMANNIA*: A SONG OF NICE ANT FIRES — F. B. ROSUMEK

We often draw attention to how difficult it is to investigate certain cryptic species in the field, or shudder at the daunting task of studying a hundred-or thousand-species rich genus. Not surprisingly, many of the largest, commonest and most widespread ant genera do not even have their taxonomy consolidated, much less other aspects of their biology. However, sometimes a species does not need to be extremely hard to observe or be part of a huge group to be unknown. All it takes is to have an outstandingly famous cousin and live in their shadow for a long time. This is the case of the little fire ants.

*Wasmannia auropunctata* has an extensive research history, not only because of its importance as a highly aggressive invasive species, but also due to its unique reproductive biology (MONTGOMERY *et al.*, 2022). Comparatively, little to nothing is known about the other ten species. As an additional problem, before Longino and Fernández (2007) taxonomic review, there were not proper identification sources in the literature, so in many cases other species were misidentified as *W. auropunctata*.

That was the case in the Atlantic Forest of southern Brazil, where previously *W. auropunctata* was thought to be common in terrestrial bromeliads, which are usually found in clusters on soil or rocks in that area (ROSUMEK *et al.*, 2008). Years later, in 2017, we looked again at those bromeliads and noticed that, while *W. auropunctata* occurs at the site, the one in the plants was *Wasmannia*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*affinis* instead, a species endemic to the Atlantic Forest and—not surprisingly—virtually unknown (ROSUMEK, 2017). This prompted us to look more closely at this curious interaction, and we performed more observations in 2023.

*Wasmannia affinis* was found on 64% of the 50 bromeliad clusters observed, a frequency higher than in previous samples on the ground. The nests were almost always located in the inner basal part of the outer leaves (dead or alive), which accumulate more soil and less water (Figure 4A-C). Although other ant nests were found during the work, *W. affinis* was by far the most common inhabitant. We found from one to five nests per cluster, and the number of nests was higher in larger clusters (Spearman, $rs = 0.5$, $p < 0.01$).

**Figure 4 -** Nests of *Wasmannia affinis* inside the bromeliad *Nidularium inocentii*. White arrows indicate clusters of light brown *Wasmannia* ants.

**Source:** (A-C) Felix B. Rosumek (2023).

Also interesting was the apparent preference for a specific bromeliad, *Nidularium inocentii*, again an endemic species to the Atlantic Forest. Nests were found almost twice as often in clusters of this species than of other bromeliads ($f = 0.70$ vs $f = 0.38$, Chi-square, $p < 0.05$). In 2017 (spring) we observed eggs and larvae, but in 2023 there was not brood during autumn, and we found eggs just in a single nest on the first days of July (winter). Thus, reproduction is seasonal, but the ants nest in the bromeliads all year round. Finally, the colonies could be polygynous, with up to three dealate queens observed in nests.

A fascinating thing about NH—and perhaps one of the reasons why we will never investigate *everything*—is how a few qualitative observations may raise intriguing questions, leading us to more systematic observations, and then to even more questions. Are bromeliads the main nesting site for *W. affinis*? They are often found in litter samples, baits, and pitfalls, thus some ground nesting would also be expected. Curiously, however, a study focused on twig nests—a common nesting resource loved by ants—found no *W. affinis* inside

them (FERNANDES *et al.*, 2020). In any case, does *W. affinis* have a preferential association with *N. inocentii*? Is it contextual or consistent across their overlapping distributional range? These questions may one day be answered, as long as curious researchers keep sitting on the forest floor, looking at little ants doing their business.

## THE EXTRAORDINARY FEMALE PHENOTYPES WITHIN *HYLOMYRMA* — M. A. ULYSSÉA

In the first taxonomic revision of the ant genus *Hylomyrma*, Kempf (1973) described a variation of *Hylomyrma reitteri* from a single specimen collected in Agudos, São Paulo, Brazil. Now recognized as *H. lopesi*, the specimen exhibits a worker-like morphology with a central ocellus and was referred to as "intercaste, pseudogyne or gynergate". Unaware at the time, Kempf's note marked the beginning of our understanding of the genus' remarkable adult female morphological diversity.

After a 48-year gap, the second revision of *Hylomyrma* nearly doubled the genus size, describing 14 new species (ULYSSÉA; BRANDÃO, 2021). This study, based entirely on museum specimens, found that 11 of the 30 recognized species present intercastes (**I**)—specimens that combine worker- and queen--like traits within a system where winged queens (**WQ**, reproductive caste) and workers (**W**, non-reproductive caste, flightless) are the extreme outcomes of a developmental pathway. Unlike most ants, where **I** are rare (MOLET; WHEELER; PEETERS, 2012), *Hylomyrma* shows a surprising frequency of such forms. Even more fascinating, three closely related species—*H. balzani*, *H. lopesi*, and *H. reitteri*—display the widest-documented range of female phenotypes (**W**, **WQ**, and four **I** phenotypes). In *H. primavesi* and *H. reitteri*, **I** outnumber **W** in collections (~78%). *Hylomyrma primavesi* is especially unique, with only ergatoid queen reported to date (**EQ**) (ULYSSÉA; FARDER-GOMES; PRADO, 2024).

Until recently, *Hylomyrma* biology was virtually unknown, limited to brief notes on *H. versuta* kept in the lab by Wilson (WHEELER; WHEELER, 1960), and scattered mentions in taxonomic revisions. In 2024, the first systematized species-level NH account was published for *H. primavesi*, an endemic species from rupestrian grassland in Santana do Riacho, Minas Gerais, Brazil (ULYSSÉA;


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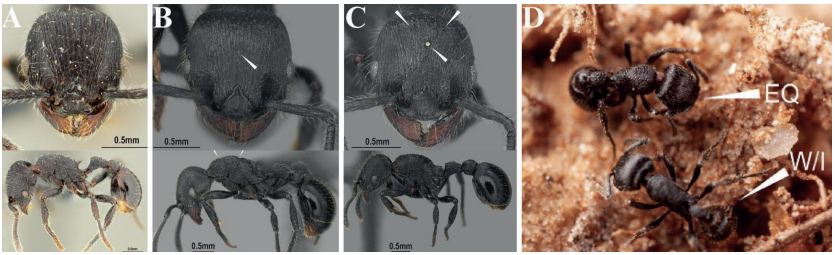
FARDER-GOMES; PRADO, 2024). Its nests, built in sandy soil, are shallow and simple, consisting of a single tunnel linking a curved nest entrance to the final chamber. Colonies are small (~7-65**W**/**I**) and have one ergatoid queen. Foraging is solitary, and prey consists of very tiny insects.

Female phenotypes in *H. primavesi* are nearly the same size (Figure 5). **EQ**s are easily distinguished under a stereoscope by their more segmented mesosoma. However, distinguishing **W** from **I** is often difficult due to the continuous morphological variation in traits like ocelli number, mesosoma segmentation, gaster size, and reproductive tract development. As such, *H. primavesi* is a rare myrmicine species with minimal differentiation between reproductive and non-reproductive castes.

**Figure 5 -** *Hylomyrma primavesi* female phenotypes. Worker (**A**), intercaste (**B**), and ergatoid queen **(C)**, external morpholo**g**y; and females inside the nest (**D**). White arrows indicate ocellus, promesonotal junction and metanotal groove in **B**, and ocelli in **C**.




**Source:** (A-C) Mônica A. Ulysséa (2017, 2021), and (D) Fabiano F. Albertoni (2024).

These data from *H. primavesi* colonies, along with morphological data from *H. balzani*, *H. lopesi* and *H. reitteri*, place *Hylomyrma* as a promising model for understanding caste evolution. It may represent a useful system for testing models of ant caste development: the standard model (WHEELER, 1986) and the hourglass model (TRIBLE; KRONAUER, 2021).

Interestingly, the seed-harvester genus *Pogonomyrmex*—sister group to *Hylomyrma*—exhibits an even broader range of female phenotypes, paralleling the diversity seen across all ants (PEETERS; KELLER; JOHSON, 2012). In *Pogonomyrmex*, the non-reproductive caste includes minor and major workers, while the reproductive caste may consist of **WQ**, **EQ**, or both. It is worth mentioning that the **EQ** is flightless and may lack wings entirely, have abnormally reduced wings, or only wing buds. Given their close evolutionary relatedness, and the fact

that species are continuously evolving, it is plausible that *Hylomyrma* species with dimorphic queens—or even minor and major workers—may eventually be found. But such discoveries will depend on continued fieldwork centered on nest collection and NH observations of these shy and inconspicuous species.

## NATURAL HISTORY BEYOND THE FIELD: INSIGHTS FROM *CAMPONOTUS* SPECIES — M. AZEVEDO-SILVA

Although NH traditionally relies on field observations, some questions are difficult to answer through direct observation alone. For instance, how can we determine a queen's mating frequency without witnessing copulation, especially since males die soon after? How do we measure polygyny and reproductive partitioning among coexistent queens without invasive approaches? And how can we study reproductive behavior and describe the following dispersal of alates if virgin queens and males commonly fly away from the paternal nest to mate? Such questions require more than field data. In these cases, NH studies may benefit greatly from molecular tools—as demonstrated in studies of two *Camponotus* species abundant in the *Cerrado* (Brazilian Savanna): *Camponotus renggeri* and *C. rufipes.*

Both species are common in *Cerrado*, feeding on extrafloral nectaries and trophobiont insects, and are considered important plant defensive mutualists (RONQUE; FOURCASSIÉ; OLIVEIRA, 2018). Their morphological similarity led to historical taxonomic uncertainty. To address this, Ronque and colleagues (2016, 2018) applied an integrative taxonomic approach and confirmed their status as distinct species based in the following traits: (i) **habitat** (*C. renggeri* nests mainly in forest-like formations, while *C. rufipes* nests almost exclusively in open *Cerrado*); (ii) **nest architecture** (*C. renggeri* nests mainly in fallen dead trunks, while *C. rufipes* builds nests using dry straw); (iii) **nest persistence** (*C. renggeri* nests are less persistent over time); (iv) **nest distribution** (random for *C. renggeri* and aggregated for *C. rufipes*); and (v) **colony size** (smaller in *C. renggeri*). Molecular data further supported this distinction, revealing separate genetic clusters with no hybridization between. Together, these multiple sources of evidence confirmed *C. renggeri* and *C. rufipes* as valid, distinct species.

Azevedo-Silva and colleagues (2020) went back to the field and conducted extensive sampling of *C. renggeri* and *C. rufipes* nests. Using a non-destructive approach and worker genotypes, they reconstructed parental lineages and described the species' breeding systems. Both species present facultative polygyny (*i.e.*, multiple queens coexisting and laying eggs in the same colony). Moreover, multiple mating (polyandry) was also observed, with *C. rufipes* queens showing higher mating frequen*cies than C. renggeri* queens. Molecular data showed that in *C. renggeri* polygynous colonies, coexisting queens are unrelated, while in *C. rufipes*, queens are closely related. For both species, queens and male mates are genetically unrelated, indicating mechanisms to avoid inbreeding. In *C. rufipes*, males are responsible for introducing new alleles into colonies, contributing to gene flow. Despite differences in breeding systems, genetic diversity within colonies did not differ, suggesting that varied reproductive strategies do not lead to distinct genetic variation in ants.

Molecular data have also been used to investigate dispersal patterns of nests, queens, and males in *C. renggeri* and *C. rufipes* (AZEVEDO-SILVA *et al.*, 2023). Using a landscape genetics approach, researchers assessed how different land-use types influence dispersal. They found that landscape composition does not affect nest relocation in both *Camponotus* species. However, dispersal of reproductive castes differs: in *C. renggeri*, queen and male dispersal is primarily limited by geographic distance, while in *C. rufipes*, dispersal is highly influenced by landscape composition—queens are more likely to disperse through forest-like formations, whereas males tend to disperse through human-modified areas.

These examples highlight the power of molecular tools in NH research. Core traits—such as reproduction, colony structure, and dispersal—were revealed, all of which are crucial for understanding population viability and survival. Although molecular methods may seem high-tech, they have opened new avenues of investigation that are difficult or impossible to answer only through NH observations alone. Still, they should not replace traditional field observations, which provide the foundational knowledge—habitats, nest structure, and colony demographics—needed to frame and interpret molecular results. The case of these two *Camponotus* species illustrate how NH can be an integrative discipline, combining diverse data sources to deepen our understanding of organisms in nature.

## PERSPECTIVES

In this chapter, we have explored various aspects of ant NH across different species, biomes, and research approaches. These exciting studies underscore the undeniable importance of NH as both a foundation for new scientific questions and as a framework for interpreting molecular, ecological, and morphological data. We hope to inspire both aspiring and experienced myrmecologists to engage more deeply with ant NH—an area still rich with unanswered questions, especially within Brazil's diverse biomes and remarkable ant diversity. To conclude,, we offer the following recommendations:

1) Simple, opportunistic observations of the natural world can spark new research avenues, help answer long-standing questions, and lead to important discoveries. So, during your fieldwork, take time to simply observe what ants are doing. Be careful to not hastily label a few interesting observations as a "pattern", but also do not dismiss them as mere anecdotes.

2) If you are a NH enthusiast, make sure to publish your observations or archive your data—these records are essential for advancing scientific knowledge (SHEEHAN; MILLER, 2021). Platforms like AntWeb serve as valuable repositories. Although descriptive NH data has often been overlooked by journals favoring hypothesis-driven research, this is beginning to change. In 2020, *Ecology and Evolution* introduced a *Nature Notes* manuscript category, followed by *Biotropica*'s *Natural History Field Notes* in 2021 (POWERS, 2025). You may still face resistance from some editors/reviewers wanting to cut side observations from broader ecological papers—but sometimes, it is worth the fight.

3) Even if you are more of a "lab person" than a "field person", NH is still for you! Many open questions in ant NH require molecular, chemical, morphological, or technological approaches. It is time to recognize NH as an integrative area—one that embraces diverse methods to deepen our understanding of ants' world.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4) If you lead a research group, NH offers an excellent entry point for undergraduate students to science. You can encourage them to observe nature carefully, ask questions, and seek answers. NH projects are also flexible in location and typically low-cost, making them ideal for training the next generation of scientists.

5) When submitting a manuscript or conference abstract, consider whether your work includes elements of ant NH. If it does, explicitly include the term "natural history" in your keywords or abstract. This simple step helps other NH scientists find your work and increases NH visibility—an important contribution in today's era of "big data" science.

6) Always support fellow researchers working with ant's NH. Cite their work, foster fruitful collaborations, and discuss your findings with them. Since NH data are not always publicly available, these exchanges can offer valuable insights for all.

7) Finally, NH needs the support of students, faculties, administrators, and funding agencies. Even if NH is not the central focus of your work, include NH data and highlight its relevance in your projects, manuscripts and talks. This collective effort is crucial to countering the ongoing decline in NH research.

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# 06

# DIET AND FORAGING BEHAVIOUR IN BRAZILIAN PONERINAE ANTS: A COMPREHENSIVE SYSTEMATIC REVIEW

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# ABSTRACT

This chapter provides a systematic review of the diet, period of activity, foraging strata and foraging strategy of Brazilian ants in the subfamily Ponerinae, synthesizing over six decades of research. Ponerinae ants exhibit diverse foraging strategies, ranging from solitary foraging to mass group raids, and occupy varied ecological niches, from omnivory to highly specialist predation. Despite their biological and ecological importance, research has focused predominantly on a few genera, leaving significant knowledge gaps for smaller, cryptic, or nocturnal genera. Using the Preferred Reporting Items for Systematic Reviews and Meta-Analyses guidelines, this systematic review analyzed 110 studies covering 65 species from 13 genera. The results highlight the evolutionary and ecological adaptations of Ponerinae ants, such as their recruitment strategies and prey specialization. These findings emphasize their potential as models for studying social behaviour, phenotypic plasticity, and ecological interactions. However, most genera remain understudied, limiting comprehensive understanding. This review calls for expanded research efforts on neglected genera using modern tools and interdisciplinary collaboration. Additionally, it emphasizes the applied relevance of studying Ponerinae ants, from biological pest control to forensic science, showcasing their broader scientific and economic significance.

**Keywords:** Behavioural ecology; ethology; foraging strategies; predatory behaviour; social insects.

## INTRODUCTION

Foraging encompasses a range of behaviors that enable animals to acquire food resources, playing a critical role in survival (reviewed in LIMA VIEIRA; CHAMERON; CHÂLINE, 2024). It involves not only the consumption of food but also activities related to locating, exploiting, processing, and sometimes storing resources (TRANIELLO, 1989). In social insects, which display a social division of labor, foraging is performed by a subset of workers called foragers. Foragers are usually the older, less fertile, and more fat-depleted workers in the colony (see review in BESHERS; FEWELL, 2001).

The subfamily Ponerinae is a diverse group of ants with 17 genera and over 170 valid extant species described in the Brazilian territory (FEITOSA; DIAS, 2024). Although they are mostly solitary predators, with extensive diurnal activity in tropical forests (DELABIE *et al.*, 2015), their foraging habits and behavioral repertoires are notably vast. These ants occupy diverse ecological niches and present feeding habits that range from omnivores (consuming both animal prey and plant items) to generalist or highly specialized predators (SCHMIDT; SHATTUCK, 2014). In addition to solitary foraging, in which there is no cooperation among nestmates, remarkable phenomena can be observed in some species, such as the group raiding recruitment of thousands of workers to a termite nest (e.g., *Neoponera laevigata* species-group: HÖLLDOBLER; TRANIELLO, 1980; LEAL; OLIVEIRA, 1995).

The subfamily Ponerinae is often considered one of the most studied ant groups (DELABIE *et al.*, 2015), especially regarding their foraging habits. Therefore, this review aims to (1) systematically synthesize the knowledge about the foraging of ponerine species; (2) identify possible research biases; and (3) propose insights through which new research can be developed. This review will not only facilitate access to information published over the past 60 years on this group but will also encourage new research, particularly for neglected groups.

## LITERATURE REVIEW

For this systematic review, 1,390 studies were initially identified, and 110 met the inclusion criteria (Methods and Supp. Tables S1 and S2 available


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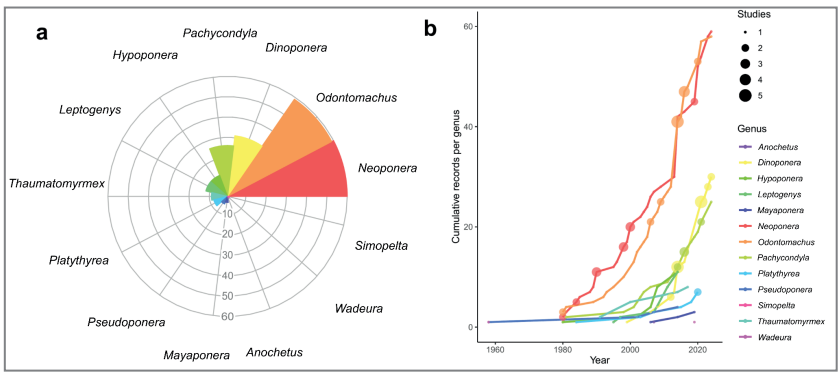
at https://doi.org/10.5281/zenodo.16228589). These studies accounted for 219 independent records on the foraging habits of 65 species from 13 genera of Ponerinae ants. There is an expressive bias in the number of studies and information recorded for Ponerinae ants, with many genera containing little or no information. In contrast, a few others have been extensively studied over the years (Fig. 1). Of the 17 genera distributed in Brazil, most studies focused on *Neoponera* Emery, 1901, *Odontomachus* Latreille, 1804, *Dinoponera* Roger, 1861 and/or *Pachycondyla* Smith, 1858 (Fig. 1a), which together account for 78.5% of all records (n = 172). Studies with a focus on *Neoponera* and *Odontomachus* species grew from the 1980s onwards, while those dedicated to *Dinoponera* and *Pachycondyla* became more frequent from the 2000s onwards (Fig. 1b). The remaining nine genera are significantly less studied, with none having more than 11 records and accounting together for only 47 records. This review was not able to find any foraging information for Brazilian species of the following four genera: *Centromyrmex* Mayr, 1866, *Corrieopone* Esteves & Fisher, 2021, *Igaponera* Troya, Marcineiro, Lattke & Longino, 2022 and *Rasopone* Schmidt & Shattuck, 2014. For this reason, these genera will not be further mentioned.

**Figure 1 -** Overall trends in publications on foraging habits of Brazilian ants in the subfamily Ponerinae: **(a)** Distribution of records according to ant genera. The number of records is greater than studies since a single study can evaluate different taxa; **(b)** Cumulative records over time exhibiting the number of published articles per year for each ponerine genus.




The main information on foraging habits (diet, activity pattern, foraging strata, foraging strategy) of ants of the subfamily Ponerinae was summarized in Supp. Table S3 (available at https://doi.org/10.5281/zenodo.16228589). In general,

ants of the subfamily Ponerinae that occur in Brazil are omnivorous and forage solitarily during the day or night. However, ponerines may present a wide behavioral diversity within the same genus, and even among populations (Supp. Table S3). For this reason, detailed information is provided below for each genus (genera appear in alphabetical order).

### *Anochetus* Mayr, 1861

*Anochetus* is a large genus with 115 species, 14 of which occur in Brazil. It is a widespread and abundant genus in the tropical and subtropical regions of the world (FERNANDES *et al.*, 2021). These ants, such as the genus *Odontomachus* (see below), have jaws modified for rapid prey capture (known as 'trap-jaw ants'). Trap-jaw ants usually walk with their mandibles open, and, after prey detection, the mandibles snap shut on a broad variety of invertebrate prey. Such a reflex catapult mechanism is triggered by mandibular hairs controlled by giant motor neurons (reviewed in LARABEE; SUAREZ, 2014). This rapid predation mechanism was later co-opted as an escape mechanism since, when directed towards the ground, it allows the ants to perform jumps that quickly move them away from danger (TORRES; SNELLING; JONES, 2000). In addition, the "popcorn effect" of multiple ants performing escape jumps could serve to confuse potential predators (PATEK *et al.*, 2006). Despite their abundance, wide distribution and trap-jaw mechanism, we have little information about *Anochetus* foraging habits, probably because they are nocturnal, smaller and more cryptic than *Odontomachus* (SCHMIDT; SHATTUCK, 2014). Individuals of *A. mayri* (Emery, 1884) reported in the field are probably epigeal foragers (QUIROZ-ROBLEDO; VALENZUELA-GONZÁLEZ, 2007).

### *Dinoponera* Roger, 1861

With exclusive distribution in South America, the genus *Dinoponera* has eight species, all occurring in Brazil. These ants are notorious for their large size (body length > 3.5 cm; DIAS; LATTKE, 2021). They mainly consume insects but also feed on inactive extrafloral nectaries from fallen flowers, fruits and seeds, therefore being considered generalist predators or scavengers (e.g., ARAÚJO;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RODRIGUES, 2006; FOURCASSIÉ; OLIVEIRA, 2002). Foraging usually takes place during both day and night, but some species have more nocturnal or diurnal habits (e.g., *D. gigantea* (Perty, 1833): FOURCASSIÉ; OLIVEIRA, 2002; *D. lucida* Emery, 1901: CURBANI *et al.*, 2021).

Foraging occurs almost exclusively on the soil surface (HANISCH *et al.*, 2023). The foraging strategy used by this group is exclusively solitary foraging (e.g., FOURCASSIÉ; HENRIQUES; FONTELLA, 1999; FOWLER, 1985). Individual foragers leave the nest slowly, exploring the environment with their antennae. After finding food, they return to the nest quickly in an almost straight line (e.g., MEDEIROS *et al.*, 2012, 2014). They exhibit directional fidelity, travelling in the same region—although not necessarily the same route—while searching for food (e.g., AZEVEDO; MEDEIROS; ARAÚJO, 2014). Foraging success can be high as reported for *D. lucida* (78%; CURBANI *et al.*, 2021) and *D. quadriceps* Kempf, 1971 (50%-76%; ARAÚJO; RODRIGUES, 2006; AZEVEDO; MEDEIROS; ARAÚJO, 2014; LIMA VIEIRA *et al.*, 2024) or low as reported for *D. grandis* (Guérin-Méneville, 1838) (31%; HANISCH *et al.*, 2023) and *D. gigantea* (10%; FOURCASSIÉ; OLIVEIRA, 2002).

Foragers have been observed on routes that lasted hours (mean of 30 to 50 minutes: e.g., ARAÚJO; RODRIGUES, 2006; FOURCASSIÉ; OLIVEIRA, 2002, HANISCH *et al.*, 2023) and covered long distances of 30-40 meters (FOWLER, 1985; LIMA VIEIRA *et al.*, 2024). *Dinoponera* workers tend to display the highest foraging activity at milder temperatures and in areas with greater prey abundance. This results in many cases in a peak of activity in the early morning and late afternoon (e.g., CURBANI *et al.*, 2021; MEDEIROS *et al.*, 2012, 2014). Even with directional fidelity, *Dinoponera* foragers are capable of altering their path with the addition of new obstacles (e.g., AZEVEDO; MEDEIROS; ARAÚJO, 2021). Additionally, it was historically believed that only visual cues were used during foraging (FOURCASSIÉ; HENRIQUES; FONTELLA, 1999), but more recent studies have also demonstrated the role of chemical cues (AZEVEDO *et al.*, 2022; LIMA VIEIRA *et al.*, 2024).

The most studied species is *D. quadriceps*, which is considered the most important high-quality disperser of the Caatinga dry forest, dispersing seeds up to 25 m (LEAL; ANDERSEN; LEAL, 2014; OLIVEIRA *et al.*, 2024). Despite no recruitment, there is evidence of social facilitation (i.e. positive feedback

between the incoming food and the activation of new foragers) (NASCIMENTO *et al.*, 2012). The biology of some species of this genus is still completely unknown: *D. hispida* Lenhart *et al.*, 2013, *D. mutica* Emery, 1901 and *D. nicinha* Dias & Lattke, 2021 (Supp. Table S3).

### *Hypoponera* Santschi, 1938

With 154 valid species, *Hypoponera* is considered the world's most common ponerine genus (SCHMIDT; SHATTUCK, 2014). However, given their small size, cryptobiotic habits, and the likely occurrence of cryptic species complexes, little work has been done on the ecology and behaviour of *Hypoponera*. They are typically reported to be generalist predators or scavengers searching in the leaf litter and trees for small arthropods (e.g., MORINI *et al.*, 2006). Foraging is probably performed by solitary workers, though recruitment with unknown mechanisms is known for a few species (e.g., SCHMIDT; SHATTUCK, 2014). In Brazil, 29 species can be found, with one being exotic: *H. punctatissima* (Roger, 1859) (FEITOSA; DIAS, 2024). Studies on seed dispersal show that *Hypoponera* ants interact with different seeds and diaspores. These ants are attracted to and interact with seeds but do not actively remove them due to their small size (e.g., PASSOS; OLIVEIRA, 2002). Interestingly, in three non-identified species of *Hypoponera* collected in Southeast Brazil, recruited workers partially removed the pulp of synthetic seeds (BIEBER *et al.*, 2014). The vast majority of articles found in this review did not provide a valid species identification, using only the genus name.

### *Leptogenys* Roger, 1861

*Leptogenys* is the largest ponerine genus with 320 species. *Leptogenys* foragers are typically nocturnal or crepuscular epigean predators (e.g., DÉJEAN; EVRAERTS, 1997). Their foraging strategies can be summarized into three categories: solitary foraging, group recruitment by a scout or swarm raiding (similar to army ants). Twenty-four species can be found in Brazil and at least one is invasive: *L. maxillosa* (Smith, 1858). Native of continental Africa, this species inhabits major harbors in urban areas. It nests in wall cracks, performs nest emigration with high frequencies and feeds on isopods (FREITAS, 1995).


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Most global and Brazilian species forage solitarily and are specialist predators of isopods (e.g., *L. bohlsi* Emery, 1896; LENKO, 1966; *L. wheeleri* Forel, 1901; DÉJEAN; EVRAERTS, 1997), although some Brazilian species also consume earwigs, termites (*L. unistimulosa* Roger, 1863; LATTKE, 2011) and harvestmen (*L. famelica* Emery, 1896; LATKKE, 2011).

The frequent specialization in isopod prey is considered a unique ecological characteristic of *Leptogenys* and is probably a plesiomorphic condition within the genus (DÉJEAN; EVRAERTS, 1997). The mandibles of *Leptogenys* are long, narrow and curved (e.g., DÉJEAN; EVRAERTS, 1997), making them well-suited to clasp round objects such as rolled-up isopods (LATKKE, 2011). The behavioral sequence employed by foragers while preying on isopods depends on the length of its mandibles and the species and size of the isopod (DÉJEAN; EVRAERTS, 1997).

Raid-group predation is frequently seen towards clustered or large prey in several African and Asian species (SCHMIDT; SHATTUCK, 2014), and evidence of this foraging strategy was never found in any *Leptogenys* with distribution in the Americas (LATTKE, 2011). The ancestral *Leptogenys* likely foraged alone, specializing - at least partially - in isopods. Over time, mass-raiding species are thought to have evolved from solitary through intermediate stages toward collective foraging (SCHMIDT; SHATTUCK, 2014).

### *Mayaponera* Schmidt and Shattuck, 2014

*Mayaponera* is a small genus with largely unknown habits. Two of the seven described species occur in Brazil: *M. arhuaca* (Forel, 1901) and *M. constricta* (Mayr, 1884) (FEITOSA; DIAS, 2024; LONGINO; BRANSTETTER, 2020). Workers of this genus usually forage at night on the leaf litter or trees (e.g., LONGINO, 2010). Currently, we have only detailed information on the biology of *M. constricta*. This species apparently uses tandem running to recruit nestmates to food sources (S. Levings, personal communication in HÖLLDOBLER & WILSON, 1990), although this behaviour has never been confirmed. It was demonstrated that this species has magnetic particles that allow them to use the geomagnetic field as an orientation cue, but neither migratory nor nomadic behaviour was ever reported (ESQUIVEL *et al.*, 2019).

***Neoponera* Emery, 1901**

With 38 of the 58 extant species known to occur in Brazil, this is one of the most behaviorally diverse genera of ponerine ants. *Neoponera*'s feeding habits comprise specific termite predation with group foraging similar to raids (namely the *Neoponera laevigata* species-group) or a generalist diet with solitary foraging (all other species) (e.g., FRESNEAU, 1985; LEAL; OLIVEIRA, 1995). The stratum where foraging occurs is also diverse with terrestrial and arboreal species (e.g., QUIROZ-ROBLEDO; VALENZUELA-GONZÁLEZ, 2007). In many cases, arboreal *Neoponera* species have a mutualistic relationship with their host trees: the ants defend the plant from herbivores and receive nest sites and food from extrafloral nectaries and Müllerian bodies (e.g., *N. goeldii* Forel, 1912: ORIVEL *et al.*, 2000; *N. luteola* (Roger, 1861): YU; DAVIDSON, 1997).

*Neoponera* foragers can be active during the day (e.g., *N. apicalis* (Latreille, 1802): FRESNEAU, 1985), night (e.g., *N. goeldii*: ORIVEL *et al.*, 2000) or both (e.g., *N. marginata* (Roger, 1861): LEAL; OLIVEIRA, 1995). When exiting the nest, foragers randomly search for food. Upon the discovery of a prey item, they grab it, sting and rapidly transport it to the nest almost in a straight line (e.g., DÉJEAN; CORBARA, 1998). In addition to its predatory habit, *Neoponera* species are known to perform pseudo-trophallaxis, also called 'social bucket'. These ants use their mandibles as an external crop, collecting and exchanging drops of liquid food between their mandibles (e.g., *N. apicalis*: FRESNEAU; DUPUY, 1988).

The four *Neoponera* species formerly placed in the genus *Termitopone* (*N. commutata* (Roger, 1860), *N. laevigata* (Smith, 1858), *N. marginata* and *N. mashpi* Troya & Lattke, 2022) are mass-raiding termite specialists and nomads (e.g., SCHMIDT; OVERAL, 2009), possibly using the Earth's magnetic field to orient during emigrations (e.g., ESQUIVEL *et al.*, 2019). Prey preference is related to species size (e.g., WHEELER, 1936). In these species, scout ants slowly search for termite parties. When the prey is successfully detected, scouts return quickly and directly to the nest (e.g., HÖLLDOBLER; TRANIELLO, 1980). During this course, their gaster is bent downwards, laying trails by the secretions from the pygidial gland, which has Citronelal as the trigger component of trail recruitment (HÖLLDOBLER *et al.*, 1996). Shortly after this, the first raiding column emerges from the nest (e.g., MILL, 1984). Both termite soldiers and workers are attacked


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by stinging, and then immobilized termites are quickly retrieved to the nest in a reversed raiding route (e.g., LEAL; OLIVEIRA, 1995).

The foraging behaviour of generalist species has also been extensively studied (especially *N. apicalis*, *N. verenae* Forel, 1922 and *N. villosa* (Fabricius, 1804) complexes). Visual orientation, polarized light and canopy navigation were hypothesised as mechanisms used by homing *Neoponera* workers (e.g., FRESNEAU, 1985). In *N. apicalis*, individual route and directional fidelity are very stable and precise (for details see '*Dinoponera*' section; FRESNEAU, 1985). *Neoponera apicalis* foraging behaviour became a model (GOSS *et al.*, 1989) and was used to develop highly efficient search algorithms for complex problems in computer science (e.g. WANG; IP, 2005). Moreover, *N. apicalis* role as an efficient seed disperser was investigated, with workers transporting seeds over long distances and removing arils (HORVITZ, 1981; HORVITZ; BEATTIE, 1980). This species also slows the decomposition process of carcasses by feeding on flies (PAULA *et al.*, 2016).

Although certain species groups have become model systems for studies of social and foraging behaviour, *Neoponera* characteristics are very unique, but detailed information is lacking for the majority of the species in the genus. Phylogenetic evidence indicates that the ancestral *Neoponera* was a ground-dwelling generalist predator and scavenger. From this origin, two major evolutionary shifts occurred: the ancestor of the *N. laevigata* group became a specialized termite mass-raider, while the ancestor of most *Neoponera* (s.s.) species transitioned to an arboreal lifestyle (SCHMIDT; SHATTUCK, 2014).

### ***Odontomachus*** **Latreille, 1804**

*Odontomachus* contains 79 extant species and, like *Anochetus*, is a trap-jaw ant (GRONENBERG; TAUTZ; HÖLLDOBLER, 1993) widespread and abundant in the tropics and subtropics. These ants can forage during the day, night (e.g., *O. chelifer* (Latreille, 1802): RAIMUNDO; FREITAS; OLIVEIRA, 2009; *O. hastatus* (Fabricius, 1804): RODRIGUES; OLIVEIRA, 2014), or both (e.g., *O. bauri* Emery, 1892: SOUZA; FRANCINI, 2010). Depending on the species, *Odontomachus* foragers may search for food from the ground to the vegetation canopy (e.g., QUIROZ-ROBLEDO; VALENZUELA-GONZÁLEZ, 2007) and can

consume invertebrate prey (e.g., EHMER; HÖLLDOBLER, 1995), insect honeydew (e.g., SOUZA; FRANCINI, 2010) and floral and extrafloral nectaries (e.g., BIEBER; PEREIRA; BOTTCHER, 2020), seeds and fruits (e.g., BOTTCHER *et al.*, 2016). When detecting a food item, workers inspect it with the antenna and snap its mandibles in only 60 m/s and generate forces over 300 times their body weight (LARABEE; SUAREZ, 2015). Stinging is more observed when capturing dangerous prey such as termite soldiers (e.g., NAYA; ÁVILA-NÚÑEZ; CALCAGNO-PISSARELLI, 2016). Despite being solitary foragers, these ants present social facilitation (for details see '*Dinoponera*' section; e.g., CAMARGO; OLIVEIRA, 2012). Social facilitation is not considered recruitment, since new foragers do not receive any clues about the food location. Some *Odontomachus* species can perform pseudo-trophallaxis or stomodeal trophallaxis (e.g., ÁVILA NÚÑEZ *et al.*, 2011).

There are 17 *Odontomachus* species occurring in Brazil (FEITOSA; DIAS, 2024). The type of cue used during spatial navigation varies with the species. For example, foraging workers of *O. bauri* and *O. hastatus* navigate using visual cues from the forest canopy overhead (e.g., CAMARGO; OLIVEIRA, 2012; RODRIGUES; OLIVEIRA, 2014), while chemical cues are important in *O. bauri* and *O. brunneus* (Patton, 1894) (DOS SANTOS *et al.*, 2024; OLIVEIRA; HÖLLDOBLER, 1989). Due to its large size, *Odontomachus* (and also *Pachycondyla,* see below) is considered one of the greatest seed dispersers among the ants of the Atlantic Forest of Southeastern Brazil. The workers can transport fallen diaspores for over 5 m (e.g., PASSOS; OLIVEIRA, 2002, 2003, 2004). They also clean and discard them on the colony's refuse pile (e.g., PIZO; OLIVEIRA, 2001). By transporting the seeds, they provide dispersal service for the plant and may even prevent the seed from rodent predation as they abandon them under the leaf litter (PIZO; OLIVEIRA, 1998). By removing the pulp or aril of the diaspores, ants enhanced germination success and prevent seed death due to fungi infestation (e.g., HORVITZ; BEATTIE, 1980). Although *O. chelifer* has a predominantly carnivorous diet (RAIMUNDO; FREITAS; OLIVEIRA, 2009), they also consume lipid-rich seed arils of *Cabralea canjerana* (Meliaceae) (BOTTCHER *et al.*, 2014). Around the nest, the chance of seed germination and seedling recruitment is increased (e.g., HORVITZ, 1981). In addition to their relevance as seed dispersers, *Odontomachus*' role in decomposition related to forensic science has recently been investigated. *Odontomachus chelifer* and *O. meinerti*


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Forel, 1905 slowed the decomposition process by consuming brood and adults of flies present on carcasses (PAULA *et al.*, 2016).

Many environmental factors may affect the foraging behaviour of these ants. In *O. chelifer*, the daily activity is negatively affected by ground temperature in the wet/warm season, thus ants forage intensively throughout the night. In the cold/dry season colony foraging activity decreases, and very few ants are seen only at night (RAIMUNDO; FREITAS; OLIVEIRA, 2009). In the Cerrado savanna near forest edges, the more variable abiotic conditions (higher temperature and lower humidity) decrease the residence time of *O. chelifer* colonies (CHRISTIANINI; OLIVEIRA, 2013). Colonies of *O. hastatus* fed on a high-protein diet had a higher daily foraging activity than colonies fed on a high-carbohydrate diet. At the individual level, when encountering a high-protein diet, foragers had a low probability of (1) feeding, (2) bringing food back to the nest, and (3) leaving the nest for another foraging visit (BAZAZI *et al.*, 2016).

### *Pachycondyla* Smith, 1858

*Pachycondyla* has a complex taxonomic history. Since its description in 1858, the genus has split and synonymized multiple genera on different occasions (for more details see MARCINEIRO; LATTKE, 2024; SCHMIDT; SHATTUCK, 2014). Today, the genus contains 17 extant species, and it is one of the most studied genera of Ponerinae, even though there is a bias for a few species (namely *P. crassinoda* (Latreille, 1802), *P. harpax* (Fabricius, 1804) and *P. striata* Smith, 1858). These ants are diurnal generalist predators and scavengers, foraging in the leaf litter via solitary foraging and tandem running. They consume mainly arthropods, dead or alive, but also lipid-rich arils/pulps (e.g., TUMA; EGGLETON; FAYLE, 2020). There is one record for feeding on extrafloral nectaries (BYK; DEL-CLARO, 2010), but usually, these species restrict their foraging activities to the soil (SCHMIDT; SHATTUCK, 2014). At least one species, *P. striata*, is also well-adapted to urban areas.

Ten species occur in Brazil (MARCINEIRO; LATTKE, 2024), but all detailed studies are found for only three species: *P. crassinoda*, *P. harpax* and *P. striata*. Researchers have evaluated how environmental factors affect the foraging of these ants. In *P. crassinoda* foraging activity is greatest during the warmest part

of the day and sharply reduced during and soon after rain (TUDOR; STARR; MOHAMMED, 2016). For *P. striata*, ants travelled faster when relative humidity (RH) was higher, and the duration of solitary trips significantly decreased at lower temperatures (SILVA *et al.*, 2021). Other studies aimed to quantify in which conditions tandem running is performed rather than solitary foraging. In *P. striata* more trips, both tandem runs and solitary foraging, were taken to near distances and protein sources. When far from the nest, the percentage of ants performing tandem running was higher with very large food sources and high RH (SILVA *et al.*, 2021). For *P. harpax*, there is an increase in the probability of performing tandem running when food items were larger and located far away from the nest (GRÜTER *et al.*, 2018). These studies conclude that recruitment through tandem running in *Pachycondyla* is expected to help colonies access and monopolise food sources in competitive environments (GLASER *et al.*, 2021; GRÜTER *et al.*, 2018; LANHOSO *et al.*, 2024).

The role of *Pachycondyla* ants in dispersing seeds was also largely investigated (e.g., *P. crassinoda*: TUDOR; STARR; MOHAMMED, 2016, *P. harpax*: HORVITZ, 1981, *P. striata*: BOTTCHER *et al.*, 2016). As reported above for *Odontomachus*, *Pachycondyla* plays a key role in seed dispersal in the Atlantic Forest of Southeastern Brazil. The large workers (body size > 10 mm) can transport fallen diaspores for more than 10 meters (e.g., PASSOS; OLIVEIRA, 2002, 2003, 2004; PIZO; OLIVEIRA, 1998) to their nest, where they fed for a few hours (*P. harpax*) or days (*P. striata*) on the arils and deposited the cleaned intact seeds on refuse piles (HORVITZ; BEATTIE, 1980; PASSOS; OLIVEIRA, 2004; PIZO; OLIVEIRA, 2001). The predatory behaviour of *P. striata* has also been used in applied approaches such as carcass decomposition studies in forensic science (PAULA *et al.*, 2016) and biocontrol of agricultural pests (ABEIJON *et al.*, 2019).

### ***Platythyrea* Roger, 1863**

This pantropical genus is the only member of Platythyreini and contains 40 species, and usually forages on vegetation (e.g., BROWN, 1975). *Platythyrea* move fast; this, combined with their potent venomous stings, allows foragers to effectively capture and subdue a wide range of prey (e.g., DJIÉTO-LORDON; ORIVEL; DÉJEAN, 2001a, 2001b). *Platythyrea* workers typically perform solitary


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foraging. Some species are described as generalist predators, others as specialized in termites, and at least one species is a specialist on adult beetles (SCHMIDT; SHATTUCK, 2014). They also present unusual behaviors rare for Ponerinae, such as collecting nectar onto part of their body surface for transport to the nest (*P. conradti* Emery, 1899; DÉJEAN; SUZZONI, 1997) and carrying their larvae directly to feed on their prey, rather than bringing the prey back to their nest (*P. modesta* Emery, 1899; DJIÉTO-LORDON; ORIVEL; DÉJEAN, 2001a).

Five species have a known distribution in Brazil. Of these, only the biology of *P. punctata* (Smith, 1858) has been widely investigated. Foraging activity is concentrated in the daytime, especially afternoon (HARTMANN *et al.*, 2020). Foragers use solitary foraging (SMITH, 1936) to capture insect prey, especially lepidopteran and coleopteran larvae (TORRES, 1984). Foragers of *P. punctata* are usually older and more fat-depleted than nurses (BERNADOU *et al.*, 2020; BERNADOU; BUSCH; HEINZE, 2015). A decrease in fat content level or ovary development is associated with an increase in foraging effort (BERNADOU *et al.*, 2020). Additionally, experimentally rearing individuals in high temperature, stress, injury and low nutritional status can increase their propensity to become subordinate foragers (BERNADOU *et al.*, 2018). Workers from smaller colonies start foraging earlier and have a shorter lifespan than workers from the largest colony (HARTMANN *et al.*, 2020).

### *Pseudoponera* Emery, 1900

Very little is known about the ecology and behaviour of *Pseudoponera*, probably because all six species share a small body size and apparently cryptobiotic habits (SCHMIDT; SHATTUCK, 2014). Three species are distributed in Brazil: *P. gilberti* (Kempf, 1960), *P. stigma* (Fabricius, 1804) and *P. succedanea* (Roger, 1863). All information available in the literature refers to *P. stigma* in Neotropical and Palearctic regions, and the general conclusion is that species in this genus are probably generalist predators and scavengers. In New Guinea, *P. stigma* is forest-dwelling, nests under the bark of rotting logs and performs solitary foraging (WILSON, 1958). In Paraguay, *P. stigma* nests in rotting wood and forages in leaf litter (WILD, 2002), while in Costa Rica, the small colonies of this species have been found from the ground layer up to the canopy

(LONGINO, 2010). In Mexico, *P. stigma* forages in the trees (QUIROZ-ROBLEDO; VALENZUELA-GONZÁLEZ, 2007).

### *Simopelta* Mann, 1922

*Simopelta* is a ponerine genus with at least two, and presumably all species, presenting the army ant syndrome: workers forage in columns up to several hundred individuals and attack colonies of other ants (e.g., KRONAUER, 2009). Of the 22 species of *Simopelta* described, five are distributed in Brazil. Although this genus occurs widely throughout the Americas' tropics and has been collected repeatedly, virtually nothing is known about its foraging habits apart from anecdotal accounts. Regarding the species that occur in Brazil, we have only the following statement by Mann (1916) concerning *S. jeckylli* (Mann, 1916), suggesting raid recruitment: "The type colony was discovered quite accidentally, by scratching away some of the leaves and debris with which the ground in the forest is everywhere covered. As far as I could ascertain, the ants were travelling in a definite direction.". Little research has been performed on the habits of *Simopelta*, but based on morphology and on anecdotal observations, it appears that *Simopelta* has converged extensively on a true army ant lifestyle (SCHMIDT; SHATTUCK, 2014).

### *Thaumatomyrmex* Mayr, 1887

With 13 species (BOLTON, 2024; FEITOSA; DIAS, 2024), *Thaumatomyrmex* is a ponerine genus known for its unusual pitchforked mandibles carrying 3 to 4 long, slender teeth (e.g., DELABIE; FRESNEAU; PEZON, 2000). These species are remarkable for their exceptional behaviour as specialist predators of Polyxenida millipedes. Workers manage to seize these millipedes with their mandibles, despite their defensive porcupine-like setae and can strip the setae from the body of their prey using the long-hardened setae of their anterior legs (e.g., BRANDÃO; DINIZ; TOMOTAKE, 1991). Little is known about the seven *Thaumatomyrmex* species occurring in Brazil. Initially, it was hypothesized that this genus could be a termite specialist since some species, such as *T. mutilatus* Mayr, 1887, were seen in association with termite nests (KEMPF, 1975). It was


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only in the 90s that the predation behaviour of these ants was formally described. The predatory sequence was detailed in *T. atrox* Weber, 1939 and is expected to be similar in other species (BRANDÃO; DINIZ; TOMOTAKE, 1991). Workers forage alone and actively search for prey, apparently using olfactory stimuli. Upon detection, the prey is inspected, then snapped with the mandibles, stung at the intersegmental membranes, and rapidly brought to the nest. During all capture steps, contact between the ants and the millipede's unpalatable hairs never occurs. In the nest, the prey is turned ventral side up and has all its setae torn out using the ant's fore tarsi. The worker thrusts the prey back and forth within its mandibles until the millipede is completely divested of its setae covering. After that, workers and larvae are free to feed on the millipede (BRANDÃO; DINIZ; TOMOTAKE, 1991). Delabie *et al.* (2000) conducted detailed observations on *T. atrox*, *T. contumax* Kempf, 1975 and *T. mutilatus* in the field and laboratory, confirming specialization in millipedes. Recently, a new species that is not a strict predator of millipedes was found in northeastern Brazil. *T. fraxini* D'Esquivel & Jahyny, 2017 is a smaller species that also consumes Collembola (Hexapoda, Insecta), but no further details were reported (D'ESQUIVEL *et al.*, 2017).

### *Wadeura* Weber, 1939

*Wadeura* is a ponerine genus recently revived and contains all the South American species previously attributed to *Cryptopone* (e.g., BRANSTETTER; LONGINO, 2022). Three of the four species known occur in Brazil: *W. guianensis* Weber, 1939, *W. holmgreni* (Wheeler, 1925), and *W. pauli* (Fernandes & Delabie, 2019) (FEITOSA; DIAS, 2024). Since they are rare and have a hypogeal habit, only some information can be attributed to these ants. Despite being hypogaeic, *W. holmgreni* workers can forage for short periods on the ground (FERNANDES; DELABIE, 2019). A morphological convergence with *Centromyrmex* suggests that *W. holmgreni* could be specialist predators of termites living in the ground (DELABIE; AGOSTI; NASCIMENTO, 2000), but to this day, this has not been formally confirmed.

## DISCUSSION

The subfamily Ponerinae is often reduced to a group of ants that have basal characteristics. However, this review illustrates how the foraging biology of this group is far from being understood by this mere generalization. Ponerine ants that occur in Brazil have varied diets, foraging strata, and recruitment strategies within the same genus and even species. Available information also comes from several research scopes, ranging from natural history to molecular studies. In addition to the compilation of knowledge, this review highlights research biases and patterns to provide suggestions and new perspectives for future studies. Despite being considered one of the most studied groups of ants, it is possible to identify that many gaps remain to be explored, especially experimental studies with cryptic, nocturnal, and/or inconspicuous ants.

Brazilian ants in the subfamily Ponerinae have been studied since at least the 1960s. Despite this, it is possible to verify in notes, academic thesis and other documents excluded from this analysis (see Methods and Fig. S1 at https://doi.org/10.5281/zenodo.16228589) that myrmecologists have been interested in investigating the foraging of ants way before (e.g., MILL, 1916). A significant increase in the number of studies began in the 1980s, with a noticeable focus on *Neoponera* and *Odontomachus*. A second peak occurred in the 2000s, with an increase in studies focusing on *Dinoponera* and *Pachycondyla*. These four genera are by far the most studied. This preference probably comes from the fact that they are generally diurnal and abundant species with large and slow workers, which are (1) more easily observable in the field (e.g., ARAÚJO; RODRIGUES, 2006; LEAL; OLIVEIRA, 1995) and (2) are easily adapted to laboratory conditions (e.g., AZEVEDO *et al.*, 2022; OLIVEIRA; HÖLLDOBLER, 1989). However, even when dealing with the most studied genera of Ponerinae, the biology of most species is still completely unknown. Therefore, to obtain a more robust and accurate view of foraging habits in Ponerinae, more efforts should be made to investigate species and genera that have little information.

The small worker size, crepuscular/nocturnal and cryptic habits, small colonies, low local abundance, absence of a clear flight period and taxonomic uncertainty are among the barriers that must be overcome when investigating some genera of Ponerinae, such as *Hypoponera*, *Centromyrmex*, *Anochetus*,


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*Rasopone* and *Simopelta*. The lack of detailed information in these cases usually leads to generalizations that come from circumstantial observations obtained from a single species, which is typically applied to the entire genus. This, if not avoided, should be carefully interpreted since feeding and foraging habits in ants are flexible phenotypes with large variation (REEVES; MOREAU, 2019) even among populations of the same species, as observed in *Pseudoponera* (LONGINO, 2010). An efficient way to overcome these obstacles is to set up collaborative projects between myrmecologists from different backgrounds and regions who have expertise in different techniques and specialties ranging from taxonomy, ecology and behaviour. Furthermore, tools have emerged that facilitate the study of animal behaviour in species that were initially considered challenging. For example, automatic tracking of workers by new software and machine learning (reviewed in PANADEIRO *et al.*, 2021), new artificial diets (LIST *et al.*, 2024), and more refined experimental manipulations can enable advances and are especially interesting to be applied to little-studied species.

Most of the information available on ant foraging, especially in less-studied genera, comes from personal observations or natural history studies. Although useful and forming the basis of what we know for many groups, this type of knowledge is sometimes limited by restricting the development of hypotheses and theories about the foraging of species between populations. I encourage researchers to take a step further and design hypotheses and bioassays in ants from other perspectives, such as behavioral ecology and ethology (TINBERGEN, 1963). This type of approach allows data to be replicable and generalized models and information to be extrapolated with more reliability (LIMA VIEIRA; CHAMERON; CHÂLINE, 2024).

Finally, foraging studies are not limited to the biological characteristics of the species, such as diet, recruitment strategy and foraging strata. Ponerine ants from Brazil are a behaviorally diverse group with the potential to be excellent study models for investigating phenotypic plasticity, individual and colonial decision-making and mechanisms that led to the diversification and evolution of foraging strategies in ants. For example, *Neoponera, Leptogenys* and *Pachycondyla* are diverse genera where a comparison between recruitment species to closely related solitary foraging ones can be drawn. Furthermore, knowledge of the foraging habits of these species has already been applied in a variety of situations, such as forensic studies, biological pest control and solving mathematical problems (e.g., ABEIJON *et al.*, 2019; MONMARCHÉ; VENTURINI;

SLIMANE, 2000; PAULA *et al.*, 2016). Therefore, in addition to the impact on basic science, studies in this area have economic potential.

## CONCLUSION AND PERSPECTIVES

Brazilian ants in the subfamily Ponerinae have been widely studied since the 1980s. However, there is a significant bias, with most studies focusing on *Dinoponera*, *Pachycondyla*, *Neoponera*, and *Odontomachus*. Even in the most studied groups, findings are limited to a few species. This bias is probably related to the conspicuity of these ants, which facilitates observations in the field and laboratory. Besides, most ant collections and observations occur on the ground during the day, excluding nocturnal arboreal/hypogeal species. The foraging habits of most groups are still today largely unknown. The main barriers to studying these species are taxonomic uncertainty, collection biases, nocturnal or cryptic habits, and small worker size. Future research may consider an interdisciplinary approach, the exploration of poorly studied species, using behavioral ecology or ethology as an approach, and new automated tools such as artificial intelligence and machine learning to access behavioral data more quickly.

## SUPPLEMENTARY FILES

Full methods, supplementary figures and tables, R script and data files are available at the free open-source Zenodo repository: https://doi.org/10.5281/zenodo.16228589.

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# 07

# CUTICULAR HYDROCARBONS IN BRAZILIAN ANTS: A SYSTEMATIC REVIEW

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# ABSTRACT

Chemical signal-mediated communication can be found in all forms of life. In ants, cuticular hydrocarbons (CHCs) are essential for mediating interactions among colony members. These compounds are present in the insect epicuticle, protecting against desiccation and playing essential roles in communication. In Brazil, the high diversity of ants suggests a broad variation in CHCs profiles, but studies on this topic remain scarce. To better understand CHC diversity in Brazilian ants, this chapter systematically reviews research conducted over the past 30 years. The review was performed using major academic databases, restricting the search to studies with ants collected in Brazil. Thirty-six articles were identified, with the highest representation in the Southeast and Central-West regions of the country. The most studied species belonged to the subfamily Myrmicinae, followed by Ponerinae, Ectatomminae, Formicinae, and Paraponerinae, belonging to 27 species. The CHCs classes found in Brazilian ants were in the following order of importance: linear alkanes > monomethyl alkanes > dimethyl alkanes > linear alkenes > branched alkenes > trimethyl alkanes > alkadienes. The total number of compounds was 354, the CHCs profiles presented both qualitative and quantitative variations, influenced by complex interactions involving environmental and genetic factors. Given the diversity of biomes in Brazil, further research at a national scale is needed to improve understanding of the ecological and evolutionary aspects of cuticular hydrocarbons.

**Keywords:** Chemical communication; chemical ecology; Formicidae.

## INTRODUCTION

All animals, irrespective of the level of sociality, need to communicate, employing different types of signals that may be audible, visual, tactile, electric, or chemical (Martin; Drijfhout, 2009a). In social insects, chemical signaling is fundamental to enable the individuals in the colonies to continuously exchange information for various purposes (Leonhardt *et al.*, 2016; Menzel; Blaimer; Schmitt, 2017). This form of communication is crucial for the ability of insects to perceive, interpret, and transmit information (Blomquist; Bagnères, 2010).

As social insects, ants primarily use two mechanisms for chemical communication, namely volatile pheromones and contact pheromones. Volatile pheromones are released from exocrine glands and have functions that include alarm signaling and trail marking (Billen; Morgan, 1998; Howard; Blomquist, 2005). On the other hand, contact pheromones are chemical compounds present in the epicuticle, which is the outermost layer of the cuticle (Blomquist; Ginzel, 2021).

The body of the ant is covered by a lipid layer mainly composed of cuticular hydrocarbons (CHCs). These compounds can be classified into two main groups: saturated hydrocarbons, including linear alkanes and methyl-branched alkanes; and unsaturated hydrocarbons, represented by alkenes and, more rarely, methyl-branched alkenes and alkadienes (Blomquist; Bagnères, 2010). The CHCs have essential functions as a barrier to prevent desiccation and to protect against pathogens. Over time, they have also been co-opted to chemical communication (Lockey, 1988; Singer, 1998).

Studies have investigated CHCs in ants from different perspectives, including their roles as signals for nestmate identification (Souza *et al.*, 2006), fertility (Evison *et al.*, 2012), sex (Campos *et al.*, 2012), caste (Nascimento *et al.*, 2013; Santos *et al.*, 2022), and age (Valadares; Nascimento, 2017). They can act in kin recognition (Fox *et al.*, 2012) determining foraging behavior (Santos *et al.*, 2024) and may be used in establishing taxonomic relationships (Fox *et al.*, 2017). These studies have yielded intriguing results demonstrating the plasticity of CHCs in response to genetic and environmental factors (Menzel; Blaimer; Schmitt, 2017; Menzel; Zumbusch; Feldmeyer, 2018; Duarte *et al.*, 2019).

Linear alkanes are primarily associated with impermeabilization, due to their molecular characteristics such as strong adhesion between atoms and

excellent stability provided by van der Waals forces (Sprenger; Menzel, 2020). Alkenes and branched alkanes exhibit weaker intermolecular adhesion (Menzel; Blaimer; Schmitt, 2017), making them more fluid in the epicuticle and, therefore, more functional in information exchange. However, chemical communication involves mixtures of compounds that can have multiple functions (Chung; Carroll, 2015). The linear alkanes, which are more associated with the physical barrier function, can also be effective in communication, transmitting information that is less complex (Akino *et al.*, 2005; Hora *et al.*, 2008; Martin; Drijfhout, 2009b). An example is provided by the species *Ectatomma tuberculatum*, where a higher proportion of heptacosane is a signal of fertility (Hora *et al.*, 2008).

The complex interplay of these functions, under the influence of biotic and abiotic variables, makes the evolution of CHCs a dynamic, but an underexplored process. Considering the size of Brazil and its high species diversity, the investigation of chemical communication in the myrmecofauna of the country can provide valuable information for elucidating how the composition of these compounds relates to their functions within a species. To assist in understanding the dynamics of CHCs profiles, a systematic review was made of studies conducted over the past three decades, concerning the chemical diversity of the ant epicuticle. This review compiles information on the techniques and tools used to study CHCs, as well as the diversity of these compounds in Brazilian ants, across different regions and biomes.

## METHODOLOGY

### Bibliometric data

A thorough systematic review was conducted using the SciELO, Google Scholar, ISI, Web of Science, and Scopus databases. The keywords used were *cuticular hydrocarbons*, *ants*, *Formicidae*, *Hymenoptera*, *chemical ecology*, *contact pheromones*, and *Brazil*, with combinations of these words. The selection of studies was limited to articles published in indexed journals that addressed the analysis of cuticular hydrocarbons in ants collected in Brazil, from the earliest record to the most recent publication found (1998 to 2024).

Considering that a systematic review may have certain limitations related to aspects such as incomplete information about the collected data, sample sizes, and research and publication biases, efforts were made to minimize possible inconsistencies. To this end, all the species studied were reviewed and updated according to their most recent taxonomic nomenclature.

Analysis was made of the progression of publication of articles across a 30-year period, which was systematically divided into three distinct decades, to enable a comparative assessment of trends over time. The geographic distribution of the publications was grouped by Brazilian states, based on the number of publications in a heatmap (Figure 1). This map was created to represent the numbers of studies of CHCs in Brazilian ants, according to biome. In cases where the article did not mention the biome where the ants were collected, it was identified using information about the collection location and geographical coordinates. Three categories of occurrence were used: low (one study), medium (five to eight studies), and high (more than eight studies). The categorization was defined by linear interpolation, with equal value intervals of records, based on the number of studies conducted in each Brazilian biome. Biomes with no study records were represented by lighter colors on the map, with the color intensity increasing as the number of publications increased. The Kernel intensity estimator was applied to provide a spatial view of the first-order distribution of points, reflecting the number of studies per state (Figure 1), with larger circles indicating a higher number of publications (Furtado; Moraes; Machado, 2008).

**Procedures for cuticular hydrocarbon analysis**

Information was gathered about the methods, including the collection technique, the numbers of colonies and individuals analyzed, and the euthanasia method. The CHCs extraction methods were also evaluated, considering the type and volume of solvent used, sample immersion time, and CHC extraction and analysis techniques.

After selecting the articles, a detailed analysis was made of the ant species and castes investigated. The data were organized into a table, enabling identification of the studied species and taxonomic groups (See Table S1 in the supplementary material, https://dx.doi.org/10.6084/m9.figshare.29825978).


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### Diversity of cuticular hydrocarbons

Determination of the CHCs classes in each subfamily studied was based on the hydrocarbons identified in the published articles. The classes considered were linear alkanes, monomethyl alkanes, dimethyl alkanes, trimethyl alkanes, linear alkenes, branched alkenes, and alkadienes. For data standardization, only data referring to the cuticular chemical profiles of worker ants were used. Other cuticular lipids that were not CHCs were excluded.

### Statistical analysis

The CHCs found in the articles were grouped to calculate the total numbers of compounds according to species, genus, subfamily, and biome (Figures 2 and 3). In addition, the number of CHCs, chain length, and predominant class were grouped by genus, to compare the variation of these compounds (Table 1).

To relate the cuticular hydrocarbon profiles to geographic distances and test for correlation, distance matrices were generated (using Jaccard and Euclidean distances, respectively), with application of the Mantel test. The results were compared to those obtained after simulating 9,999 random permutations of one of the matrices. Non-metric multidimensional scaling (nMDS) was then used to visualize the ordering of the different cases, considering genus, subfamily, and biome, based on the CHCs profiles, to determine whether the hydrocarbon composition data were grouped according to genetic and/or environmental factors. These analyses were performed using the R software (Team, 2020).

## RESULTS

### Bibliometric data

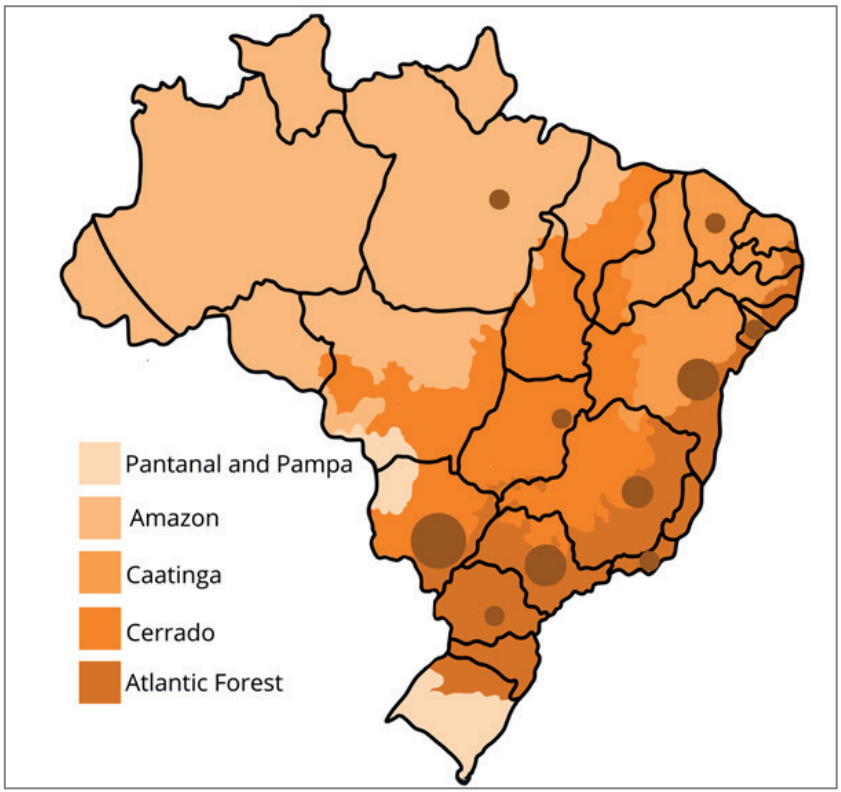
A total of 36 articles involving CHCs analysis were identified, with the earliest study dating back to 1998. Bibliometric analysis revealed a progressive increase in the number of publications. Seven publications were recorded in the first period, from 1998 to 2004, increasing to 13 from 2005 to 2014, and reaching 16 publications in the most recent period, from 2015 to 2024. Hence, there was

an 86% increase between the first and second periods (1998-2004 and 2005-2014), followed by a 24% increase between the two later periods.

The published articles were from research groups located in all regions of Brazil (Figure 1). Most of the studies used samples collected in a single state, except for three studies that analyzed samples from two states in different regions. In these cases, CHCs variation was assessed according to different ant populations. The greatest number of studies were undertaken by researchers affiliated with institutions in the Southeast region, followed by the Central-West and Northeast regions. Among Brazilian states, Mato Grosso do Sul had the highest number of publications, followed by Bahia and São Paulo (Figure 1).

In terms of biome, samples were collected in areas of the Atlantic Forest (13 studies), the Cerrado (5 studies), both the Atlantic Forest and the Cerrado (3 studies), the Caatinga (2 studies), and the Amazon (1 study) (Figure 1). No evidence or citations were found for studies conducted in the Pantanal or Pampa biomes. Twelve of the studies did not mention the biome where the analyzed ants were collected; in these cases, the biomes were identified from information given in the articles about the collection locations and geographic coordinates (See Table S1 in the supplementary material, https://dx.doi.org/10.6084/m9.figshare.29825978).

**Figure 1 -** Heatmap indicating biomes with publications related to hydrocarbons in ants from Brazil. The intensity of the colors represents the number of studies per biome, the greater color intensity, the higher the number of publications. The size of the circles indicates the number of studies according to state (a larger circle corresponds to a greater number of publications).




## Procedures for cuticular hydrocarbon analysis

Several different CHCs extraction and analysis methods were employed in the reported studies. A majority (27) used gas chromatography coupled with mass spectrometry (GC-MS), eight employed Fourier transform infrared photoacoustic spectroscopy (FTIR-PAS), and three used solid phase microextraction (SPME).

Different methods were also used for extraction of the cuticular compounds. In the eight studies that used FTIR-PAS, the analysis was performed directly on the insect cuticle. Twenty-three studies used solvents to extract the cuticular compounds, while no solvent was used in the five studies employing SPME, this is because it is used as a solvent-free sample preparation technique

that uses a coated fiber or Arrow to concentrate volatile and semi volatile compounds from a sample (Verma; Arya; Singh, 2025). The most widely used solvent was hexane (19 studies), followed by pentane (2) and dichloromethane (1), all of which have nonpolar characteristics. Only one study did not specify which solvent was used for extraction.

The shortest time for extraction of the cuticular compounds was 10 seconds, while the longest recorded time was one hour (S1). The most frequently used immersion times were two minutes (8 studies) and 10 minutes (6 studies). The ant euthanasia method varied among the studies, with freezing being most common (16 studies). One study used euthanasia by immersion in alcohol, while another immersed the ants directly in the extraction solvent. However, the euthanasia method was not specified in eighteen of the articles.

**Diversity of cuticular hydrocarbons**

Considering all the studies, the CHCs profiles of 27 ant species were examined. The most studied subfamily was the Myrmicinae, with 12 species, followed by Ponerinae (7), Ectatomminae (4), Formicinae (3), and Paraponerinae (1) (Table 1). The most frequently studied genera were *Ectatomma* (7 studies), *Atta* (6) and *Odontomachus* (4) (S1). At the species level, *Atta sexdens* was the most studied (5 studies).

Most of the studies focused on behavioral aspects and intraspecific relationships, assessing the effects of factors such as diet, temperature, or population differences on the hydrocarbon profiles. Several studies explored the taxonomic functionality of CHCs (S1). The worker caste was the most frequently analyzed, followed by queens. Some studies also investigated the influence of sex on CHCs profiles, using males as models (S1).

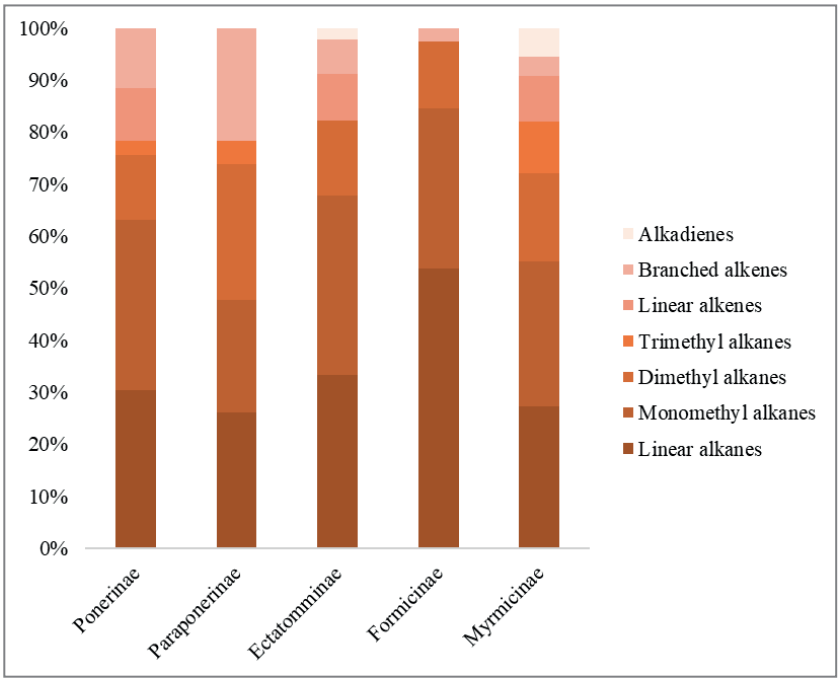
The total number of identified compounds was 354, and varied among the ant genera (10 to 90), and chain lengths from $C_{15}$ to $C_{43}$. The three compound classes with the greatest numbers of CHCs among the genera (predominance) are shown in Table 1.

**Table 1 -** Variation of cuticular hydrocarbons in ant genera from Brazil. N.C.= number of compounds; C.C.L.= carbon chain length; LA = linear alkanes; TR = trimethyl alkanes; ME = monomethyl alkanes; DI = dimethyl alkanes; BKE = branched alkenes; LKE = linear alkenes.

| Subfamily | Genus | N.C. (min. and max.) | C.C.L. | Predominance |
|---|---|---|---|---|
| **Myrmicinae** | *Atta* | 10 to 27 | $C_{15}$-$C_{40}$ | LA, TR, ME |
| | *Acromyrmex* | 19 to 20 | $C_{21}$-$C_{36}$ | LA, DI, ME |
| | *Solenopsis* | 18 to 23 | $C_{22}$-$C_{31}$ | ME, LA, BKE |
| | *Wasmannia* | 36 | $C_{19}$-$C_{31}$ | LA, ME, LKE |
| | *Cephalotes* | 11 | $C_{19}$-$C_{32}$ | LKE, ME, LA |
| | *Cardiocondyla* | 61 | $C_{19}$-$C_{39}$ | DI, ME, LKE |
| | *Odontomachus* | 12 to 30 | $C_{20}$-$C_{32}$ | ME, LA, DI |
| **Ponerinae** | *Dinoponera* | 12 to 81 | $C_{21}$-$C_{37}$ | LA, ME, BKE |
| | *Pachycondyla* | 15 to 40 | $C_{31}$-$C_{43}$ | ME, LA, DI |
| | *Neoponera* | 12 to 82 | $C_{20}$-$C_{41}$ | ME, LA, LKE |
| **Paraponerinae** | *Paraponera* | 49 | $C_{15}$-$C_{35}$ | LA, DI, ME |
| **Ectatomminae** | *Ectatomma* | 25 to 47 | $C_{16}$-$C_{33}$ | ME, LA, DI |
| **Formicinae** | *Camponotus* | 10 to 90 | $C_{19}$-$C_{34}$ | LA, ME, DI |

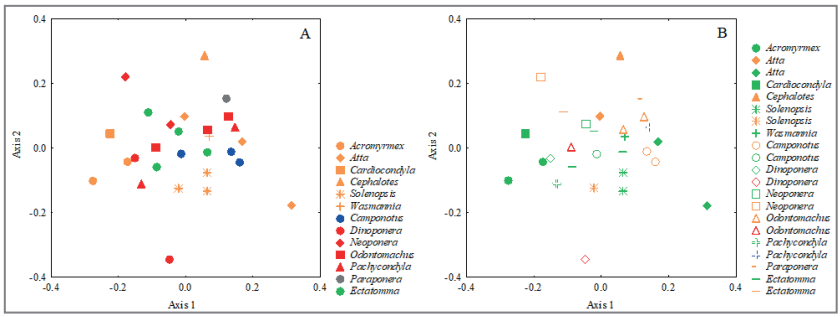
In all the subfamilies, the most numerous compound classes were the linear and monomethyl alkanes, followed by dimethyl alkanes and branched alkenes (Figure 2). Linear alkenes were only found in the cuticles of ants from the subfamilies Myrmicinae, Ectatomminae, and Ponerinae. Trimethyl alkanes were only present in Myrmicinae, Paraponerinae, and Ponerinae, while alkadienes were only found in Myrmicinae and Ectatomminae. The lowest chemical diversity was in the Formicinae subfamily, with only four classes of compounds (Figure 2).

**Figure 2 -** Distribution of cuticular hydrocarbon classes found in ant subfamilies in Brazil.




No spatial correlation was observed between the collection locations of the ant genera and their hydrocarbon profiles ($r = 0.01$; $p = 0.47$), indicating that geographic distance alone was unable to explain the differences in CHCs. The nMDS analysis showed the distributions of the genera according to subfamily (Figure 3A) and biome (Figure 3B). Overall, for all the genera, no consistent pattern of grouping related to environmental or genetic factors was observed. However, in some cases, there appeared to be an influence of biome on the distance between samples of the same genus, such as for *Dinoponera* from the Caatinga and Atlantic Forest biomes, as well as a separation according to biome for the genera *Camponotus*, *Pachycondyla*, and *Neoponera* (Figures 3A and 3B). Only *Solenopsis* showed an apparent domination of genetic over environmental (biome) factors (Figures 3A and 3B).

**Figure 3 -** Non-metric multidimensional scaling (nMDS) analysis of the distribution of genera according to (A) subfamily and (B) biome. In (A), the colors indicate the subfamily: orange = Myrmicinae; blue = Formicinae; red = Ponerinae; gray = Paraponerinae; green = Ectatomminae. In (B), the colors indicate the biome: green = Atlantic Forest; orange = Cerrado; red = Caatinga; blue = Amazon. In (A) and (B), the symbols indicate the genera.




## DISCUSSION

### Bibliometric data

This is the first study to provide an overview of the methodologies and results reported in published articles concerning the CHCs of ant species in Brazil, aiming to understand the chemical diversity of cuticular compounds and their variations among ant species in the country. The number of published papers on this topic has progressively increased over the years, since the first report by Monnin, Malosse and Peeters (1998), reflecting the increasing interest of researchers globally in understanding chemical communication involving CHCs (Martin; Drijfhout, 2009a; Kather; Martin, 2015). However, despite Brazil being the country with the greatest diversity of ant genera and the second greatest diversity of ant species (Baccaro *et al.*, 2015), CHCs have so far been studied in only 27 species.

The highest number of samples were collected in the Atlantic Forest biome, followed by the Cerrado, Caatinga, and Amazon (only one study). There were no reports of studies of CHCs in ants of the Pampa and Pantanal biomes, for which fewer ant species have been described (Feitosa *et al.*, 2022). However, a new study investigating the effect of biome on hydrocarbons of the ant *Ectatomma brunneum* is the first to use ants collected in the Pantanal biome

(Antonialli-Junior *et al.*, 2025). The number of studies of species in a specific biome may also be related to the region where the researchers are based, facilitating the collection of samples in that environment.

Brazil is a country with continental size and high biome and phytophysiognomy diversity, which influences the distribution of ant species and their CHCs composition, as observed for different populations by Menzel, Blaimer and Schmitt (2017). Brazilian biomes impose environmental challenges that shape the diversity and composition of CHCs. In areas with hot and humid climates, such as the Atlantic Forest, there may be a reduced need for linear CHCs or long-chain compounds, due to lower water loss by evaporation (Menzel; Zumbusch; Feldmeyer, 2018). On the other hand, hot and dry climates, such as in the Cerrado, may favor cuticular compositions with higher saturated and long--chain compounds, to prevent desiccation (Blomquist; Bagnères, 2010). Since environmental conditions can directly affect the compounds present, enabling adaptation to the ecosystem, studies in different biomes, including those where there have been few or no studies (such as the Pantanal and Pampa biomes), are needed to understand how CHCs have evolved across all the Brazilian biomes.

**Procedures for analysis of cuticular hydrocarbons**

The methods used for extraction of the CHCs varied among the studies. The majority employed methods involving solvents, although some utilized techniques that did not require extraction of the compounds. This could have influenced the numbers of compounds found in the ant cuticles, because different techniques vary in their efficiency, selectivity, and potential for compound degradation (Pechal *et al.*, 2014). For example, immersing insects in organic solvents can extract other lipids from their bodies, depending on the immersion duration and type of solvent (Butterworth *et al.*, 2020). Some techniques, such as SPME, may recover smaller amounts of CHCs, compared to solvent-based methods (Pechal *et al.*, 2014).

The analysis technique most widely adopted in the studies was GC-MS, which has been employed since the 1970s. In mass spectrometry, the spectra are interpreted by means of the mass-to-charge ratio, enabling confirmation of the identity of compounds detected in the sample (Blomquist; Bagnères, 2010). The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second most used technique was FTIR-PAS, which identifies functional groups, rather than compounds. This can be advantageous when the main objective is to evaluate qualitative differences in chemical composition, since FTIR-PAS is a less expensive technique that does not use solvents or cause abrasion to the cuticle, so the sample remains intact after the analysis (Blomquist; Bagnères, 2010).

**Diversity of cuticular hydrocarbons**

Most studies have investigated ants from the subfamily Myrmicinae, especially species of fungus-cultivating ants from the genera *Atta* and *Acromyrmex*. Due to their herbivorous behavior, leafcutter ants are of significant economic interest, since they can cause substantial losses in various crops (Della Lucia; Gandra; Guedes, 2014), consequently attracting the interest of the scientific community. Given that CHCs influence the complex relationships among ants, studying these compounds could be valuable for species management practices.

The second most studied subfamily was Ponerinae, with many investigations of the role of CHCs in discriminating castes and species, assisting in understanding the behavioral and evolutionary aspects of various Ponerinae species. However, there are many gaps in knowledge about different aspects of these ants, which exhibit basal behavior and present little morphological differentiation between castes (Lattke, 2015). The use of CHCs as a complementary tool for taxonomy has been promising, assisting in rearranging unnatural or divergent clades (Lucas *et al.*, 2002; Martins; Serrão, 2011; Chen *et al.*, 2020).

Variation in the number and chain length of the hydrocarbons, among the genera of the different subfamilies, could have been influenced by the high diversity of species, different collection sites, distinct ecological strategies, and specific physiological requirements (Blomquist; Ginzel, 2021). Even within a single species, the number and abundance of cuticular compounds can vary during the year, such as between different seasons, as shown by Lima *et al.* (2025). The present findings are consistent with the review by Martin and Drijfhout (2009a), who reported the existence of nearly a thousand different compounds in 78 ant species worldwide. It was pointed out that although each species may have a unique pattern of CHCs, there is no clear association between chemical profile and phylogeny. Elsewhere, van Wilgenburg, Symonds and Elgar (2011) observed

a positive correlation between ants from rainy environments and compounds with shorter chains. However, this trend was not observed here, even though many of the ant samples were collected in the Atlantic Forest biome. It is likely that the observed numbers of compounds and chain lengths could have been influenced by the different analysis techniques, columns, extraction times, and solvents employed.

In all the subfamilies, the most numerous compound classes (in decreasing order of abundance) were linear alkanes, monomethyl alkanes, and dimethyl alkanes. The same trend was reported by Martin and Drijfhout (2009a), who reviewed the CHCs of ants and observed that linear and monomethyl alkanes occurred in all species, while most dimethyl alkanes were species-specific, indicating that these compounds could be used to discriminate species and nestmates, maintaining functional equilibrium in recognition.

The predominance of linear and monomethyl alkanes in all the ant subfamilies appeared to be a strategy to ensure that the cuticle could perform the two essential functions of impermeabilization and communication. The linear alkanes with relatively high melting points could protect against water loss, while the branched alkanes could have greater potential in terms of information content, due to variations in the number of branches, their positions in the molecule, and their optical configuration (Hefetz, 2007). Hence, environments that are open and dry, where foragers are exposed to heat and low humidity, would favor linear alkanes, rather than branched alkanes with greater permeability (Wagner; Tissot; Gordon, 2001). The presence of monomethyl alkanes could facilitate communication by increasing cuticular fluidity, helping to maintain sufficient permeability to allow the diffusion of chemical signals. In *Temnothorax*, especially in foragers, monomethyl alkanes were shown to increase under hot and humid conditions (Menzel; Zumbusch; Feldmeyer, 2018) and are also important for impermeabilizing the cuticle (Chung; Carroll, 2015; Baumgart *et al.*, 2022; Lima *et al.*, 2025).

The subfamily with the highest number of linear alkanes was Formicinae, with almost two-fold more compounds of this class, compared to the other subfamilies. The predominance of these compounds could be explained by environmental and genetics factors, since 75% of the ants in this subfamily were collected in the Cerrado and 50% belonged to specie *Camponotus textor*,


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leading to similarity in the cuticle characteristics. This could also explain the smaller number of compound classes (only four) in this subfamily. The Cerrado has an extended dry season (May to September), with low relative humidity of the air and high temperatures (Ratter *et al.*, 1997). Furthermore, the open vegetation of the Cerrado exposes ants to high levels of UV radiation and thermal fluctuations, especially since many Formicinae in the Cerrado nest in the soil or in scrub vegetation, which are environments where temperature and humidity vary significantly. Consequently, linear alkanes are favored in Formicinae inhabiting this biome, since these compounds are less volatile and more effective in reducing water loss (Gibbs, 1998).

Trimethyl alkanes (TMAs) were only found in the subfamilies Myrmicinae, Ponerinae and Paraponerinae (in that order of importance, in terms of numbers). These results indicate that the ability to synthesize TMAs already existed in the hymenopteran ancestors, including parasitic wasps and less derived ants, suggesting that the biosynthetic pathways were present in the early evolution of ants and were co-opted for different functions (Martin; Drijfhout, 2009a; Kather; Martin, 2015; van Wilgenburg; Symonds; Elgar, 2011). Differences in hydrocarbons among ants may result, in part, from the activation or deactivation of specific biosynthetic pathways in different lineages (van Wilgenburg; Symonds; Elgar, 2011).

TMAs are common in species from high humidity regions, where the adaptive impermeabilization is less rigid, favoring the diffusion of chemical signals (Menzel; Blaimer; Schmitt, 2017; Sprenger *et al.*, 2018). In Myrmicinae, which often inhabit humid tropical forests, and in Ponerinae/Paraponerinae, which nest in humid soils, this trend is favored by local rainfall regimes. In addition, the complexity of TMAs (with multiple isomers) provides a greater repertoire of chemical signals, which may be crucial for recognition in ants that have large colonies, as in the case of Myrmicinae species (Guerrieri *et al.*, 2009). Ponerinae and Paraponerinae, considered basal lineages within Formicidae, presented chemical profiles that were more diverse, possibly because of adaptations to humid tropical environments (Dijkstra; Boomsma, 2006).

Linear alkenes were only identified in the cuticles of ants belonging to the subfamilies Mymicinae, Ectatomminae, and Ponerinae, while branched alkenes were present in members of all the subfamilies. Alkenes play an important

role in chemical communication, with the linear and branched compounds being associated with nestmate recognition (Martin *et al.*, 2008). According to Martin; Drijfhout (2009a), species that produce branched alkenes containing both double bonds and methyl branches are rare, because this architecture is chemically complex (van Wilgenburg; Symonds; Elgar, 2011). However, this appeared to be a common characteristic of ants found in Brazil, since, despite the methodological differences, the CHCs profiles of all the species analyzed included this class of compounds.

The alkadienes class was only found in the subfamilies Myrmicinae and Ectatomminae. The results showed that most of the species in these subfamilies were from humid environments, such as the Atlantic Forest biome. Species from humid environments are more likely to incorporate alkadienes into their chemical profiles, because water loss is low and the biosynthesis of unsaturated compounds, such as alkadienes, is favored (van Wilgenburg; Symonds; Elgar, 2011).

There was no significant correlation between the CHCs and the biomes where the ants were collected. This indicates that the cuticular chemical profile in most cases appears to be a combination of both genetic and environmental factors. Nonetheless, in some cases, the composition was more influenced by genetic or environmental factors, the in genera *Camponotus*, *Pachycondyla*, *Neoponera* and *Dinoponera*, the biome was a determining factor for the ants' grouping.

The CHC profile of *Dinoponera quadriceps* from the Caatinga biome showed highly distinct characteristics from ants of the same species from the Atlantic Forest biome, which could be explained by the semiarid climate of the Caatinga in Northeastern Brazil, with low precipitation and high temperatures (Marengo *et al.*, 2018). These conditions could induce changes in the chemical composition of the cuticle, stimulating the plasticity of the hydrocarbon profile when exposed to environmental stress (Wagner; Tissot; Gordon, 2001; Menzel; Zumbusch; Feldmeyer, 2018). Populations adapted to different environments differ in their CHCs profiles due to factors such as geographic isolation, diet, and varying abiotic conditions (Menzel; Zumbusch; Feldmeyer, 2018). Similar results were found in *Ectatomma brunneum*, where the type of biome was a determining factor in CHC composition, indicating that these compounds have potential for assessing biogeographic differences (Antonialli-Junior *et al.*, 2025).


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The grouping of the cuticle composition of ants of the genus *Solenopsis* indicated a greater influence of genetic factors. Although the CHCs composition was modulated by environmental factors, in *Solenopsis* this effect could apparently be lowered by reduced environmental heterogeneity, since the nests of many species are constructed in similar microhabitats (underground, where conditions are more stable), as well as low genetic diversity and the presence of homogeneous supercolonies of these ants (Wagner; Tissot; Gordon, 2001; Ajayi *et al.*, 2020).

Therefore, CHC profiles in Brazilian ants vary according to a combination of genetic and environmental factors. Each biome has distinct environmental characteristics that reflect both evolutionary adaptations and the plasticity of CHCs in ant populations, making CHCs promising ecological and taxonomic markers.

## CONCLUSION

In the last three decades, there has been an increase in the number of publications concerning ants CHCs in Brazil, with a similar trend worldwide, probably driven by technological advances and the democratization of science. In Brazil, published articles have mainly been from research groups in the Southeast and Central-West regions, due to the concentration of investments and infrastructure, although relevant studies have also been undertaken in other regions. Consequently, most research has been conducted in the Atlantic Forest and Cerrado biomes, while others, such as the Amazon, Pantanal and Pampa, remain underrepresented. Further studies of CHCs across all regions and biomes are needed, especially in areas where knowledge gaps persist and habitat loss is ongoing. Research in these regions could provide insights into the ways that different species can modulate their hydrocarbon profiles in response to environmental changes.

The methods for collecting and extracting CHCs varied among the studies, which could have influenced the observed diversity of the compounds, because different techniques and solvents extract compounds with varying characteristics. Moreover, studies involving samples from different biomes did not analyze CHCs separately, as this was not the focus of the research. This factor limited the ability to establish CHCs profiles according to biome. Nonetheless, when

analyzed in a standardized way and for the same objective, CHC profiles can be valuable tools for obtaining information about species diversity, relationships, and distributions.

Most studies have investigated the ways that CHCs are used in intra-colonial relationships, including the differences in the profiles of these compounds between castes. However, there have also been studies evaluating the effects of environmental factors on hydrocarbon profiles. The published results have shown that the cuticle composition is determined by complex interactions between environmental and genetic factors, associated with different strategies that are species-dependent. Despite the increase in publications over the years, studies about CHCs in ants in Brazil are still scarce, considering the importance of these compounds. Since CHCs reflect both genetic and environmental factors, they can be used as indicators of ecological impacts, as well as in species taxonomy and as tools in management strategies.

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# 08

# ADVANCES IN UNDERSTANDING THE MICROBIOTA OF ANTS IN BRAZIL: REVIEW AND FUTURE PERSPECTIVES

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# ABSTRACT

Since the advent of DNA sequencing and the introduction of new sequencing technologies such as Next Generation Sequencing, we have advanced our understanding of ants, including the host-microbe interactions maintained within their bacterial communities, sometimes spanning 50 million years. This significant advancement has been attributed to exploration of non-cultivable bacteria, yielding unprecedented data. Considering that Brazil harbors one of the world's largest ant diversities, exclusively unique biomes, it is expected that bacterial diversity is equally extraordinary. Thus, this study systematically reviews and shows meta-analysis aiming to provide a comprehensive view of ant microbiota in Brazil, identifying the studied ant species and genera, mapping the explored biomes, and delineating the functional traits of studied ants, ultimately outlining future perspectives. This includes identifying hotspots for subsequent studies, and identifying biomes that have not yet been investigated. This study, for the first time, highlights gaps in ant subfamilies/genera, and areas that are still under-investigated in the context of host-microbe interactions in Brazil. Results of this study reveal that bacterial community composition is significantly affected by biome, subfamily, and diet type, being the first study of its kind to do so on such a large scale. Additionally, it can serve as a guide for the myrmecology community to direct future microbiota studies, aiming to expand both the number of ant species and investigated locations. Furthermore, this study has the potential to unravel more about Neotropical microbiological diversity, contributing significantly to understanding the ecological and evolutionary mechanisms underlying ant-bacteria associations.

**Keywords:** Microbial ecology; neotropical insects; symbiosis; Formicidae; 16S rRNA gene.

## INTRODUCTION

Advancements in DNA sequencing technology and bioinformatics continue at an unprecedented pace, enabling us to uncover species interactions that were previously unidentified and poorly understood. This allows us to investigate interactions from the present, and from the deep evolutionary history of taxa. Ants serve as excellent models for investigating these interactions due to their global distribution and extraordinary diversity, encompassing more than 16,000 species that exhibit remarkable variation (HOLLDOBLER; WILSON, 1990). This includes individual and colony size, morphology, ecological roles, niche exploitation, and behavior. As one of the most ecologically successful insect groups, ants alone contribute to about 6% of the terrestrial arthropod biomass, approximately 33% more biomass than that of wild mammals and birds combined (HOLLDOBLER; WILSON, 1990; SCHULTHEISS *et al.*, 2022). Furthermore, their evolutionary history, spanning approximately 150 million years, is deeply intertwined with interactions involving other taxa (RUSSELL *et al.*, 2009; MOREAU, 2020).

It is well-established that bacteria can be both harmful and beneficial to their hosts, and ants are no exception. Bacteria provide various functions that support their ant hosts, including nutritional benefits. A well-known example is the long-standing association between ants of the Camponotini tribe and their bacterial symbiont *Blochmannia*, a relationship that has persisted for over 50 million years (RAMALHO *et al.*, 2018; RAFIQI *et al.*, 2020). Numerous studies have shown that many ant species rely on a diverse and functional bacterial symbiont community (RUSSELL *et al.*, 2012; MOREAU; RUBIN, 2017; MARTINS; MOREAU, 2020; RAMALHO; MOREAU, 2023). However, this dependence is not universal across all ants; for example, species within the genus *Crematogaster* do not appear to rely on functional bacterial communities (MOREAU 2020).

Brazil encompasses a vast array of biomes, including the Amazon Rainforest, Cerrado, Atlantic Forest, Caatinga, Pantanal, and Pampas, each hosting unique ecosystems and contributing to the country's status as one of the most biodiverse nations globally (MAKSIC *et al.*, 2022). Situated predominantly within the Neotropical region, Brazil's rich biodiversity is a result of millions of years of isolated evolution, leading to high levels of endemism (JOLY, 2008).


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Given the country's vast size and exceptional biodiversity, our understanding remains in its early stages, merely scratching the surface of the immense microbial diversity linked to these highly diverse ants. Since Brazil harbors one of the world's largest ant diversities and diverse biomes, including unique ones, bacterial diversity is expected to be equally extraordinary. Thus, this systematic review and meta-analysis aim to provide a comprehensive view of ant microbiota in Brazil, identifying the studied ant species and genera, mapping the explored biomes, and delineating the functional attributes of the studied ants, ultimately outlining future perspectives for this area. This includes identifying hotspots for subsequent studies and providing guidelines for collecting, analyzing, and presenting data to build a comparable database of ant-microbe interactions in Brazil. We hope this guides the myrmecology community in directing future microbiome studies and will contribute significantly to understanding the ecological and evolutionary mechanisms underlying ant-bacteria associations.

## METHODS

We conducted a systematic search for published studies that used NGS to do 16S rRNA amplicon metabarcoding (Supplementary Table 1[1] has a glossary with all the relevant terms we use) to identify the bacterial community of ants collected in Brazil. We searched Web of Science and Google Scholar without restricting the year of publication; studies from all publication years were considered. We used combinations of the following terms: 'Ants', 'Formiga', 'Formicidae', 'NGS', '16S rRNA', 'microbiota', 'bacterial communities', 'Brazil', and the names of Brazilian biomes (Atlantic Rainforest, Amazon Rainforest, Caatinga, Cerrado Savanna, Pampa, and Pantanal). We also looked in the references of these articles for more studies that we could have missed in our initial search. The inclusion criteria were: use of 16S rRNA metabarcoding through NGS techniques; collection of ant samples within Brazilian territory; bacterial data identified to at least the order level; and availability as published articles, articles

[1] https://figshare.com/articles/dataset/Supplementary_Material_Advances_In_Understanding_The_Microbiota_Of_Ants_In_Brazil_Review_And_Future_Perspectives/29795342?file=56832941.

in preparation by the authors of this study, or through direct contact with authors to confirm the origin of the samples. Authors of studies with partial sampling in Brazil were contacted to discriminate which samples were from Brazil and subsequently included in our analyses. The exclusion criteria were: studies on other microbial taxa (i.e., fungi), with other sequencing techniques (like Sanger sequencing), or outside of Brazil-although some with ant species also found in Brazil-were not included, and publications that analyzed bacterial taxa to a higher phylogenetic level than order (e.g., class, phylum). The last criterion led to the removal of Sanders *et al.* (2014) from the meta-analysis, but findings are still discussed (Supplementary Table 2[2]). The study selection process identified 12 manuscripts that met the inclusion criteria and were considered for the systematic review (Supplementary Table 2). The screening process involved reading the titles, abstracts, and then the full texts, conducted by all the authors. The data extraction and organization were based on the metadata from these studies. We compiled key functional traits into tables that included the analyzed ant genera and species or morphospecies, diet, nesting habit, biome (https://ecoregions.appspot.com/; DINERSTEIN *et al.*, 2017), habitat and locality, developmental stage, body part sampled, whether ants were maintained in the laboratory or collected from the wild, and the equipment and methodologies used for sequencing and bioinformatic analysis. Finally, we extracted the three most common bacterial orders associated with the core microbiota of the ants in each study. Each different observation, defined in this study as the significant presence of a bacterial order(s) within the composition of a bacterial community, within a study was entered as a separate row in the meta-data; i.e., one row in the meta-data represented one observation. Therefore, one study could contribute multiple observations (i.e., multiple rows) if it investigated multiple species, different body parts, habitats, localities, or other key functional traits.

In the meta-analysis, we used Pearson's $\chi 2$ to explore the associations among biome, subfamily, and diet type variables. Simulated p-values were generated through Monte Carlo simulation, with 5,000 replications

[2] https://figshare.com/articles/dataset/Supplementary_Material_Advances_In_Understanding_The_Microbiota_Of_Ants_In_Brazil_Review_And_Future_Perspectives/29795342?file=56832941.


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performed. To summarize bacterial order frequencies across subfamilies, diet types, and biomes, contingency tables were created to calculate relative abundances of observations and identify the top three most frequently reported bacterial orders across studies. All analyses were carried out using R software (R Development Core Team, 2023), utilizing the tidyverse (WICKHAM *et al.*, 2019), dplyr (WICKHAM *et al.*, 2023), and ggplot2 (WICKHAM, 2009) packages. The map of ant sampling localities was produced in QGIS 3.26.1 software and is divided into biomes according to the divisions of IBGE (Instituto Brasileiro de Geografia e Estatistica) (IBGE, 2025).

## RESULTS AND DISCUSSION

### The Current State of Brazilian Ant Microbiota Studies

Brazil is the epicenter of ant diversity, being in the top 10% of species richness globally across taxa (FEITOSA *et al.*, 2022). In addition to myrmecological diversity, Brazil hosts a notoriously wide variety of microorganism diversity (SANTOS *et al.*, 2024). Each biome plays a unique and pivotal role in biodiversity and climate regulation. The study of ant microbiota is relatively recent and geographically restricted in Brazil with 12 studies compiled in our systematic review, with the first article characterizing the ant microbiota published in 2014 (SANDERS *et al.,* 2014) and most of the sampling done in the Southeast region (Figure 1 and Supplementary Table 2). The range of habitats sampled in the Cerrado goes from pine reforestation forests to Cerrado *stricto sensu*, Cerradão, and the Campos Rupestres; the last three are natural physiognomies that are quite distinct from each other. On the other hand, the range of habitats sampled in the Atlantic Rainforest range from forests surrounding lake systems to Restinga forest, a type of lowland forest formation found right next to the sea in stretches of sand before the mountain ranges. Some specimens from the Brazilian Amazon, Caatinga dry forest, and Pampa grasslands were included in those widely distributed studies, with the exception of a study with *Paraponera clavata* which was restricted to the Amazon (MOREAU; RUBIN, 2017). In relation to wild or laboratory colonies, all 12 studies characterized the bacterial communities

of wild colonies of ants, while one also characterized a laboratory colony for comparison purposes (GIANARIS *et al.*, *in prep*).

## The Bacterial Communities of Brazilian ants

Five of the 12 subfamilies found in Brazil have been studied: Dolichoderinae, Formicinae, Myrmicinae, Paraponerinae, and Ponerinae. Although Formicinae and Myrmicinae are the most common ant subfamilies observed in Brazil (Figure 2), the majority of studies focus on Myrmicinae, the largest ant subfamily worldwide (BOLTON, 2022). Myrmicinae remarkably displays evolutionary adaptation, with species within this subfamily found to have nuanced social structures such as the highly conserved subcaste divisions, detailed behavior regimens, and complex nest structures of *Atta* (DELLA-LUCIA; GANDRA; GUEDES, 2013; CALHEIROS *et al.*, 2019) and *Cephalotes* spp. (GORDON *et al.*, 2019; OLIVEIRA *et al.*, 2021). Less studies focused on subfamilies such as Ponerinae, Paraponerinae, and Dolichoderinae. Our results identified association with ant subfamilies studied with biome distribution (p-value < 2.2e-16; Pearson's Chi-squared test).

**Figure 1 -** Map of sampling localities obtained from the reviewed ant microbiota studies in Brazil. The sampled genera are identified with different dot colors and the Brazilian biomes are seen in the background. The four genera in white were sampled at the same location.

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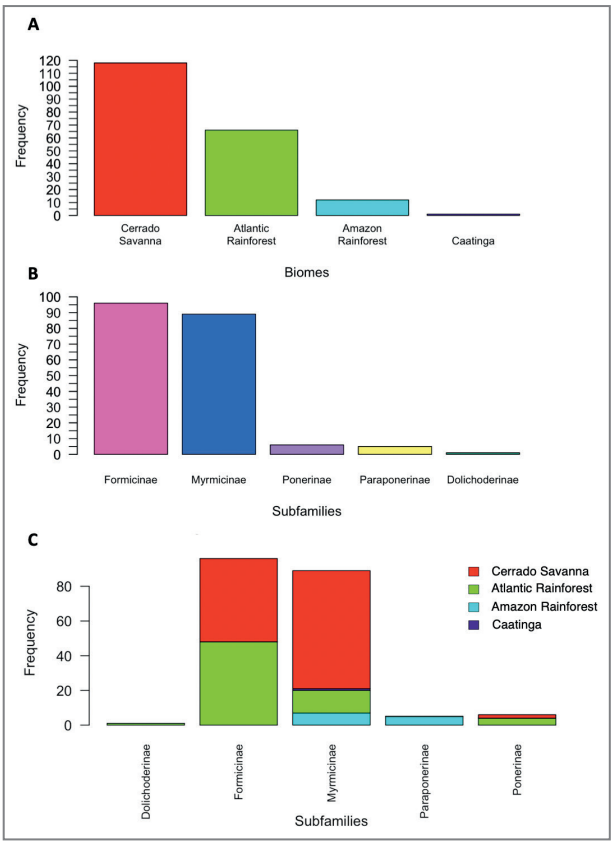
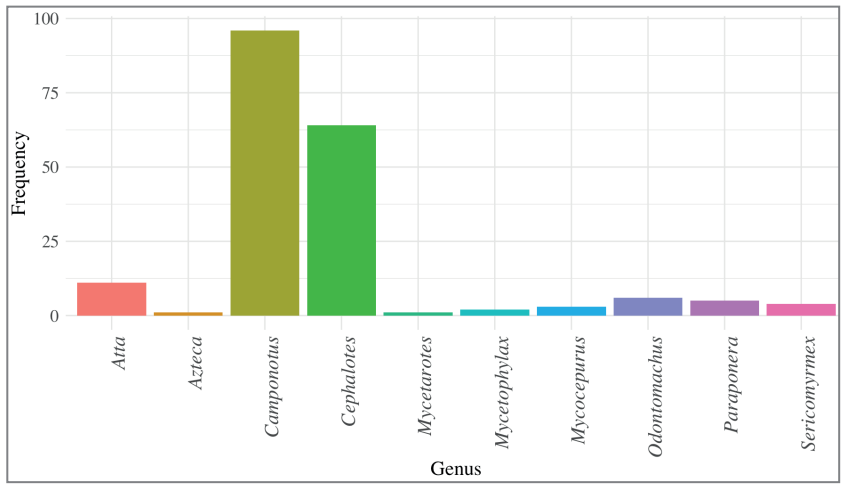
**Figure 2 -** Frequency of biome and subfamily observations within ant-microbiome studies across Brazil **A.** Distribution of ant-microbiome studies focusing on biome frequency across Brazil. The bar graph represents the number of observations present from studies in each biome. **B.** Distribution of subfamilies reported in bacterial diversity studies across Brazil in review. **C.** Distribution of subfamilies across different biomes in bacterial diversity studies from Brazil in review. The stacked bar graph shows frequency of each subfamily in the Cerrado Savanna, Caatinga, Atlantic Rainforest, and Amazon Rainforest.




Of the 117 genera found in Brazil (BOLTON, 2022), there are 12 genera of ants with their microbiota studied: *Atta, Azteca, Camponotus, Cephalotes, Crematogaster, Mycetarotes, Mycetophylax, Mycocepurus, Odontomachus, Paraponera, Pseudomyrmex,* and *Sericomyrmex* (Figure 3 and Supplementary Table 2). The studies covered 56 species, 1 subspecies, and 14 morphospecies (Supplementary Table 2) from a total of 1,684 species found in Brazil (BOLTON, 2022).

**Figure 3 -** Frequency of genera observations in bacterial diversity studies across Brazil in review. The bar chart reads from most frequently observed (*Camponotus*) to least frequently observed (*Mycetarotes*).




By exploring how bacterial diversity is distributed through different ant subfamilies and biomes, we can start to unravel connections between resource availability, potential environmental stressors impacting observations and subsequent types of interactions with hosts and functions they may have.

As important as investigating the influence of phylogenetic history in host-associated bacterial community structure, researchers were also concerned in relating different functional or ontogenetic attributes of ants to their bacterial communities, including their diet, body parts, castes, and development stages.

Six studies investigated the worker as a whole; two the cuticle; two the gut; four investigated the gaster as a proxy for the gut community; one divided the worker into its three main body parts (head, mesosoma, and gaster); and finally, one study investigated the queen postpharyngeal gland and midgut. As studies had multiple foci, the numbers found here are greater than the number of studies. All these divisions serve different purposes in these studies as they focus on the acquisition and maintenance of bacterial communities from the environment, from social interactions, and from diet. In relation to castes and development stages, all studies focused on adult workers, apart from one study that included all castes and immature stages beyond the workers (HU *et al.*, 2023).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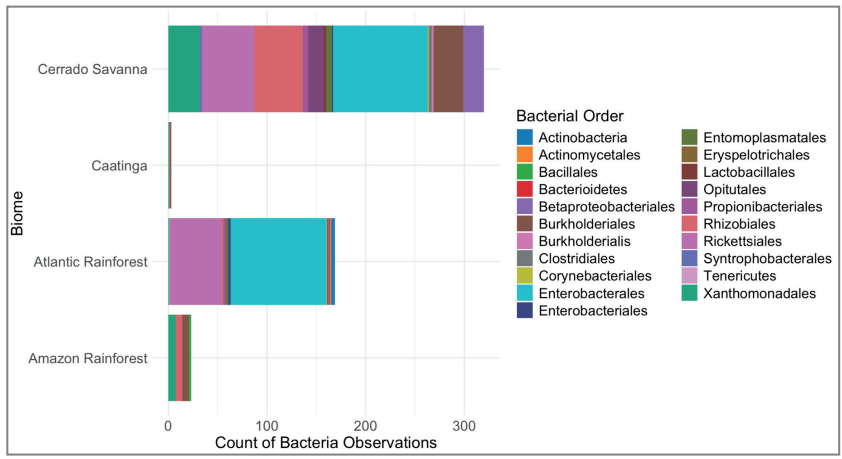
Finally, while most studies used the Illumina platform to conduct their sequencing (nine out of 12), there were two studies that used 454 pyrosequencing, and one that used Ion Torrent.

**Bacterial communities within Biomes, Subfamilies, and Diet**

The observations of each ant species across all studies were compared to find any significant correlation between biome, subfamily and diet type.

The four biomes explored across all studies were the Cerrado Savanna; Atlantic Rainforest; Amazon Rainforest; and Caatinga (Figure 4). The most common biome studied was the Cerrado Savanna and the most infrequently studied biome was the Caatinga, besides Pantanal, and Pampas with no data. There was a significant correlation found between ant bacteria observations and biome (Chi-Square Test, X-square = 226.37, df = 60, p-value < 2.2e-16). A contingency table reveal that the most bacterial diversity (with 17 bacterial orders found in total) was found in the Cerrado Savanna with the three most common bacterial orders being Enterobacterales (29%), Rickettsiales (16%), and Rhizobiales (15%). The Atlantic Rainforest was the second most diverse biome with 15 different bacterial orders found across observations. Enterobacterales comprises 57% of observations in the Atlantic Rainforest followed by Rickettsiales (31%), and Actinomycetales (2%). The only observation from the Caatinga presented Burkholderiales, Rhizobiales, and Xanthomonadales. These are bacteria commonly found in ants, such as the *Cephalotes* (FLYNN *et al.*, 2021;GRABER *et al.*, 2023; RAMALHO; MOREAU, 2023). This showcases the importance of future research within the least studied biomes, like the Caatinga.

**Figure 4 -** Bacterial order observations in biomes, Amazon Rainforest, Atlantic Rainforest, Caatinga, and Cerrado Savanna, reported in studies across Brazil. Significant correlation found between observation composition and biome type (Chi-Square Test, X-square = 226.37, df = 60, p-value < 2.2e-16).




Enterobacterales was found to be most observed in both the Cerrado Savanna and Atlantic Rainforest. This may be due to Enterobacterales being the bacterial order for *Blochmannia* which is highly observed in *Camponotus* ants which reside in both biomes, serving as the primary symbiont involved in nitrogen recycling (CHANSON; MOREAU; DUPLAIS, 2023). *Blochmannia*, a well-known ant symbiont, vertically transferred to offspring, important to Camponotini ant development (RAMALHO *et al.*, 2018; RAFIQI *et al.*, 2020). This vertical transfer of the endosymbiont eventually results in *Blochmania* becoming a part of the midgut epithelium of *Camponotous* (RAFIQI; RAJAKUMAR; ABOUHEI, 2020) and is essential in nutrient metabolism, important to offspring survival and host development throughout the Camponotini tribe (DEGNAN *et al.*, 2004; WERNEGREEN *et al.*, 2009; RAMALHO *et al.*, 2018; JACKSON *et al.*, 2022; WANG *et al.*, 2022). In the Camponotini tribe, *Blochmannia* is also linked to decreased efficacy in raising larvae to pupae when eliminated with antibiotic treatment, presenting a trade-off between essential nutrients for development and rearing young (ZIENTZ *et al.*, 2006; PREUSS *et al.*, 2023).

Rickettsiales, the second most observed order in the Atlantic rainforest, is an order of the genus *Wolbachia*, another symbiont unknown in its exact functional role. Rickettsiales and *Wolbachia* still remain enigmatic in function to

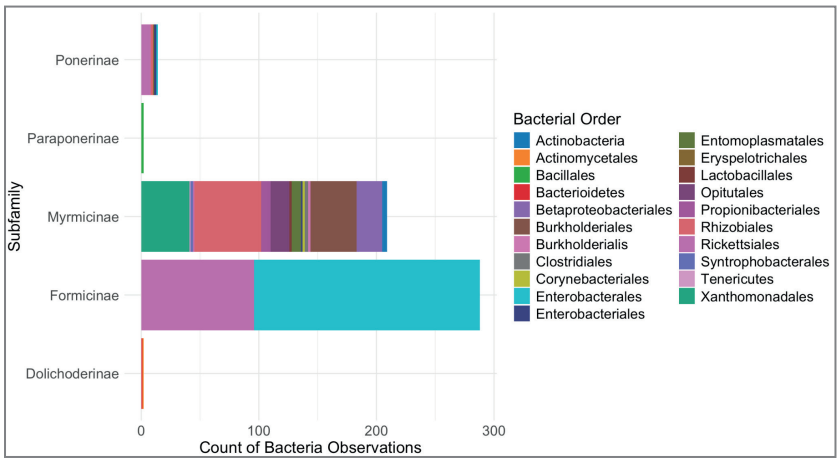
their host with theorized nutritional value to host, potentially in vitamin B supplementation when in higher abundance (ANDERSEN *et al.*, 2012; CHENG *et al.*, 2019). Phylogenetic analysis shows that Rickettsiales is interestingly aquatic in origin with adaptive shifts to terrestrial based habitats (SCHÖN *et al.*, 2022). Rickettsiales has not always been involved in mutualism independently evolving to be a part of insect-bacteria interactions. The origin of this is thought to be related to evolution of Rickettsiales living in protist-associated ancestors and over time, transitioning to insects and mammals as symbionts (SCHÖN *et al.*, 2022). In Camponotini, *Wolbachia* has a prominent presence in *Polyrhachis* and *Camponotus* resulting from vertical transmission (RAMALHO *et al.*, 2018; RAMALHO; MOREAU, 2020; WEBB *et al.*, 2023). *Wolbachia* has been found absent from the germarium, the region of egg cell formation during the start of oogenesis. This indicates that to ensure next generation transmission, the bacterium must follow an alternate route to reach the nurse chamber later on (RAMALHO *et al.*, 2018).

*Wolbachia* has been found in abundance in *Cephalotes* species (KELLY *et al.*, 2019; FLYNN *et al.*, 2021) and in traces of attine species across *Atta* (VAN BORM *et al.*, 2001) and *Acromyrmex* (ANDERSEN *et al.*, 2012; SAPOUNTZIS *et al.*, 2015). In *Acromyrmex* species, *Wolbachia* was highly abundant and free-living in the foregut, which supports a mutualistic role of *Wolbachia* (SAPOUNTZIS *et al.*, 2015). When deprived of fungal gardens, *Wolbachia* was virtually eliminated from the bacterial community composition of *Acromyrmex octospinosus* (which typically present *Wolbachia* in fecal droplets), suggesting a mutualistic role in fungal cultivation and relation to diet (ANDERSEN *et al.*, 2012; SAPOUNTZIS *et al.*, 2015). *Aphaenogaster* in North America was highly infected with several strains of *Wolbachia* (KELLEHER; RAMALHO, 2025), although we still don't know the impact of *Wolbachia* associated with the majority of the ant diversity (RAMALHO; MOREAU, 2020). Interestingly, this meta-analysis does not show Rickettsiales as one of the top three most abundant bacteria taxa in fungivores in this study nor within the subfamily Myrmicinae where fungivores (leaf cutting ants) samples are from. Rickettsiales was, however, found to be most abundant in the Atlantic Rainforest and Cerrado Savanna, the environment of many fungivores and Myrmicinae samples in this study. This stresses the importance of

further research of environmental and biome effects on Ricketiales and *Wolbachia* in observations.

The five subfamilies present across all studies were Formicinae, Myrmicinae, Ponerinae, Paraponerinae and Dolichoderinae (Figure 5). The most common subfamily studied was Formicinae, and the fifth and least most commonly studied was Dolichoderinae. There was a significant correlation found between bacteria observations and subfamily (Chi-Square Test, X-square = 1605.9, df = 88, p-value < 2.2e-16). A contingency table revealed that the highest bacterial diversity (with a total of 18 bacterial orders found in total) was found in the Myrmicinae subfamily with the three most common bacterial orders being Rhizobiales (26%), Xanthomonadales (19%), and Burkholderiales (16%) in order of highest to lowest abundance among observations studied. All herbivorous ants reviewed in this study belong to the Myrmicinae subfamily, which may help explain the observed abundance of Xanthomonadales (present in 23% of herbivorous samples) across both herbivores and Myrmicinae.

**Figure 5 -** Bacterial order observations in subfamilies Formicinae, Myrmicinae, Ponerinae, Paraponerinae and, Dolichoderinae, reported in studies across Brazil. Significant association found between bacteria observations and ant subfamily (Chi-Square Test, X-square = 1630.6, df = 80, p-value < 2.2e-16).




Betaproteobacteriales has been associated closely with the order Burkholderiales (RAMALHO; MOREAU, 2023). Significant presence of Burkholderiales has been found in the abdomens of attine species, *Acromyrmex coronatus,*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*Atta sexdens,* and *Atta laevigata* (ZANI *et al.*, 2021), as well as in *Atta colombica* dumps collected in a moist subtropical biome (LEWIN *et al.*, 2016). This order has been strongly associated with bacterial communities of fungi, serving as a fungal endohyphal symbiont (PARTIDA-MARTINEZ *et al.*, 2007), and found to control fungal reproduction (MONDO *et al.*, 2017; OKRASINSKA *et al.*, 2021). The results of this study show significant observations of Burkholderiales in herbivores, Myrmicinae subfamily, and Caatinga biome.

The subfamily with the second highest bacterial diversity was the Ponerinae subfamily, with five different bacterial orders observed, although it is the second-most underrepresented subfamily among all 12 papers analyzed in this study. Rickettsiales comprised the majority (57%) of observations within the Ponerinae subfamily followed by Enterobacterales (14%), and Rhizobiales (14%). The most common subfamily studied, Formicinae, was not found to be very diverse with only 2 different bacterial orders observed: Enterobacterales (67%) and Rickettsiales (33%) - *Blochmannia* and *Wolbachia*.

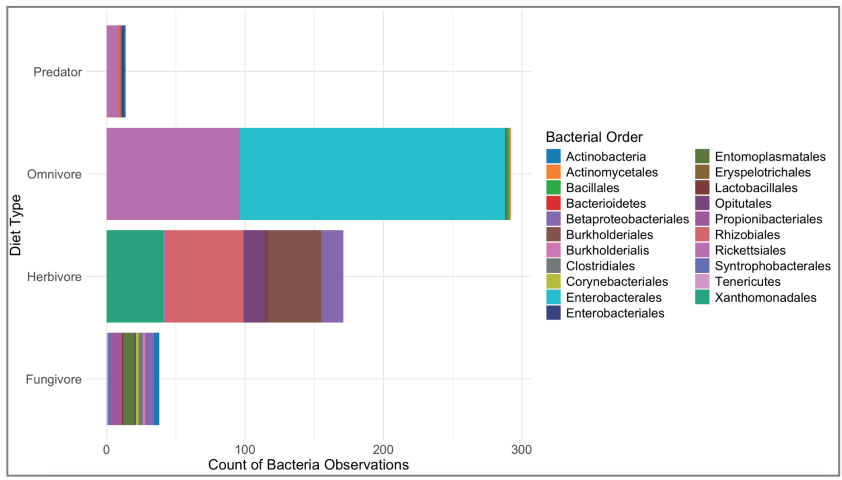
The fifth and least studied subfamily, Dolichoderinae, had only two different bacterial orders observed. While Dolichoderinae ants in this study are omnivorous, the only genus of this subfamily observed, *Azteca,* is well-known to have a mutualistic relationship with fungal mycelium for nest structures (VASSE *et al.*, 2017; DEJEAN *et al.*, 2023). Actinomycetales was observed in all *Azteca* observations present in the study. Although the majority of Actinomycetales microbes are free living, this order has a rich history with mutualism. In ants, Actinomycetales have an established mutualism (LI *et al.*, 2018; DIARRA; OSBORNE-NAIKATINI; SUBRAMANI, 2024). This may be due to the antibiotic producing benefits of this bacterial order, contributing to overall host immunity and defence against parasites (KOEHLER, 2014; DOUGLAS, 2015).

The subfamily with the lowest bacterial diversity was Paraponerinae, with only Bacillales and Erysipelotrichales orders present in over 50% of samples (MOREAU; RUBIN, 2017). Bacillales have previously been strongly associated with fungivores and are theorized to have mutualistic function to *Atta* and *Acromyrmex* spp. (SCOTT *et al.*, 2010; VIEIRA *et al.*, 2017). Erysipelotrichales is a common order found in animal guts, including other predatory and omnivorous ants (LUKASIK *et al.*, 2017; ROCHA *et al.*, 2023). However, its role in ants, if there is any, is still unknown. Further research is needed to understand the

host-symbiont association present, or absent (HAMMER; MORAN, 2019), in this unique subfamily.

The four diet types present across all studies were fungivore, herbivore, omnivore, predator (Figure 6). The most common diet type present among studies was omnivores comprising 102 observations separated by species and body part of ant studied. Herbivore diet types comprised 68 observations, fungivores comprised 21 observations, and the rarest diet type was predator, with only 6 observations. There was a significant correlation found between bacteria observed and diet type (Chi-Square Test, X-square = 1026.3, df = 60, p-value < 2.2e-16). A contingency table revealed that the most bacterial diversity (with 11 bacterial orders found in total) was found in observations belonging to fungivores, with the three most common bacterial orders being Entomoplasmatales (21%), Propionibacteriales (21%), and Betaproteobacteriales (16%) in order of highest to lowest abundance among observations studied.

**Figure 6 -** Bacterial order distribution in diet types fungivore, herbivore, omnivore, predator, reported in studies across Brazil. Significant correlation found between bacteria observations and ant diet (Chi-Square Test, X-square = 1026.3, df = 60, p-value < 2.2e-16).




Entomoplasmatales is strongly suggested to be correlated to fungus mutualism and present as a top three driver in the bacteria observations of fungivores. Research corroborates this idea, with high abundance in *Atta sexdens rubropilosa* queens (VIEIRA *et al.*, 2017) and *Atta sexdens* workers (RAMALHO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*et al.*, 2020; GIANARIS *et al.*, *in prep*) suggested to play a role in lipid metabolism (DECIO *et al.*, 2016; VIEIRA *et al.*, 2017) and chitin processing (SAPOUNTZIS *et al.*, 2018; ZHAO; ZHANG.; ZHU, 2019). Other studies, however, suggest that Entomoplasmatales is related to a carnivorous diet among Paraponerinae (genus *Paraponera*); Ponerinae (genera *Anochetus, Neoponera,* and *Odontomachus*); and Dorylinae (genera *Eciton* and *Labidus*) subfamilies (CHANSON; MOREAU; DUPLAIS, 2023). Evidence from Sapountzis *et al.* (2019) shows that the presence of Entomoplasmatales is associated with the predatory attine *Paratrachymyrmex cornetzi*, and further suggests that Entomoplasmatales may function in chitin processing for both predators, feeding on insects with chitinous cuticles, and fungivores, consuming chitin-rich fungal cell walls. The lack of high abundance of this order in predator diets in this study suggests that future research is important to explore the function in chitin processing further.

The function of Propionibacteriales is unknown and only recently discovered to be found in observations of *Atta* ants (GIANARIS *et al.*, *in prep*). This order has only been found in fungal gardens of lower attines but not in their observations (MA *et al.*, 2023). Propionibacteriales may be involved with propionic acid production in mammal gastrointestinal tracts, identified as anti-inflammatory for mammal gut health (GRINSTEAD; BAREFOOT *et al.*, 1992). There is much still to unravel about the presence of this order; more studies need to be conducted to explore its presence in fungivore diet types and environmental effect (PLÉ *et al.*, 2016).

Betaproteobacteriales was found to be prevalent in fungivores in this study, found as a top three most observed bacteria within this diet type. The function of this order remains unclear, however Betaproteobacteriales has been found in high relative abundance in fungus mutualistic *Atta* species (GIANARIS *et al.*, *in prep*). Betaproteobacteriales has also been found prevalent in *Bolitophagus reticulatus*, a frugivorous beetle (KACZMARCZYK-ZIEMBA *et al.*, 2019). Significant observations of this bacterial order outside of fungivorous organisms were found within guts of herbivorous (POTTER; HELD, 2002), Japanese beetle *Popillia japonica* (AVILA-ARIAS *et al.*, 2022) as well as caterpillars, whose gut bacterial communities were found to reflect the microbial composition of their surrounding soil environment (GOMES *et al.*, 2020).

The second most diverse diet type was herbivores with 9 different orders observed and Rhizobiales being the most abundant, present in 31% of herbivore observations, followed by Xanthomonadales (23%), and Burkholderiales (20%). Rhizobiales has strong links to herbivory across a wide range of ant genera notably including *Cephalotes*, *Dolichoderus*, *Procryptocerus*, and *Pheidole* (RUSSELL *et al.*, 2009; REEVES *et al.*, 2020; ZHUKOVA *et al.*, 2022). The order Rhizobiales is agriculturally salient, especially in roots of crops (ESCOBAR *et al.*, 2018), known to provide function in recycling nitrogenous waste products (GARRIDO-OTER *et al.*, 2018; ZHUKOVA *et al.*, 2022). Recent studies have shown a significant difference in the presence of Rhizobiales in host plants that have a parasitic relationship with *Liriomyza* (GAO *et al.*, 2024) and *Meloidogyne* (LI *et al.*, 2023). These two pest types have been shown to be rampant parasitising crops broadly across Brazil (CARNEIRO *et al.*, 2014; SOUSA *et al.*, 2022), perhaps providing a connection to the significance of this order in herbivore nutrient sources.

While Rhizobiales has also been well documented in fungus farming ants such as *Atta* and *Acromyrmex* ants (PINTO-TOMÁS *et al.*, 2009; SAPOUNTZIS *et al.*, 2015; ZHUKOVA *et al.*, 2022), the function of Rhizobiales found in herbivorous ants seems to differ slightly in nitrogen recycling function. Rhizobiales in herbivorous ants has been found to provide arginase and urease, producing ammonia (ZHUKOVA *et al.*, 2022). This allows for usage of ammonia for nitrogen source, supplementing the nitrogen-poor diet in herbivores (RUSSELL *et al.*, 2009; ZHUKOVA *et al.*, 2022). In fungus farming ants, urease genes have been discovered to be lost (ZHUKOVA *et al.*, 2022). Fungivore ants source arginine from their fungal symbiont, *Leucoagaricus gongylophorus*, and instead release urea, less harmful than ammonia to the symbiont (ZHUKOVA *et al.*, 2022). The presence of Rhizobiales in fungivores has therefore been suggested to serve as a backup-mechanism to process excess arginine (ZHUKOVA *et al.*, 2022). This bacteria has also been documented in predatory ants (NEUVONEN *et al.*, 2016; RAMALHO *et al.*, 2020; ZHUKOVA *et al.*, 2022).

Xanthomonadales has been found to be highly associated with herbivorous ants (KAUTZ *et al.*, 2013; CHANSON; MOREAU; DUPLAIS, 2021; FLYNN *et al.*, 2021; CHANSON; MOREAU; DUPLAIS, *et al.*, 2023; RAMALHO; MOREAU, 2023). Xanthomonadales is notable in its abundance within *Cephalotes* and lower in attine workers (KELLNER *et al.*, 2015). Xanthomonadales has been theorized to be


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involved with nitrogen recycling from its presence alongside other nitrogenous recycling bacterial orders (CHANSON; MOREAU; DUPLAIS, 2023).

The least diverse diet types with 5 bacterial orders observed among each were omnivore and predator. Omnivore diet types had a large presence of Enterobacterales being present in 66% of omnivore observations followed by Rickettsiales (33%), and Bacillales (1%). *Blochmannia*, a well-known endosymbiont within order Enterobacteriales, may be a source of nitrogen in ants from an omnivorous diet. *Camponotus* ants have an omnivorous diet and often will have arthropods (FELDHAAR *et al.*, 2007) in their diet, which are a nitrogenous source. In *Camponotus*, genes for urease in *Blochmannia* has been found in fact, perhaps suggesting that *Blochmannia* is serving the host in nitrogen recycling function, aiding in the metabolism of urea to avoid urea toxicity (DEGNAN *et al.*, 2004; WERNEGREEN *et al.*, 2009). *Camponotus* suggests having a longstanding relationship with *Blochmannia* originated more than 45 million years ago, being phylogenetically conserved (WERNEGREEN *et al.*, 2009) and reliant on its host (KIERSTEAD, 2023). The most common bacterial order in predator diet types was Rickettsiales (57%), followed by Enterobacteriales (14%), and Rhizobiales (14%).

## BEST PRACTICES AND FUTURE DIRECTIONS

### Best Practices for Future Studies

Due to the paucity of data regarding the ant microbiota in Brazil, and the expected growing interest in the topic - driven by decreasing costs and greater accessibility to equipment, methods, and analysis pipelines; we would like to offer guidelines for metadata collection and results presentation. We hope these guidelines allow future systematic comparisons, like this one, with greater data to answer the hardest questions on host-microbe interactions, microbial ecology, and the evolution and co-evolution of symbiosis.

Previous articles have reviewed a list of practices and considerations when designing or executing research (POLLOCK *et al.*, 2018; DADA *et al.*, 2021; COMBRINK *et al.*, 2023). These should be considered standard for developing the field in Brazil and for future comparisons of the Brazilian ant microbiota. Focused on mosquito communities, Dada *et al.*, (2021) provide a complete list

of important metadata to collect during a field or laboratory-based study. These considerations can mostly be followed by ant researchers when thinking about their study design and execution. However, attention must be paid to taxa-specific details to answer your questions properly. This includes the particularities of ants' nesting and feeding habits (i.e., soil in different depths, hollow stems, domatia, leaves, roots, fungus gardens, extrafloral nectaries, etc.), which might impact how you include environmental controls in your design. Furthermore, particularities of their sociality should be considered when thinking about replication and hypotheses to test. For example, ants have different castes, polygyny, polydomy, grooming, and trophallaxis to consider; thus, replication within and between colonies should be considered.

Apart from these considerations, we want to stress the importance of giving the most complete details possible from the data and metadata in your publications. Finally, consider the proper processing and statistical analyses for your questions (PALIY; SHANKAR, 2016).

## Future directions

Brazil's biodiversity is disappearing at an alarming rate, outpacing our ability to study and understand it. The country is home to a vast diversity of ants and bacteria, many of which remain undescribed. To prevent irreversible losses, conservation efforts must prioritize protecting these ecosystems before species vanish. Additionally, future studies should explore uncharted ant biomes and genera, which could offer valuable insights into the complex interactions between ants and their microbial partners.

Two complementary directions could enhance our understanding of ant--bacteria diversity. Firstly, researchers should delve into ant genera and species that exhibit restricted distribution ranges, unique functional traits, or distinct phylogenetic histories — particularly those endemic to Brazil — as these could provide valuable insights into diet specialization, functional or phylogenetic correlations, and ant–bacteria coevolution. Conversely, exploring the common ants with wide distributions is an opportunity to research the importance of bacterial communities to their widespread hosts, as well as possible trade-offs


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from harboring bacteria, and the importance of environmental and genetic factors in determining the structure of these communities.

Given Brazil's rich biodiversity and varied biomes, which serve as potential research hotspots, numerous ecological and evolutionary questions arise. Are there any specific ASVs or groups of ASVs that have co-evolved with particular ant groups? Do certain ant taxa exhibit independence from or reliance on bacteria? Additionally, do particular biomes (dry forests, wet forests, savannas, grasslands) or microhabitats (hypogeic, epigeic, canopy, domatia) favor specific types of bacteria or interactions with bacteria, indicating convergence patterns, or is the distribution random? Furthermore, while herbivorous ants are known to rely on bacteria, exploring the microbiota of other functional groups, such as predators and fungivores, is equally crucial to understand diet-related patterns in ant-bacteria interactions.

Finally, exploring the potential of utilizing ant microbiota as a supplementary data source for ant taxonomy in Brazil, especially in cases involving cryptic species or species complexes, could offer new avenues for research. Although the microbiota might be less efficient than genetic or genomic information in these scenarios, interesting findings could arise for the ant taxonomy and the microbial ecology fields.

## CONCLUSIONS

This systematic review and meta-analysis provided a comprehensive and unprecedented overview of the current state of the knowledge on the bacterial microbiota associated with Brazilian ants. We compiled 12 studies published since 2014, identifying a strong concentration of the studies in the Southeast, and predominance of studies on the Myrmicinae subfamily. Notably, only a fraction of genera and biomes have been investigated, with gaps in the Caatinga, Pantanal, and Pampa biomes. Our findings reveal that bacterial community composition is significantly affected by biome, subfamily, and diet type. This study is the first of its kind to do so on such a large scale, providing a guide for the myrmecology community to direct future microbiota studies.

Despite Brazil's unparalleled ecological wealth - encompassing its vast ant diversity, microbial communities, and dynamic ecosystems - these biological

treasures remain under perpetual threat from habitat degradation and climate change. Safeguarding Brazil's biodiversity is not merely a function of conservation but crucial for advancing scientific discovery. Ant-microbe interactions hold profound insights into evolutionary biology and ecological resilience- insights that may remain undiscovered if unprotected. By fostering international collaboration, preserving Brazil's ecosystems will shape the future of global scientific research and discoveries for generations to come.

## Tables and Figures

**Supplementary Table 1 -** Glossary of relevant terms.

| Term | Definition |
|---|---|
| **Amplicon** | A fragment of DNA or RNA amplified naturally or artificially with a specific primer set using, for example, PCR (Combrink *et al.,* 2023). |
| **ASV** | Amplicon Sequence Variant - individual sequences that differ from others by as little as one nucleotide with no fixed dissimilarity threshold but frequently 1% of dissimilarity. See also OTU (Weinroth *et al.,* 2022). |
| **Core microbiota** | Members of a microbial community shared by particular habitats and are important for understanding the system's properties, like stability, plasticity, and functioning (Berg *et al.,* 2020). |
| **Marker gene** | A gene used in broad sequencing studies for its benefits, like broad prevalence in the studied taxa and low mutation rate. One example is the 16S rRNA gene of bacteria. |
| **Metabarcoding** | The technique is used to sequence the marker gene of the whole community of a sample at the same time (i.e., soil, water, tissue, organism). See also 'Metataxonomics' in Marchesi & Ravel (2015). |
| **Microbiota** | The community of microbial organisms in an environment or sample, including protozoans, fungi, bacteria, and viruses (Marchesi & Ravel, 2015). Used sometimes as a synonym for the bacterial community of an organism or sample. |
| **Microbiome** | The microbiome is a microbial community in a well-defined habitat and its specific physio-chemical properties (Berg *et al.,* 2020). |
| **NGS** | Next Generation Sequencing - the generation of parallel sequencing techniques that can produce millions of amplicon sequences per run, like Illumina, Ion Torrent, and others. (Slatko *et al.,* 2018). |
| **OTU** | Operational Taxonomic Unit - sequencing reads that differ from each other by less than a fixed dissimilarity threshold. Usually, 3% of dissimilarity is used. See also ASV (Weinroth *et al.,* 2022). |
| **Observation** | In this study, an 'observation' refers to the significant presence of a bacterial order(s) within the composition of a bacterial community. Bacterial communities were separated by species, different body parts, habitats, localities, etc., or all of the above. One row in the meta-data represented one observation. Therefore, one study would have multiple rows of observations if it investigated multiple species, different body parts, habitats, localities, others, or all of the above. |


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**Supplementary Table 2 -** Complete list of subfamilies, genera, and species reported in Brazilian ant microbiota publications. The table includes all ant taxa compiled from the 12 references that met inclusion criteria for our bacterial observational analysis, plus one additional reference (*) that was excluded from analysis due to bacterial data not being resolved to at least the order level. This reference is included here to provide a comprehensive taxonomic overview.

| Subfamily | Genus | Species | No. of studies | Reference |
|---|---|---|---|---|
| Dolichoderinae | *Azteca* | *Azteca chartifex* | 1 | Bitar *et al.* (2023). |
| | | *Azteca* sp. | 1 | Sanders *et al.* (2014).* |
| Formicinae | *Camponotus* | *Camponotus atriceps* | 1 | Ramalho *et al.* (2019). |
| | | *Camponotus balzani* | 1 | |
| | | *Camponotus blandus* | 1 | |
| | | *Camponotus renggeri* | 1 | |
| | | *Camponotus rufipes* | 1 | |
| | | *Camponotus senex* | 1 | |
| | | *Camponotus sericeiventris* | 1 | |
| | | *Camponotus* sp. 2 | 1 | |
| | | *Camponotus* sp. 3 | 1 | |
| | | *Camponotus* sp. 4 | 1 | |
| | | *Camponotus* sp. 5 | 1 | |
| | | *Camponotus* sp. 7 | 1 | |
| | | *Camponotus* sp. 9 | 1 | |
| | | *Camponotus substitutus* | 1 | |
| | | *Camponotus textor* | 1 | |
| | | *Camponotus vittatus* | 1 | |

| Subfamily | Genus | Species | No. of studies | Reference |
|---|---|---|---|---|
| Myrmicinae | *Atta* | *Atta bisphaerica* | 1 | Gianaris *et al. (in prep).* |
| | | *Atta capiguara* | 1 | Gianaris *et al. (in prep).* |
| | | *Atta laevigata* | 1 | Gianaris *et al.* (in prep). |
| | | *Atta sexdens* | 2 | Ramalho *et al.* (2020); Gianaris, Ramalho *et al.* (*in prep*). |
| | | *Atta sexdens rubropilosa* | 1 | Vieira *et al.* (2017). |
| | *Cephalotes* | *Cephalotes adolphi* | 1 | Ramalho & Moreau (2023). |
| | | *Cephalotes angustus* | 1 | Ramalho & Moreau (2023). |
| | | *Cephalotes* sp. angustus-group | 1 | Graber *et al.* (2023). |
| | | *Cephalotes*<br>*Cephalotes atratus* | 3 | Graber *et al.* (2023); Ramalho & Moreau (2023); Sanders *et al.* (2014).* |
| | | *Cephalotes betoi* | 2 | Graber *et al.* (2023); Ramalho & Moreau (2023). |
| | | *Cephalotes borgmeieri* | 1 | Sanders *et al.* (2014).* |

| Subfamily | Genus | Species | No. of studies | Reference |
|---|---|---|---|---|
| Myrmicinae | *Cephalotes* | *Cephalotes clypeatus* | 2 | Ramalho & Moreau (2023); Sanders *et al.* (2014).* |
| | | *Cephalotes cordatus* | 1 | Ramalho & Moreau (2023). |
| | | *Cephalotes depressus* | 3 | Graber *et al.* (2023); Hu *et al.* (2022); Ramalho & Moreau (2023). |
| | | *Cephalotes eduarduli* | 3 | Graber *et al.* (2023); Ramalho & Moreau (2023); Sanders *et al.* (2014).* |
| | | *Cephalotes grandinosus* | 4 | Graber *et al.* (2023); Hu *et al.* (2022); Ramalho & Moreau (2023); Sanders *et al.* (2014). |
| | | *Cephalotes incertus* | 1 | Ramalho & Moreau (2023). |
| | | *Cephalotes laminatus* | 1 | Ramalho & Moreau (2023). |
| | | *Cephalotes liepini* | 2 | Graber *et al.* (2023); Ramalho & Moreau (2023). |
| | | *Cephalotes maculatus* | 4 | Graber *et al.* (2023); Hu *et al.* (2022); Ramalho & Moreau (2023); Sanders *et al.* (2014).* |
| | | *Cephalotes minutus* | 2 | Ramalho & Moreau (2023); Sanders *et al.* (2014). |
| | | *Cephalotes monicaulyssea* | 1 | Graber *et al.* (2023). |
| | | *Cephalotes nilpiei* | 2 | Graber *et al.* (2023); Ramalho & Moreau (2023). |
| | | *Cephalotes notatus* | 1 | Ramalho & Moreau (2023). |
| | | *Cephalotes opacus* | 1 | Ramalho & Moreau (2023). |
| | | *Cephalotes pallens* | 1 | Sanders *et al.* (2014).* |
| | | *Cephalotes* sp. pallens-group | 1 | Ramalho & Moreau (2023). |
| | | *Cephalotes pallidoides* | 1 | Ramalho & Moreau (2023). |
| | | *Cephalotes palta* | 1 | Ramalho & Moreau (2023). |
| | | *Cephalotes pavonii* | 1 | Ramalho & Moreau (2023). |

| Subfamily | Genus | Species | No. of studies | Reference |
|---|---|---|---|---|
| Myrmicinae | *Cephalotes* | *Cephalotes pellans* | 2 | Ramalho & Moreau (2023); Sanders *et al.* (2014).* |
| | | *Cephalotes persimilis* | 3 | Graber *et al.* (2023); Ramalho & Moreau (2023); Sanders *et al.* (2014).* |
| | | *Cephalotes pilosus* | 1 | Ramalho & Moreau (2023). |
| | | *Cephalotes pinelii* | 2 | Graber *et al.* (2023); Ramalho & Moreau (2023). |
| | | *Cephalotes* sp. pinelii-group | 2 | Graber *et al.* (2023); Ramalho & Moreau (2023). |
| | | *Cephalotes* sp. pinelii-group dark | 1 | Ramalho & Moreau (2023). |
| | | *Cephalotes pusillus* | 4 | Graber *et al.* (2023); Hu *et al.* (2022); Ramalho & Moreau (2023); Sanders *et al.* (2014).* |
| | | *Cephalotes ramiphilus* | 1 | Ramalho & Moreau (2023). |
| | | *Cephalotes specularis* | 2 | Graber *et al.* (2023); Ramalho & Moreau (2023). |
| | | *Cephalotes spinosus* | 1 | Ramalho & Moreau (2023); |
| | | *Cephalotes* sp. 18 | 1 | Ramalho & Moreau (2023). |
| | | *Cephalotes targionii* | 3 | Graber *et al.* (2023); Hu *et al.* (2022); Ramalho & Moreau (2023). |
| | | *Cephalotes trichophorus* | 1 | Ramalho & Moreau (2023). |
| | *Crematogaster* | *Crematogaster* sp. | 1 | Sanders *et al.* (2014).* |
| | *Mycetarotes* | *Mycetarotes paralelus* | 1 | Ronque *et al.* (2020). |
| | *Mycetophylax* | *Mycetophylax morschi* | 1 | Ronque *et al.* (2020). |
| | *Mycocepurus* | *Mycocepurus smithii* | 1 | Ronque *et al.* (2020). |
| | *Sericomyrmex* | *Sericomyrmex parvulus* | 1 | Ronque *et al.* (2020). |
| | | *Sericomyrmex saussurei* | 1 | Ronque *et al.* (2020). |
| Paraponerinae | *Paraponera* | *Paraponera clavata* | 1 | Moreau & Rubin (2017) |
| Ponerinae | *Odontomachus* | *Odontomachus chelifer* | 1 | Rocha *et al.* (2022) |
| | | *Odontomachus hastatus* | 1 | Rocha *et al.* (2022) |
| Pseudomyrmicinae | *Pseudomyrmex* | *Pseudomyrmex* sp. | 1 | Sanders *et al.* (2014)* |

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# Ecology

# 09

# TRENDS AND GAPS IN THE STUDY OF ANTS IN ECOLOGICAL RESTORATION IN BRAZIL

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# ABSTRACT

Ecological restoration is one of the main ways of recovering degraded areas. However, considering biodiversity, we still have a 'phytocentric' view of ecological restoration, neglecting the role of animals in this process, especially insects. Ants are one of the most abundant groups of insects in terrestrial environments, performing essential ecological functions such as nutrient cycling, soil bioturbation and seed dispersal. Therefore, understanding how these insects recover and perform their ecological functions in restoration areas is essential. Here, we review the trends and knowledge gaps regarding the ants' responses to restoration in Brazil, whether through passive restoration (natural regeneration) or active restoration (using different techniques such as no-till, nucleation, soil transposition etc). We found 70 articles published in the last 30 years on almost all Brazilian biomes. Most of the studies were (i) comparisons between degraded areas and reference ecosystems, despite a considerable number of studies (ii) evaluating chronosequences. In (i) comparative studies, areas undergoing restoration showed lower richness and abundance compared to reference ecosystems, while diversity was similar and composition was different. However, in (ii) chronosequence studies, richness and diversity increased over time, while abundance decreased and the results relating to composition were uncertain. Although these results reaffirm a pattern that has already been described, the inclusion of new metrics (phylogenetic and functional diversity, and studies of ecological interactions) in the assessment of ant communities could improve our understanding. Finally, Brazil has great potential for ecological restoration due to its vast areas of degraded land and high biodiversity, and ants can be a key element in this process.

**Keywords:** Bioindicators; chronosequence; disturbance; natural regeneration; sustainable development goals (SDGs).

## INTRODUCTION

Habitat loss due to changes in land use and cover is considered one of the greatest threats to global biodiversity, being responsible for most species extinctions since 1500 (ISBELL *et al.*, 2023). The reversal, or at least mitigation of this scenario could occur both through the conservation of environments that have not yet been converted by human activities, as well as through the restoration of areas (mainly on a large scale) that have already been altered (BANKS-LEITE *et al.*, 2014). Through restoration, it is possible to increase the biodiversity of areas that have been depleted of species, also increasing the chances of reestablishing previously lost ecosystem functions and services (BENAYAS *et al.*, 2009; BARRAL *et al.*, 2015). In this sense, the United Nations highlighted the importance of this practice by declaring 2021 to 2030 as the decade of restoration (UNEP, 2021). In Brazil, for example, the federal government has updated its National Plan for the Recovery of Native Vegetation (Planaveg) with the goal of restoring 12 million hectares by 2030.

Ecological restoration, also known as biodiversity restoration is the "process of helping to re-establish an ecosystem that has been degraded, damaged or destroyed" (SER, 2004). It can generally be divided into two approaches: passive and active restoration. The passive restoration uses only the environment's intrinsic capacity to reestablish itself after a disturbance has been interrupted, i.e. the process of natural regeneration. On the other hand, active restoration involves the application of a series of techniques to accelerate the process of recovering the disturbed environment towards the local native ecosystems (ROHR *et al.*, 2018), such as erosion control, prescribed burning and reintroduction of native or exotic plant species (PALMA & LAURANCE, 2015; PILON *et al.*, 2019; ATKINSON & BONSER, 2020, SLODOWICZ *et al.*, 2023).

In this scenario, Brazil is particularly at risk because it combines high levels of habitat loss with a high biodiversity that is largely unknown (CARVALHO *et al.*, 2023), especially when we consider smaller organisms like invertebrates (ISBELL *et al.*, 2023). In this process, species are becoming extinct before they are even discovered. Despite an increase in restoration studies in Brazil over the last 30 years, the vast majority of these studies (>80%) have focused on plants, while effects on the fauna are still relatively neglected (GUERRA *et al.*, 2020). This is

particularly true for insects, even with many studies strongly suggesting that this group works well as bioindicators of environmental changes (LENHARD & WITTER, 1977; GERLACH *et al.*, 2013; CHOWDHURY *et al.*, 2023). Considering that organisms' responses to disturbances can vary greatly across taxa (BARLOW *et al.*, 2007; FILGUEIRAS *et al.*, 2019), assessing the success of ecological restoration requires a deeper understanding of how different biological groups respond to restoration.

Among insects, ants have been successfully used as bioindicators in different contexts worldwide (UNDERWOOD & FISHER, 2006; MAJER *et al.*, 2007; RIBAS *et al.*, 2012; CASIMIRO *et al.*, 2019), with numerous characteristics that make this group a potentially ideal candidate for biomonitoring. Ants are broadly distributed, being one of the most ubiquitous and diverse groups of arthropods in almost all terrestrial habitats, where they occupy a wide range of microhabitats (SCHULTHEISS *et al.*, 2022). In addition to their wide distribution, these organisms are easy to sample, which reduces costs, and they have a relatively well-resolved taxonomy (BACCARO *et al.*, 2015). The ants occupy many trophic positions, playing significant roles in several ecosystem functions (HOLLDOBLER & WILSON, 1990; DEL TORO *et al.*, 2012; DE ALMEIDA *et al.*, 2024; ROCHA *et al.*, 2024). Moreover, these ecosystem functions can be especially relevant for restoration efforts (DE ALMEIDA *et al.*, 2024), with multiple implications for its success. For example, ants can increase seed dispersal (GALLEGOS *et al.*, 2014; ANJOS *et al.*, 2020) and germination (PINEDA-LÓPEZ *et al.*, 2025), and increase the soil quality due to their role in bioturbation and nutrient cycling (DEL TORO *et al.*, 2015; DE ALMEIDA *et al.*, 2020). Moreover, the ants can prey on potential herbivores (TRAGER *et al.*, 2010; ANJOS *et al.*, 2022), increase pollination (DAS & DAS, 2023; TOREZAN-SILINGARDI & DEL-CLARO, 2024), or even affect seedling establishment through herbivory (by leaf-cutting ants) (LEAL *et al.*, 2014).

There are several studies showing how ants respond to restoration in different ecosystems, disturbances and even analyzing taxonomic and/or functional levels (ANDERSEN, 1993; DAHMS *et al.*, 2010; FAGAN *et al.*, 2010; LAWES *et al.*, 2017; CASIMIRO *et al.*, 2019; QUEIROZ *et al.*, 2021). However, despite Brazil being one of the global priority areas for ecosystem restoration (STRASSBURG *et al.*, 2020) and the increasing number of studies using ants as


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indicator species (RIBAS *et al.*, 2012), we still lack a general understanding of the patterns, trends and gaps in the relationship between the ant communities and ecological restoration in Brazil.

In this chapter, we review the current understanding of ant communities in ecological restoration in Brazil. We did that by focusing on studies that measured ant community attributes (e.g., taxonomic and functional) and their ecological functions in areas under natural regeneration (passive, i.e., without any human intervention) or active restoration. Therefore, our aim was to describe how ant community attributes respond to restoration in Brazil.

## METHODS

### Data collection

We searched for articles in Web of Science and Scopus databases using all available years up to 17st November 2024. We used the PRISMA (Preferred Reporting Items for Systematic Reviews and Meta-Analyses) protocol for paper articles (MOHER *et al.*, 1999), using the following key terms in our search: 'ant*' AND 'restoration ecology' OR 'forest recovery' OR 'afforestation' OR 'succession' OR 'chronosequence' OR 'reforestation' OR 'bioindicators' OR 'restoration' OR 'regeneration' OR 'plantation' AND 'brazil'. To complement our dataset, we searched for more studies in a recent review (see CASIMIRO *et al.*, 2019). The initial screening of titles and abstracts was carried out by two authors using the Sysrev platform (BOZADA-JUNIOR *et al.*, 2021). Studies that mentioned restoration in relation to community attributes or ecological functions were selected for the second phase of full-text screening (Figure 1). Since this review focused exclusively on studies conducted in Brazil and many of them are in Portuguese but have the abstract section in English, studies published in both languages were considered.

We evaluated the full texts based on inclusion and exclusion criteria. We selected empirical studies that assessed ant community attributes (e.g., taxonomic and functional metrics) and their ecological functions in areas undergoing either natural regeneration (passive restoration) or active restoration interventions (e.g., tree planting, soil transposition, nucleation, etc.). Studies

were included if they met at least one of the following criteria: (i) in comparative studies, at least one of the evaluated areas had experienced some form of degradation (e.g., deforestation, mining, etc.), followed by restoration (passive or active), with the degrading activity already ceased; or (ii) the study assessed a chronosequence following a disturbance (e.g., secondary forests of different ages). In comparative studies, at least one site is assumed to represent a reference ecosystem, reflecting the biotic and abiotic conditions of the community prior to disturbance (WHITE & WALKER, 1997).

From the full-text studies included in the review (n = 70), we extracted information on the restoration technique (natural regeneration or active restoration, further classified by the origin of planted species: native or exotic), the Brazilian biome (e.g., Amazon, Cerrado, Atlantic Forest etc) (see IBGE, 1993), and the previous source of disturbance (e.g., mining, livestock, fire). In each study, we extracted the time (hereafter, 'age of restoration') since the last source of disturbance of each site studied. When the authors indicated the time period of the restoration age (e.g., from 8 to 10), we calculated the average time (9 years according to the previous example). In this way, we were able to estimate the age of restoration for each restored area recorded and calculate the average restoration time for the areas studied. In addition, for each study we also extracted information about the sample technique used to collect ants, ant fauna strata (e.g., arboreal, epigeic or hypogeic), type of habitat (e.g., forest or savanna), and the measured ant community attributes (e.g., richness, abundance, diversity, composition), and ecological functions.

Since most of the studies were carried out at local scales, in each study we extracted the geographical coordinate of one of these sites to visualize the distribution of studies by biome in Brazil. When the article did not provide any kind of coordinate, we identified the location (e.g., city, park, natural reserves etc.) provided by the authors and searched for its coordinate. Since only a few studies addressed ecological functions (n = 2), this attribute was excluded from the analysis. As a result, we were able to estimate only a limited set of community attributes, such as species richness, diversity, abundance, and composition, along with some derived metrics (e.g., estimated richness, functional diversity etc). We estimated the effect of the response variable (ant community attributes) as positive, negative or neutral for two types of studies. For example, in the (i)


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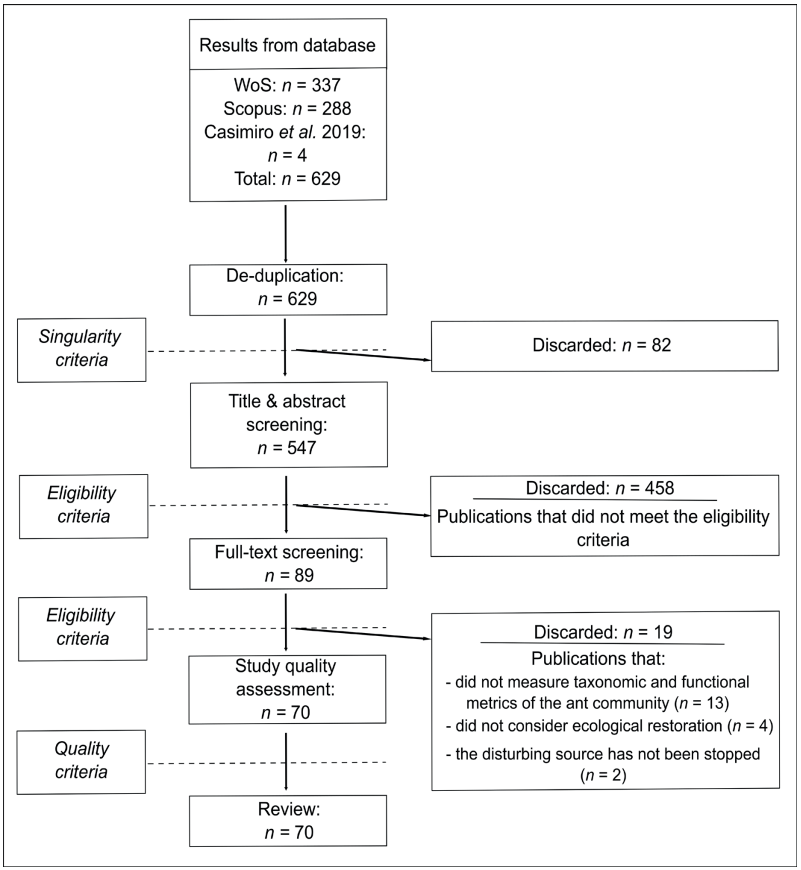
comparative studies, the positive effect represents higher richness, diversity or abundance in the restored areas compared to the reference ecosystems, and also represents the similar composition between these two areas (Table 1). Considering (ii) chronosequence studies, the decrease in richness, diversity or abundance over time represents a negative effect, as does the decrease in similarity of species composition over time. The positive effect follows the opposite reasoning. When richness, diversity, abundance and composition did not change over time, we considered it as a neutral effect, which also indicates a kind of "positive" outcome of restoration (weaker compared to the one above) (Table 1).

**Table 1 -** Criteria used to determine the effect of the response variables (e.g., ant community attributes) according to the types of studies found. '>' represents higher; '<' represents lower; and '=' represents similar effects on ant community attributes. '↑' represents increase; '↓' represents decrease in these attributes.

| | **Ant community attributes** | |
|---|---|---|
| | **Richness/abundance/diversity** | **Composition** |
| **Comparative studies (restored *Vs* reference ecosystem)** | > (positive) | similar (positive) |
| | < (negative) | different (negative) |
| | = (neutral) | |
| **Chronosequence studies** | ↑ (positive) | ↑ similarity (positive) |
| | ↓ (negative) | ↓ similarity (negative) |
| | = (neutral) | = (neutral) |

**Figure 1 -** Sequence of information in the different phases of a systematic review using the PRISMA protocol.




## Results

We identified 70 studies published from 1992 to 2024, revealing a slight increase in the number of studies starting from 2007 (Figure 2). These studies were conducted in all Brazilian biomes except the Pantanal. The majority of studies were carried out in the Atlantic Forest (55.5%), followed by Cerrado (25.0%), Amazon (13.9%) and Caatinga and Pampa (both 2.9%) (Figure 3a). Therefore, most of the studies were carried out in forest environments (81.1%) rather than open ones (18.9%). The most studied ant fauna was epigeic, followed by arboreal and hypogeic (Figure 3b). Different sampling methods were used,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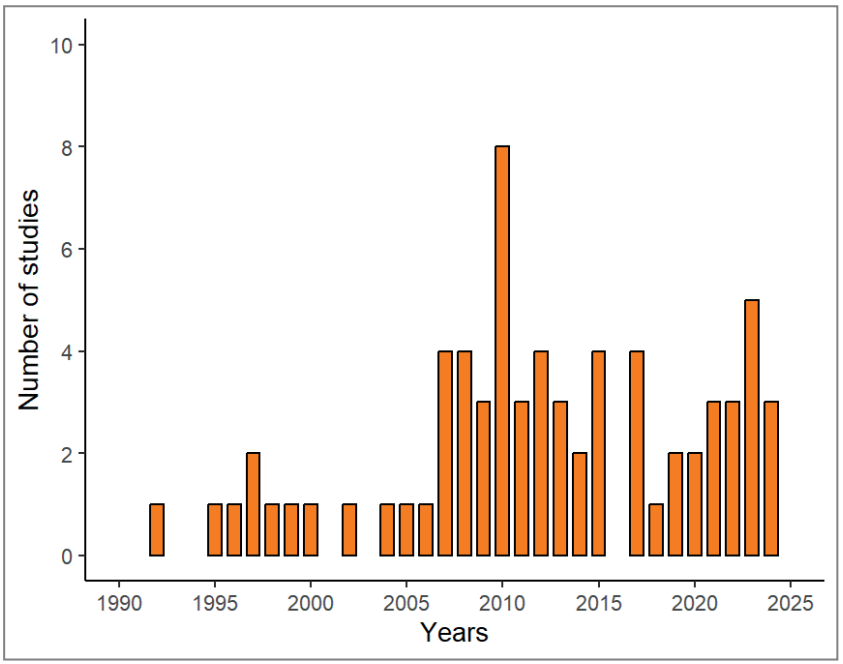
the most common were pitfall traps, followed by active collection, baits, Winkler/Berlese, beating/entomological umbrellas and others (e.g., observations, D-Vac suction, fogging etc.) (Figure 3c). Some studies (28.5%) used more than one sampling method. 11.4% of the studies investigated the effects of restoration only on populations of leaf-cutting ants (Attini), while the majority considered the effects on the entire local ant community (88.6%).

**Figure 2 -** Temporal trend in the number of studies fitting inclusion criteria.




Considering the two types of restoration evaluated (passive and active), 60.3% of the studies were carried out in areas under active restoration, with 39.7% in passive restoration areas (i.e. natural regeneration). Considering the studies with active restoration, the majority used only a single technique. Total planting was the most used restoration technique (85.3%), followed by soil transposition (9.7%), nucleation and direct seeding (both 2.5%). The most used exotic species was *Eucalyptus* spp. (66.6%), followed by *Pinus* spp. (12.1%) and others (e.g., *Acacia* spp., *Tectona* spp., *Ficus* spp., *Erythrina* spp. etc) which account for 21.3%. The planting of exotic trees, mainly *Eucalyptus* spp. and timber species,

reflects the history of land use prior to restoration. In this way, the most common source of disturbance found was logging, followed by livestock, cropping, deforestation, others (e.g., dam failure, soil degradation, water pipeline, human presence etc), mining and fire (Figure 3d). Eight studies did not report the most recent source of disturbance prior to restoration. Finally, our results showed that most of the studies focused on areas with relatively short restoration periods, with an average of 15.7 years (Figure 4).

**Figure 3 -** Distribution of sites studying the effects of restoration on the ant fauna in Brazil and their respective biomes according to the Brazilian Institute of Geography and Statistics - IBGE (a). Percentage of ant fauna studied by type of strata (b). Percentage of ant collection techniques (c). Percentage of source of disturbance before restoration (d).

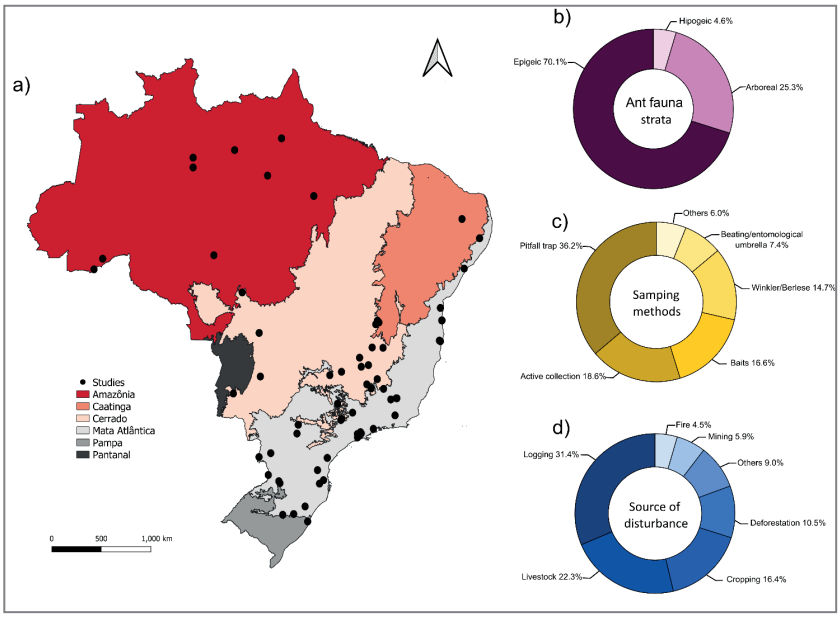
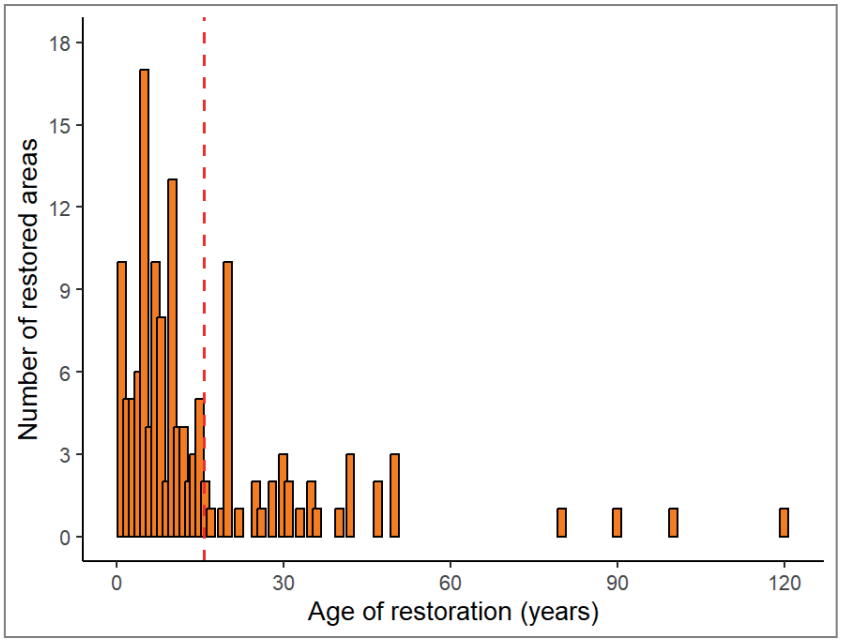


**Figure 4 -** Age of restoration (years) of the restored areas considering the ants' responses. The dashed line (red) represents the mean age considering all studies included.



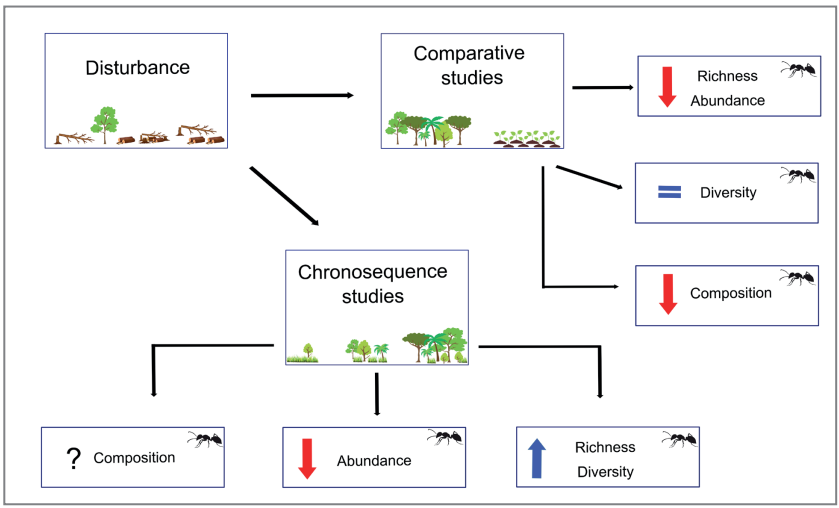

## Effect of restoration on ants

Regarding (i) comparative studies, 66.6% of the total number of articles that measured richness found a negative effect, i.e. the restored area had lower richness compared to the reference ecosystem. The same percentage of negative effects was found in the studies that measured abundance. On the other hand, half of the studies evaluating diversity found neutral effects, which may indicate good restoration results. With regard to composition, 78.2% of the studies also found a negative effect, i.e. the restored areas have a different composition to the reference ecosystems (Figure 5). These results should be interpreted with caution, as our review did not allow us to control for the effect of the age of the restoration, which is an important variable.

Regarding (ii) chronosequence studies, 61.9% of those that measured richness found a positive effect, as well those that measured diversity (83.3% found a positive effect), i.e., richness and diversity increased over time. On the other hand, in 60.0% of the studies, abundance showed a negative effect (decreasing

over time). Finally, with regard to composition, just under half (46.6%) of the studies found a positive effect, i.e., when composition becomes more similar over time (Figure 5). This result should be interpreted with caution as almost half of the studies reported no significant trend in composition over time.

**Figure 5 -** General patterns regarding the effects of response variables (e.g., ant community attributes) according to the types of studies found: (i) comparative and (ii) chronosequence studies, from any type of source of disturbance. For each community attribute, the effects were categorized as 'positive' (blue arrow), 'negative' (red arrow), 'neutral' (gray equal sign) when consistently observed in at least 50% of the studies which measured certain variables (see Table 1). In other cases (i.e., when no effect was detected, or positive/negative effects were detected in less than 50% of models), the effect was categorized as 'inconsistent' (black question sign).




## DISCUSSION

We review the state of the art on ant communities in ecological restoration in Brazil. In general, our finding supports and aligns with other studies (see CASIMIRO *et al.*, 2019). For example, the restored areas showed lower ant richness and abundance, and a different composition compared to the reference ecosystems (SILVA *et al.*, 2007; PACHECO *et al.*, 2009; DRÖSE *et al.*, 2021). Moreover, in chronosequence studies, richness and diversity of ants increased over time, while abundance decreased (VASCONCELOS 1999; NEVES *et al.*, 2006; OLIVEIRA *et al.*, 2024).

Our results demonstrated that in the most studied ant fauna was epigeic, sampled using pitfall traps. This may be because this method is more cost-effective, and provides efficient results over a shorter period of time, although with some bias as any type of sampling method (LASMAR *et al.*, 2017; DELABIE *et al.*, 2020). For example, sampling the epigeic fauna using Winkler/Berlese collects a large amount of material (including some species that are difficult to collect with other methods) and requires a long period of sorting in the laboratory, which can make the evaluation of the restoration projects more expensive.

Studies considering the entire ant community were the majority (89%). However, around 11% focused on populations of leaf-cutting ants (e.g., *Atta* and *Acromyrmex* species). Despite these ants play a fundamental role in the ecosystem, such as nutrient cycling, soil bioturbation and plant demography (LEAL *et al.*, 2014, FARJI-BRENER & WERENKRAUT, 2017), they are often seen as villains in restoration projects because they attack newly planted seedlings, causing an additional cost in restoration projects. Many restoration projects already control leaf-cutting ants, mainly through chemical control (MONTAGNINI *et al.*, 1995; BRITTO *et al.*, 2016). Prior diagnosis of the area, choice of less attractive plant species for leaf-cutting ant and greater plant functional diversity, achieved through either active restoration, are vital strategies to reduce herbivory pressure (GARCIA *et al.*, 2020). Usually, leaf-cutting ants are more abundant in recently and/or continuously impacted areas than in areas in more advanced stages of regeneration (FARJI-BRENER, 2001; VASCONCELOS & CHERRETT, 1997). Therefore, even in areas under passive restoration, the role of leaf-cutting ants can be investigated, and some kind of intervention (such as population control of these ants) may be necessary.

In the studies that have made comparisons between restored areas and reference ecosystems (i.e., comparative studies), we have found a pattern that has already been described considering ants' response to land use change (WILKER *et al.*, 2024). Regardless of the age of the restoration, restored areas showed lower species richness and abundance than reference ecosystems. Moreover, most studies found a neutral pattern for diversity; however, it is worth noting that the number of studies evaluating this metric was small (n = 6). These results imply that the restored areas have not been able to recover the number of species and number of individuals (see CASIMIRO *et al.*, 2019). We cannot

ignore, however, the fact that many studies have also been unable to effectively evaluate restoration. For example, we found that most studies evaluated the first few years after restoration, with few studies considering long-term evaluations. Depending on the source of the disturbance (e.g., mining), decades of monitoring can be required (50 -100 years, see BIHN *et al.*, 2008). Because the recovery of ant communities is influenced by the time since restoration, long-term monitoring is essential to fully understand ecosystem recovery.

As expected for disturbed areas, the composition in restored areas was different from their respective reference ecosystems (SILVA *et al.*, 2007; PACHECO *et al.*, 2009; DRÖSE *et al.*, 2021). For example, PACHECO *et al.* (2009) comparing an area reforested with *Pinus* spp. *versus* a fragment of Atlantic Forest showed that only 50% of ant species were recorded in both areas. However, the composition of terrestrial ant fauna may not be consistently distinct across a forest succession gradient (SILVA *et al.*, 2007). In successional stages of regeneration in Cerrado areas, early stages showed a higher proportion of generalist ant species, which decreased as plant succession progressed (TIBCHERANI *et al.*, 2020). These differences depend on several factors, such as the type of ecosystem, the nature of the disturbance (and its frequency and intensity), among others.

Considering the effect of time, (ii) chronosequence studies have shown that ant richness and diversity increase over time (positive effect). In the meta-analysis by CASIMIRO *et al.* (2019), the same pattern was found for species richness, but only when active restoration techniques are used - although some areas under natural regeneration have higher diversity when compared to reference areas. On the other hand, we found that ant abundance decreases over time in chronosequence studies. These patterns (i.e., an increase in species richness and diversity and a decrease in ant abundance along chronosequences) have also been described in other studies (VASCONCELOS 1999; NEVES *et al.*, 2006; OLIVEIRA *et al.*, 2024). Ants are resistant and resilient insects to anthropogenic disturbances, being one of the first groups to establish themselves in degraded areas (WILKER *et al.*, 2024). Therefore, shortly after the disturbance the abundance of these insects increases considerably (ANJOS *et al.*, 2017), mainly the generalist ones, which may imply low species richness and/or diversity. Through time and with natural succession, the competition between species increases and the levels of abundance of generalist species tends to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decrease, creating opportunities for the colonization of species less sensitive to disturbance (increasing richness species) (CERDÁ *et al.*, 2013). Slightly less than half of the studies showed which ant fauna became more similar over the restoration period. Regarding active restoration, other studies suggest a similar pattern for tropical ecosystems (CASIMIRO *et al.*, 2019). However, half of the studies in this review found no trend. Therefore, species composition and its analyses need to be better understood.

We suggest that understanding the role of ants in restored areas requires looking beyond simple measures such as species richness and the number of individuals. These metrics have been widely used despite their limitations. With the same sampling effort, it is possible to use more complex metrics that generate interesting results. For example, analysis of phylogenetic diversity measures how evolutionarily related species are to each other (FAITH, 1992; TUCKER *et al.*, 2017). Communities with high phylogenetic diversity tend to have a greater variety of traits and ecological strategies, even if richness is relatively low (LIU *et al.*, 2016). Likewise, functional diversity analysis, based on functional traits (e.g., body size, diet, type of locomotion, etc.) helps to understand how ant communities respond to environmental changes and how they influence ecosystem processes (PARR *et al.*, 2016). CASIMIRO *et al.* (2019), for example, found that reestablishment of ant functional groups occurs faster than species richness. Here, due to the small number of articles considering ant functional traits (n = 2) in ecological restoration, we cannot make any inference. Recently, DE ALMEIDA *et al.* (2024) proposed an approach based on ant traits (e.g., mandibles length, nest size, die, colony foraging strategy, etc.) to evaluate ecological restoration from different impacts caused by disturbances. This approach is based on the role of ants in the ecosystem. For example, a successful case occurred in France after the oil leak in 2009. Evaluating several traits, BULOT *et al.* (2014) chose to introduce the ant *Messor barbarous* in this affected area. Seven years later, these colonies contributed to the restoration of the ecosystem, increasing soil fertility, and plant biomass and species richness (DE ALMEIDA *et al.*, 2020). Moreover, after the dam collapse in Brumadinho – MG (Brazil) in 2019, one of Brazil's biggest environmental violations and tragedies (ROTTA *et al.*, 2020), one of the protocols for environmental analysis of the affected areas involves not only monitoring the ant community parameters, but also the ecological functions they perform (e.g., seed

dispersal). Therefore, future studies also should consider community diversity metrics beyond taxonomic diversity, as well as ant-mediated ecological functions.

Finally, it is important to consider the synergy between current climate change and environmental disturbances. For example, climate changes such as global warming can disrupt ecological functions mediated by ants which are pivotal to habitat restoration, such as nutrient cycling and seed dispersal (STUBLE *et al.*, 2014, DEL TORO *et al.*, 2015). Moreover, global warming has increased the frequency of certain disturbances such as fire (DRISCOLL *et al.*, 2021), whether in open or forested environments. We are still in the early stages of improving restoration techniques after fire disturbance. However, with the development of these techniques in burned areas, ants can be a good indicator of ecological restoration. The responses of ants are already well known, especially in cases of natural regeneration after fire in the Cerrado (VASCONCELOS *et al.*, 2017). In other semiarid grasslands around the world, such as Sevilleta National Wildlife Refuge (USA), two years after a wildfire, the harvester ant nests improved resources, leading to faster recovery of grass inflorescences than in burned controls (NICOLAI *et al.*, 2019). In this sense, it is important to evaluate the restoration process in synergy with other impacts in this changing world - something that has been completely lacking in myrmecological studies conducted in Brazil so far.

## CONCLUSION

Our study reviewed the responses of ants to ecological restoration in Brazil over the last 30 years. Community attributes such as ant species richness and abundance show useful and often predictable responses. However, long-term studies assessing the effects of restoration are still needed to better understand how ant fauna recovers in the face of anthropogenic disturbances. Furthermore, incorporating new metrics and analyses - such as functional diversity, phylogenetic diversity and ecological interaction studies - can lead to more effective outcomes, often without increasing costs. These metrics should be applied across different biomes and restoration strategies. Moreover, these innovative approaches should be adopted not only by researchers but also by environmental agencies, NGOs, and companies involved in both causing and


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mitigating environmental impacts. In addition, more effective results also depend on studies that advance in open and neglected ecosystems located into Cerrado, Caatinga, Pampa and Pantanal. Brazil hosts large and growing research groups in ant ecology and ecological restoration, providing a fertile ground for the effective use of ants in restoration initiatives.

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10

# THE DIVERSITY AND ECOLOGY OF ANT GARDENS IN THE BRAZILIAN RAINFOREST: A COMPREHENSIVE REVIEW OF A COMPLEX ANT-PLANT MUTUALISM

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# ABSTRACT

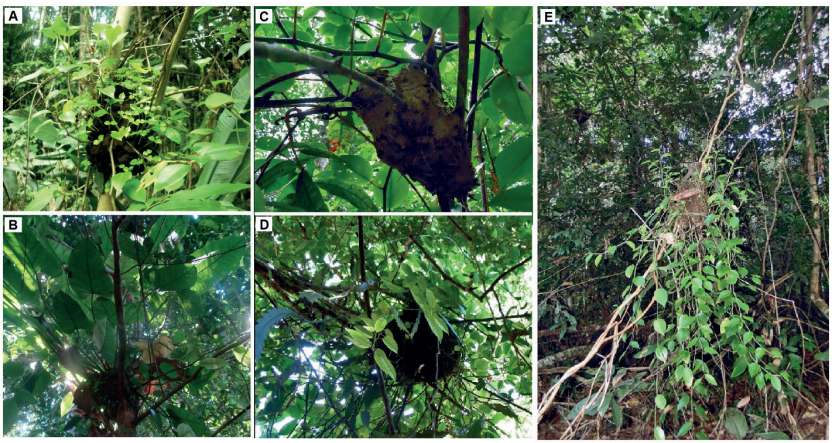
Ant Gardens (AGs) are the most complex mutualistic interaction between ants and plants that occur in tropical forests. In these systems, ants build nests on tree branches or liana crevices, incorporating epiphytic plant seeds into their walls. After germination and establishment, these epiphytes control humidity within the nests and provide structure for nest growth and food for the ants. Meanwhile, ants provide nutrients to epiphytes and protect them against natural enemies. Therefore, the interaction between ants and partner epiphytes in this system is mutualistic, with some epiphyte species being found exclusively in AGs. Thus, AGs result from a multitude of pairwise mutualistic interactions between ants and epiphytes, most of them defense and nutrition. Besides influencing the fitness of ant and epiphyte species, these interactions play a relevant ecological role, especially in directing the succession dynamics of the arboreal communities where they occur. Despite their importance and complexity, AGs are among the least studied of mutualistic ant-plant interactions, especially in Brazilian tropical forests. This review synthesizes our current knowledge on AGs, focusing on the most frequent and studied system, the parabiotic AGs of the Amazon, their ecological roles and the factors that influence their distribution and diversity.

**Keywords:** *Camponotus femoratus*; *Crematogaster levior*; dominance; mutualism; parabiosis.

## INTRODUCTION

Mutualistic interactions between ants and plants stand out as one of the most diverse and broadly distributed ecological interactions worldwide (BRONSTEIN, 1998). In these interactions, ants and plants exchange resources that are costly or impossible to obtain otherwise (HOEKSEMA & BRUNA, 2000). The most studied examples of ant-plant mutualisms are the protective ones between ants and plants with extrafloral nectaries (HEIL, 2015; DEL-CLARO *et al.*, 2016; CHINARELLI *et al.*, 2022; ALENCAR *et al.*, 2023; SOUZA *et al.*, 2024; NAKAYAMA MIRANDA *et al.*, 2025) and/or domatia - hollow cavities where ants can nest (MICHELANGELI, 2010; IZZO & BENELLI-PETINI, 2011; IZZO & VASCONCELOS, 2002; DEJEAN *et al.*, 2018a). In both cases, plants benefit from the anti-herbivory protection provided by the ants consuming extrafloral nectar and/or nesting in domatia. In turn, ants can benefit from accessing predictable and renewable sources of carbohydrates and/or nesting sites.

**Figure 1 -** Ant gardens recorded in the modules of the Biodiversity Research Program (PPBio): A) AG covered by *Peperomia macrostachyos*, B) AG covered by *Philodendron* sp., C) image showing the carton walls with *Peperomia* branches; D) ant garden with *Epiphyllum* and *Codonanthe* occupying a tangle of branches in the canopy; E) AG covered only by *Peperomia* growing on lianas attached to the forest canopy.




**Photos:** R. E. Vicente (2014).

While most ant-plant interactions involve bilateral exchanges, some systems feature multiple pairwise mutualisms simultaneously. The most striking example is the Ant Gardens (AGs), specialized niches co-constructed by

ants and epiphytes through integrated seed dispersal, nutrient exchange, and defensive interactions (ORIVEL & LEROY, 2011; VICENTE *et al.*, 2020). The AGs remain among the least studied ant-plant mutualisms, largely due to their exclusive occurrence in tropical rainforest canopies (ORIVEL & LEROY, 2011). The inaccessibility of these high-canopy habitats severely restricts field observation and monitoring, impeding a comprehensive understanding of AG functioning.

Although Orivel and Leroy's (2011) seminal synthesis consolidated early knowledge on AGs, it highlighted persistent gaps in understanding the functional mechanisms and biogeographic variation of these systems. These gaps are particularly acute in Brazilian AG systems, where species-specific interactions remain understudied compared to other regions (e.g., French Guiana). Subsequent studies have yielded valuable insights into AG complexity in Brazilian AG systems, yet their findings remain fragmented across the literature. This dispersion hinders the identification of the mechanisms governing AG formation, distribution, and ecological functioning. To address these gaps, we present a comprehensive synthesis of recent AG research advances in Brazilian AG systems, integrating three critical dimensions: (1) an updated conceptual framework capturing AG ecological complexity, (2) analysis of ant-epiphyte interaction dynamics, and (3) biogeographic drivers of AG distribution. These insights are urgently needed for tropical rainforest conservation, where AGs persist in ecosystems under escalating anthropogenic threats (GIBSON *et al.*, 2011; RIBEIRO *et al.*, 2022).

## WHAT ARE THE ANT GARDENS?

We define Ant Gardens (AGs) as a specialized mutualism which arboreal ants actively cultivate epiphytic plants within their nests through a cyclical process of reciprocal benefits. Where as some ant species form facultative associations with epiphytes through root-nesting (DEJEAN & OLMSTED, 1997; DAROCHA *et al.*, 2016), AGs emerge from a distinctly co-evolved interdependence, where ants and epiphytes collaboratively construct specialized niches. The interaction begins when ants collect seeds from the mutualistic epiphytic plants. Most of these seeds bear lipid- and protein-rich appendages that function as food rewards for ants (BENSON, 1985; DAVIDSON, 1988; RICO-GRAY & OLIVEIRA, 2007). Although such appendages are not considered true elaiosomes (e.g.,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lipidic appendages common on true myrmecochorous plants; GORB & GORB, 2003), they have been considered a functional analog, mediating the attractiveness of AG epiphyte seeds to mutualistic ants (elaiosome-like - BENSON, 1985; DAVIDSON, 1988). Evidence of that is the fact that the appendages of some epiphyte seeds can release volatile compounds attractive to AG-associated ants, favoring the seed location and further incorporation on AGs carton nest walls (YOUNGSTEADT *et al.*, 2008, 2009). The incorporation of epiphyte seed into AG walls creates a self-sustaining mutualistic system where: (1) the nest provides an ideal microenvironment for seed germination and plant growth, enriched by constant organic matter deposition (KLEINFELDT, 1978; DAVIDSON, 1988); (2) ants protect plants from herbivores through constant patrolling (VANTAUX *et al.*, 2007; VICENTE *et al.*, 2014); while (3) mature plants stabilize and expand the nest structure through their roots (YU, 1994; VICENTE *et al.*, 2020) and (4) are expected to provide food to ants via extrafloral nectaries or fleshy fruits (LEAL *et al.*, 2017). Because AG ants can forage beyond the AGs (VICENTE & IZZO, 2017, 2020), we still lack information on the importance of food resources offered by AG epiphytes for the overall colony energy intake.

So far, 30 ants and 137 epiphyte species (including obligatory and facultative ones) were found on AGs worldwide (ORIVEL & LEROY, 2011). Most of these species are strongly dependent on AGs and occur exclusively in these systems. Some species of ants and plants can occur outside the AGs, and their role in the AG functioning is mostly open to debate (see more in the sections ANT SPECIES IN BRAZILIAN AGS and EPIPHYTE COMPOSITION OF BRAZILIAN AGS). These ants and plant species are commonly found in phylogenetically distant families and represent a tiny percentage of the total diversity of ant and epiphyte species worldwide (ZOTZ, 2016; BOLTON, 2025). When we consider epiphytes, for example, approximately 0.67% of the paleotropical epiphyte species occur in AGs, and this percentage is even lower in the neotropical region (less than 0.35%), where epiphyte diversity is higher (ZOTZ, 2016; VICENTE *et al.*, 2020). This number drops by approximately half when considering the number of epiphyte species exclusively occurring in AGs (ORIVEL & LEROY, 2011).

## ANTS SPECIES IN BRAZILIAN AGS

Eleven ant species have been recorded in Brazilian AG (Table 1). These species diverge considerably in their obligate/facultative use of AGs and can be classified into three categories on this matter: true AG ants, opportunistic ants, and uncertain ant species. True AG ants actively collect and incorporate mutualistic epiphyte seeds into their carton nests, creating a suitable substrate for germination and seedling establishment (ORIVEL & LEROY, 2011). These ants commonly initiate the AGs construction, building the characteristic loamy nest structures, and exhibiting strong specificity to AG-associated plants (DAVIDSON, 1988). Opportunistic ants may nest in pre-existing AG structures but do not participate in their construction or maintenance (KAUFMANN & MASCHWITZ, 2006; ORIVEL *et al.*, 1997). Lastly, species with insufficient ecological data are classified as uncertain, still relying on more studies on their roles in AGs functioning (VICENTE *et al.*, 2020). Of the six species currently listed as true AG ants in Brazil (ORIVEL & LEROY, 2011), *Crematogaster* c*arinata* and *Crematogaster limata* are here considered uncertain due to these unresolved taxonomic and behavioral complexities (Table 1).

**Table 1 -** Ant species found on Brazilian Ant gardens. In the Status column, "True" refers to ant species obligatorily associated with AGs; "Opportunist" refers to species facultatively associated; and "Uncertain" for cases without in-depth records. Asterisks indicate ant species proposed for reclassification regarding their association category with AGs.

| Plant species | Status | Reference |
|---|---|---|
| **Dolichoderinae** | | |
| *Azteca trailii* Emery, 1893 | True | ORIVEL & LEROY, 2011, LEAL et al. 2017 |
| *Azteca paraensis bondari* Borgmeier, 1937 | True | DELABIE et al., 2007 |
| *Dolichoderus debilis* Emery, 1890 | Uncertain | VICENTE et al., 2020 |
| *Dolichoderus decollatus* F. Smith 1858 | Uncertain | VICENTE et al., 2020 |
| **Formicinae** | | |
| *Camponotus femoratus* (Fabricius, 1804) | True | ORIVEL & LEROY, 2011, PAOLUCCI et al., 2016; LEAL et al., 2017, VICENTE et al., 2020 |
| **Myrmicinae** | | |
| *Crematogaster carinata* Mayr, 1862* | Uncertain | proposed in this chapter |
| *Crematogaster levior* Longino, 2003 | True | ORIVEL & LEROY, 2011, PAOLUCCI et al., 2016; LEAL et al., 2017 |


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| Plant species | Status | Reference |
|---|---|---|
| *Crematogaster limata* Smith, 1858* | Uncertain | proposed in this chapter |
| *Solenopsis picea* Emery, 1896 | Opportunist | VICENTE et al., 2020 |
| **Ponerinae** | | |
| *Neoponera goeldii* Forel, 1912 | True | ORIVEL & LEROY, 2011 |
| *Odontomachus mayi* Mann, 1912 | True | ORIVEL & LEROY, 2011, VICENTE et al., 2020 |

Although eight from the 11 ant species located on Brazilian AGs have been classified as true AG species in previous studies (ORIVEL & LEROY, 2011), recent evidence suggests that the status of *Crematogaster carinata* and *Cr. limata* as true AGs requires reevaluation. These species were historically conflated under *Cr. limata parabiotica* (Forel, 1904) until Longino (2003) described *Cr. levior* as a distinct AG specialist with smooth pronotal morphology and obligatory association with *Camponotus femoratus* in AGS. Crucially, *Cr. carinata* (with pronotal carinulae) shows variable AG association patterns, including opportunistic nesting in pre-existing structures without active seed transplantation (DAVIDSON, 1988; DAVIDSON *et al.*, 1990). Because of this behavioral plasticity and morphological intermediacy, we classified here *Cr. limata* and *Cr. carinata* as uncertain species pending further studies on their role in AGs.

## PARABIOTIC AGS: A MODEL SYSTEM

Most of the AGs occurring in Brazil are observed in the Amazon region, being formed by arboreal nests shared between *Camponotus femoratus* (Fabricius, 1804) (Formicinae) and *Crematogaster levior* Longino, 2003 (Myrmicinae) (DAVIDSON, 1988; YOUNGSTEADT *et al.*, 2010; VICENTE & IZZO, 2017; QUINTEROS-GÓMEZ *et al.*, 2024). Despite cohabiting the same nest, each ant species maintains separate broods and distinct cuticular profiles in an interaction called parabiosis (e.g: EMERY & TSUTSUI, 2013, 2016; SPRENGER *et al.*, 2019). Although it is still open to debate, the current evidence indicates that the trade-off between the costs and benefits of this interaction is favorable to both ant species occurring in AGs (DACQUIN *et al.*, 2021; MENZEL *et al.*, 2014a, b). For instance, when preying within and outside the AGs, *Ca. femoratus* take advantage of the

ability of *Cr. levior* to discover prey, usurping them during agonistic interactions, especially towards protein resources (VANTAUX *et al.*, 2007; VICENTE & IZZO, 2021). However, *Cr. levior* largely benefits from *Ca. femoratus* ability in defending the shared nest, including the epiphyte plants structuring it (e.g., VICENTE *et al.*, 2014; LEAL *et al.*, 2017; ANJO-PEREIRA *et al.*, 2021). Another evidence of the mutualistic nature of *Cr. levior* and *Ca. femoratus* parabiosis is the existence of pre-adaptations favoring niche partitioning between the two species, such as altered cuticular hydrocarbon profiles compared to non-parabiotic species and low levels of interspecific aggression towards each other (MENZEL *et al.*, 2014b). Temporal partitioning of foraging activity minimizes competitive pressure, with Cr. *levior* foraging nocturnally (18:00-03:00) and *Ca*. *femoratus* diurnally (06:00-15:00) (VANTAUX *et al.*, 2007). This inversion of typical circadian rhythms, which the larger *Camponotus* forages diurnally, likely optimizes niche partitioning: *Ca*. *femoratus* capitalizes on visual advantages for nest defense, while *Cr*. *levior* exploits night conditions for efficient resource exploitation. Importantly, as with all mutualisms, the cost-benefit balance of this parabiosis is context-dependent, varying with abiotic and biotic factors (CHAMBERLAIN & HOLLAND, 2009). So far, we still lack evidence about the forces mediating the outcome of ant parabiotic interactions, an important gap which is still preventing a proper identification of the nature and functioning of this interaction.

This context-dependency is further illustrated by the presence of other ant species in AGs, such as the kleptobiotic *Solenopsis picea* (Emery, 1896). Through lestobiosis, *S. picea* stealthily exploits resources from parabiotic nests, building satellite chambers to steal food and brood (DAVIDSON, 1988; ORIVEL *et al.*, 1997; ANTWIKI, 2025). Unlike the mutualistic parabiosis, this interaction represents a facultative parasitism, highlighting how AGs balance costs and benefits under dynamic biotic pressures.

A question still open to debate is how these shared nests are formed. Evidence from Guyanese AGs indicates that only *Ca. femoratus* can build nests suitable for AG formation (DAVIDSON, 1988; ORIVEL & LEROY, 2011). However, observations from the Brazilian Amazon AGs indicate that *Cr. levior* may also initiate nest structures. For instance, *Cr. levior* frequently establishes small satellite nests (smaller than a tennis ball) in branch forks, liana villi, cavities of palm or dead branches (VICENTE *et al.*, 2020). These nests, however, are


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not colonized by epiphytes, suggesting that their subsequent occupation by *Ca. femoratus* is a necessary step for the development of a true AG (VICENTE *et al.*, 2020). Additional support for this sequential founding pattern comes from the higher ratio of *Cr. levior* to *Ca. femoratus* workers in younger AGs, which are gradually shifting toward *Ca. femoratus* dominance as the garden matures (DACQUIN *et al.*, 2021). Taken together, these findings suggest that *Cr. levior* may initiate nests that are later transformed into AGs by *Ca. femoratus*. It is important to note, though, that divergent evidence on who initiates the AGs relies on some historical biases of AG studies. Early studies developed prior to the recognition of parabiotic associations (ORIVEL *et al.*, 1997), described *Ca. femoratus* as the sole founder of AG nests (ULE, 1901; KLEINFELDT, 1978; DAVIDSON, 1988), likely because of limitations in detecting *Cr. levior* in the AGs, which is smaller and more cryptic than *Ca. femoratus*, and primarily nocturnal. Regardless of which species initiates the nest, the establishment of parabiosis between the two species appears to be a pivotal step driving the dynamics and likely the success of AG formation in this region (MENZEL & BLÜTHGEN, 2010; MENZEL *et al.*, 2014a).

## EPIPHYTE COMPOSITION OF BRAZILIAN AGS

After discussing the role of ants in AGs, it is essential to understand which epiphytes are found on Brazilian AGs and how their occurrence on them is shaped by environmental factors. In the Neotropical region, 53 species of epiphytes have been recorded in AGs (ORIVEL & LEROY, 2011), and more than 20 epiphyte species have been observed in AGs from Brazil (Table 2). These plants belong to seven different families, with Araceae and Gesneriaceae being the richest ones (six and five species, respectively). Here, we focus on the often--underestimated diversity of epiphyte species associated with Ant Gardens (AG epiphytes), an underestimation exacerbated by sampling biases toward ants, taxonomic complexities, high spatial turnover, and constrained canopy access.

Just like AG ants, AGs epiphytes can be grouped as follows, according to the degree of their association with AGs:

**1. 'True AG epiphytes'** – Obligate mutualists exclusive to AGs and/or dis-

persed and planted exclusively by mutualistic ants in AGs (e.g., *Codonanthe*, *Peperomia*; ORIVEL & LEROY 2011). This includes species like *Codonanthopsis ulei*, where field evidence confirms restriction to AGs despite limited dispersal studies (LEAL et al., 2017).

2. **'Facultative AG epiphytes'** – Species that colonize AGs opportunistically but also grow independently on non-AG substrates (e.g., *Aechmea mertensii*; YU 1994; LEROY et al. 2017).

3. **'Uncertain' –** Species with insufficient ecological data to confirm their association level.

While these categories provide an initial framework for studying AGs epiphytes composition, recent studies have revealed some exceptions. For example, the bromeliad *Aechmea mertensii*, traditionally classified as a true AG epiphyte, exhibits remarkable phenotypic plasticity in response to light, substrate, and ant partner identity (LEROY *et al.* 2017). This plasticity includes shifts in rosette architecture (crateriform vs. urceolate), leaf thickness, and resource allocation, enabling survival in both shaded (AG-like) and sun-exposed (non-AG) microhabitats. Field observations report occasional occurrences on non-AG substrates (BENZING 1990), and experimental evidence shows that even AG-derived seeds can germinate independently (though with reduced survival; LEROY *et al.* 2017), demonstrating that this species spans a continuum from ant-dependent to ant-independent states. This plasticity has cascading ecological effects: AG-associated *Aechmea* populations house richer aquatic microcosms in their leaf tanks than non-AG counterparts (CÉRÉGHINO *et al.*, 2011; CARRIAS *et al.*, 2012), likely due to defensive benefits from parabiotic ants. Future studies comparing genetic and morphological traits between AG and non-AG populations could clarify whether these differences reflect plastic responses or local adaptations.

**Table 2 -** Epiphyte species found on Brazilian Ant gardens. In the Status column, "True" refers to ant species obligatorily associated with AGs, able to build or restricted to AGs; "Opportunist" refers to species facultatively associated with AGs; and "Uncertain" for cases without in-depth ecological studies. Asterisks indicate epiphyte species proposed for reclassification regarding their association category with AGs.

| Plant species | Category | Reference |
|---|---|---|
| **Araceae** | | |
| *Anthurium gracile* Lindl. | True | ORIVEL & LEROY, 2011, Leal et al. 2017 |
| *Anthurium obtusum* (Engl.) Grayum | Facultative | LEAL et al. 2017 (syn. *Anthurium trinerved* Miq.) |
| *Anthurium* sp.1 | Uncertain | LEAL et al. 2017 |
| *Anthurium* sp.2 | Uncertain | LEAL et al. 2017 |
| *Philodendron megalophyllum* Schott | Facultative | LEAL et al. 2017 |
| *Philodendron* sp. | Uncertain | LEAL et al. 2017 |
| **Bromeliaceae** | | |
| *Aechmea mertensis* Schult. F.* | Facultative | ORIVEL & LEROY, 2011 |
| *Aechmea* sp. | Uncertain | LEAL et al. 2017 |
| *Streptocalyx longifolius* (Rudge) Baker | True | ORIVEL & LEROY, 2011 |
| **Cactaceae** | | |
| *Epiphyllum phyllanthus* (L.) Haw. | True | ORIVEL & LEROY, 2011 |
| **Clusiaceae** | | |
| *Clusia* sp. | Uncertain | LEAL et al. 2017 (syn. *Oedematopus* Planch. & Triana) |
| **Gesneriaceae** | | |
| *Codonanthopsis calcarata* (Miq.) Chautems & Mat. Perret | True | ORIVEL & LEROY, 2011, LEAL et al. 2017 |
| *Codonanthopsis crassifolia* (H. Focke) Chautems & Mat. Perret | True | ORIVEL & LEROY, 2011, LEAL et al. 2017 |
| *Codonanthopsis ulei* Mansf. | True | LEAL et al. 2017 |
| *Codonanthopsis uleana* (Fritsch) Chautems & Mat. Perret | True | ORIVEL & LEROY, 2011, VICENTE et al. 2014 |
| *Codonanthopsis sp.* | Uncertain | LEAL et al. 2017 |
| **Moraceae** | | |
| *Ficus paraensis* (Miq.) Miq. | True | ORIVEL & LEROY, 2011 |
| *Ficus* sp. | Uncertain | LEAL et al. 2017 |
| **Piperaceae** | | |
| *Peperomia macrostachyos* (Vahl) A.Dietr. | True | ORIVEL & LEROY, 2011, PAOLUCCI et al., 2016; LEAL et al. 2017, VICENTE et al. 2014 (= *P. macrostachya*) |
| **Rubiaceae** | | |

| Plant species | Category | Reference |
|---|---|---|
| *Psycotria* sp. | Uncertain | LEAL et al. 2017 |
| **Solanaceae** | | |
| *Markea formicarum* Dammer | True | ORIVEL & LEROY, 2011 |
| *Markea longiflora* Miers | Facultative | VICENTE et al. 2014 |

At a local scale, there is a marked variation in the frequency of these epiphytes' occurrence in the AGs. Some epiphyte species are consistently found on most, if not all, AGs in each site, with the less frequent species always occurring in AGs in which the most frequent local epiphyte species also occurs (VICENTE *et al.*, 2014; PAOLUCCI *et al.*, 2016). These obligatory epiphytes are commonly True AGs epiphytes. Among these, *Peperomia macrostachyos* (Piperaceae) deserves special attention, since it stands out as the most frequent epiphyte species in AGs from different study sites in the Brazilian Amazon Forest (VICENTE *et al.*, 2014; PAOLUCCI *et al.*, 2016; LEAL *et al.*, 2017). In some cases, *P. macrostachyos* can even be the unique epiphyte species in some AGs, commonly the smaller ones (PAOLUCCI *et al.* 2016). It suggests that *P. macrostachyos* is a key species for AGs formation in the Brazilian Amazon region. Together, these patterns highlight how ant-epiphyte interactions and species-specific traits shape Brazilian AG epiphyte assemblages at the local scale, from obligate true AG species to context-dependent facultative species.

While ant gardens (AGs) enhance epiphyte diversity by hosting specialized species (CÉRÉGHINO *et al.*, 2011), their composition of non-specialized epiphytes appears largely independent of surrounding epiphyte communities. This suggests strong ecological filtering mechanisms acting primarily on non-true AG species. Multiple lines of evidence support this filtering hypothesis: (1) AG epiphytes can have allelopathic effects against non-partner plants in controlled experiments (ANJO-PEREIRA *et al.*, 2021), (2) parabiotic ants are more likely to prune non-mutualistic seedlings than the mutualistic ones (ANJO-PEREIRA *et al.*, 2021), mirroring behaviors observed in domatia systems (FREDERICKSON, 2005), and (3) field observations show striking compositional differences between AGs and background epiphyte communities (VICENTE & LEAL, personal observation). It is important to note, though, that the first and


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second evidence come from experimental studies using a crop plant species (cucumber - *Cucumis sativus* (Curcubitaceae)) as a model for non-mutualistic plants, and we still lack evidence for such effects on non-mutualistic species from the habitat of AGs. While the exact efficacy against native non-mutualistic epiphytes requires further study, the combined evidence of chemical inhibition, behavioral exclusion, and field patterns strongly suggests that both true AG epiphytes and ants might act as complementary filters, shaping AG composition through allelopathy and pruning of colonizing species.

At the regional scale, the restricted distributions of true AG epiphytes drive spatially heterogeneous biodiversity patterns in the Brazilian Amazon region. These context-dependent AG epiphytes assemblages manifest as discrete communities per locality, with regional floristic shifts occurring predominantly via species turnover (PAOLUCCI *et al.*, 2016). It suggests that regional AG diversity in the Brazilian Amazon region emerges from the interaction between ant-mediated dispersal and local ecological filters (ORIVEL & LEROY 2011, PAOLUCCI *et al.*, 2016). As we demonstrate in the subsequent SPATIAL PATTERNS AND ECOLOGICAL FILTERS section, these distributional patterns vary markedly across Amazonian habitats. Nevertheless, significant knowledge gaps persist regarding both the Neotropical taxonomic composition of AG epiphytes and the functional roles of true, facultative, and opportunistic AG epiphytes in this mutualistic system. Urgently needed broader-scale studies must address: (1) the mechanisms underlying the biogeographic patterns and (2) the mechanistic drivers structuring these unique communities across the Brazilian Amazon region. Beyond shaping AG composition across spatial scales, AG epiphytes also interact with other organisms and contribute to broader ecosystem functions.

## SPATIAL PATTERNS AND ECOLOGICAL FILTERS

Ant Gardens formed by *Cr. levior* and *Ca. femoratus* parabiosis represents approximately 95% of the AGs occurring in forested areas of the Brazilian Amazon region (DAVIDSON, 1988; YOUNGSTEADT *et al.*, 2010). These AGs commonly occur in clusters, distributed vertically throughout the forest strata, from 30 cm above the ground to over 20 m high, following canopy openings created by natural treefall events (VICENTE *et al.*, 2020). The AGs within these

clusters function as satellite nests of the same colony, with younger nests being formed either by worker displacement from older nests or by queens from the same colony, given their polygynous nature (DACQUIN *et al.*, 2021; VICENTE & LEAL, personal observation). The complexity of these clusters varies markedly, with *Ca. femoratus-Cr. levior* colonies sometimes include up to 33 satellite nests, while other AG ant species rarely exceed two satellite nests per colony (VICENTE *et al.*, 2020).

While *Cr. levior-Ca. femoratus* associations dominate the AG systems, field surveys in the Brazilian Amazon Forest have located AGs also inhabited by *Azteca* sp., mixed colonies of *Odontomachus mayi* Mann, 1912 and *Dolichoderus debilis* Emery, 1890 and *Odontomachus mayi* with *Dolichoderus decollatus* F. Smith 1858 (VICENTE *et al.*, 2020). Field surveys have documented *Odontomachus mayi* and *Dolichoderus* spp. co-occurring in the same AGs (VICENTE *et al.*, 2020). However, unlike the obligate parabiosis of *Camponotus femoratus* and *Crematogaster levior*, there is no behavioral evidence confirming true parabiosis between these species. Ant gardens formed by these non-parabiotic associations are rare in the Amazon region, where *Cr. levior-Ca. femoratus* AGs dominate both numerically and behaviorally. Such dominance is largely attributed to *Ca. femoratus'* extreme aggressiveness (it has been ranked among the most aggressive ant species globally; WILSON, 1987), which increases their ability to monopolize resources and defend colonies effectively (DAVIDSON, 1988; VASCONCELOS *et al.*, 2003; MERTL *et al.*, 2010; VICENTE *et al.*, 2014). Interestingly, this dominance may explain why *Cr. levior* did not exhibit chemical defenses typical of non-parabiotic *Crematogaster* species (LONGINO, 2003).

In the Brazilian Amazon forest, parabiotic AGs are documented primarily in forest gaps such as those formed by fallen trees, riverbanks and abandoned roads, where light availability favors epiphyte performance (DAVIDSON, 1988; VICENTE *et al.*, 2014; PAOLUCCI *et al.*, 2016; LEAL *et al.*, 2017; VICENTE & IZZO, 2017; QUINTEROS-GÓMEZ *et al.*, 2024). Within these gaps, AG epiphyte assemblages become more dissimilar as the distance between gardens increases, a pattern likely driven by stochastic limitation of seed dispersal by parabiotic ants (PAOLUCCI *et al.*, 2016; YOUNGSTEADT *et al.*, 2008, 2009, 2010). At regional scales, non-linear responses to light-moisture gradients further filter internal taxonomic and functional AG epiphyte composition. For instance, AGs at forest


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edges – where plants are under higher solar incidence and face hotter and drier conditions - host fewer epiphytes with extrafloral nectaries compared to those in the forest interior (consistent with unimodal optima; LEAL *et al.*, 2017).

An interesting aspect to be considered is the difference in the patterns of AGs local and regional geographic distribution within the Amazon region. In the Guyanese Amazon, ant species establish clear dominance hierarchies, leading to spatially segregated territories dominated by different ant species (MAJER, 1993). Because of that, Guianese AGs form spatially interspecific mosaics, determined by the dominance of different AG ant species (DEJEAN *et al.*, 2018b). However, patterns in the Brazilian Amazon seem to be more complex than that. While *Cr. levior-Ca. femoratus* AGs in the Amazon forest from Mato Grosso state are approximately 2 km apart from *Azteca* AGs (VICENTE *et al.*, 2020), parabiotic and *Azteca* AGs can co-occur less than ten meters from each other in the Amazon forest of Amazonas state (Leal, L.C., personal observation). These contrasting patterns suggest that AG distribution at local scales results from multiple and spatially variable interacting mechanisms. Key among these are biotic factors, like *Ca. femoratus'* aggressive competitive exclusion of other ant species (DAVIDSON, 1988; VICENTE & IZZO, 2021), and abiotic factors, including canopy architecture and microclimatic conditions that mediate both nest establishment and epiphyte colonization (BENZING, 1990; CALLAWAY *et al.*, 2002; VICENTE & IZZO, 2017). Future studies should focus on disentangling how these biotic and abiotic factors interact to shape the distributional mosaics of AGs across different Amazonian landscapes.

## CONCLUSION AND PERSPECTIVES

Ant gardens represent complex ecological interactions that integrate multiple forms of mutualistic relationships between ants and plants, such as ant parabiosis, ant seed dispersal, and epiphyte biotic defense against herbivores. Among the AGs, those of *Camponotus femoratus* and *Crematogaster levior* appear to exhibit particularly sophisticated interactions and the greatest diversity of associated species. Their ecological dominance in successional habitats - through aggressive territoriality, numerical abundance, and frequent activity - positions them as potential ecosystem engineers in three key ways: (1)

by altering invertebrate community structure and nutrient flows through their extensive nest networks; (2) by mediating epiphyte establishment that may influence epiphyte local communities and ultimately canopy sucessional dynamic; and (3) through effects on soil enrichment due to accumulation of organic material discarded by AGs in forest gaps. While these broader impacts require empirical verification, the common occurrence of AGs in forest gaps and other disturbed areas, such as forest edges, suggests that these mutualistic systems may contribute to forest regeneration by creating favorable microsites for plant recruitment, within and outside the AGs. It is important to notice that AGs can also influence the animal communities in the forest canopies and gaps. The most remarkable example of such influence came from AGs sheltering *Aechmea* species (Bromeliaceae). Like other bromelia species, these plants house a microcosm of microorganisms and aquatic insects inside their leaf pitcher (CÉRÉGHINO *et al.*, 2011; CARRIAS *et al.*, 2012). However, *Aechmea* species from AGs house a richer and more diverse microcosm than non-AG tank bromeliads, likely due to the direct and indirect defensive benefits provided by the AG ants (CÉRÉGHINO *et al.*, 2011; CARRIAS *et al.*, 2012). Thus, AG formation potentially generates still unknown cascade effects altering core mechanisms that regulate canopy community dynamics across space and time. Given the accelerating threats to tropical ecosystems, future research should prioritize: quantifying AGs' roles in forest dynamics; elucidating the physiological mechanisms maintaining these partnerships; and evaluating their resilience to anthropogenic change. Such work will be crucial for preserving both these intricate mutualisms and their potential contributions to ecosystem recovery.

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11

# CARRION-VISITING ANTS IN BRAZIL: A 26-YEAR SYSTEMATIC REVIEW

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# ABSTRACT

Carrion decomposition is mediated by microorganisms and a diverse community of detritivorous and necrophagous insects. Among these, ants play an important role by either preying on other insects or fragmenting vertebrate carcasses, potentially delaying or accelerating the decomposition process. However, little is known about their diversity and ecological dynamics on carcasses in Brazil. This chapter presents a systematic review of research conducted in Brazil over the past 26 years involving ants and carcasses. During this period, 49 studies identified ants on carcasses, but most focused on other insect groups. A total of 162 ant species were recorded, likely an underestimate, as only 16% of studies identified ants to species level. The most frequently recorded genera were *Camponotus*, *Pheidole*, *Solenopsis*, and *Crematogaster*, which are also widely found in Brazil. Several ecological guilds were observed engaging in both necrophagy and predation. This lack of specificity suggests that ants' role in carcass decomposition might not be strictly tied to their ecological guild. Instead, traits such as morphology could be more important than feeding or nesting habits in determining ants' role and impact in decomposition. We propose a new research direction focusing on interactions and communities of frequently observed ant species with varying morphology and behavior in cadaveric contexts, alongside hypothesis-driven investigations in decomposition ecology and forensic entomology. Given the high species richness and research interest in the country, Brazil presents a promising scenario for studies on ants in carcasses and applied forensic entomology.

**Keywords:** Decomposition; ecology; forensic entomology; Formicidae; vertebrate carcass.



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## INTRODUCTION

Dead organic matter (i.e., detritus) is the foundation of many trophic webs and plays a crucial role in nutrient cycling within ecosystems (Moore *et al.*, 2004). Among the several types of detritus, vertebrate carcasses (henceforth referred to as carrion or carcass) are considered a high-quality resource (Carter; Yellowlees; Tibbett, 2006). Carrion is ephemeral, patchy, and unpredictable, introducing heterogeneity into ecosystems and influencing biological communities (Barton *et al.*, 2013; Carter; Yellowlees; Tibbett, 2006). Insects, particularly necrophagous species, are key drivers of carcass decomposition, as they actively feed on decomposing tissue during at least one stage of their life cycle (Begon; Townsend, 2020).

Necrophagous flies (Diptera) and beetles (Coleoptera), which rely on carrion for reproduction and completion of their life cycles, are the primary insects associated with vertebrate carcasses (Byrd; Tomberlin, 2019). Predatory arthropods can also influence decomposition dynamics and necrophagous activity by preying on or parasitizing species attracted to carcasses; they are drawn by the cadaveric fauna and may also use carcasses as mating sites (Olea; Mateo-Tomás; Sánchez-Zapata, 2019). Some species can shift roles depending on their life stage or the stage of decomposition, functioning as both predators and necrophages, and are often considered omnivores (Olea; Mateo-Tomás; Sánchez-Zapata, 2019; Byrd; Tomberlin, 2019). However, not all arthropods found on carrion are directly or indirectly involved in the decomposition process, and some are considered incidental. Ants are also part of the cadaveric fauna, represented by species from all functional groups. They are found in most terrestrial habitats (Hölldobler; Wilson, 1990), and contribute to key ecosystem services, including nutrient cycling and decomposition (Del Toro; Ribbons; Ellison, 2015; Elizalde *et al.*, 2020). Despite specific diet preferences, ants can opportunistically exploit diverse food sources (Hölldobler; Wilson, 1990).

Ants can be present on carcasses throughout all stages of decomposition, regardless of changes in resource type and quality over time (Bornemissza, 1957; Dawson *et al.*, 2022). They remove pieces of carrion, feed on decomposing exudates, and prey on other insects (Payne, 1965). It is often suggested that some species' necrophagous activity might accelerate carrion decomposition

by creating favorable sites for fly oviposition and larval development, and tissue removal (Paula *et al.*, 2016). However, by preying on other detritivores, some other ant species may also slow decomposition by removing necrophagous larvae and disrupting fly colonization (Pereira *et al.*, 2017; Singh *et al.*, 2020; Stoker; Grant; Bradleigh Vinson, 1995; Wei *et al.*, 2023). Given this variability, the role of ants in carrion decomposition cannot be generalized, as it likely depends on species-specific traits and environmental or biological factors (Nooten *et al.*, 2022; Adetimehin *et al.*, 2023).

Beyond ants' role in decomposition, they have important implications for forensic entomological analysis. By altering decomposition dynamics, ants can affect the precision of minimum post-mortem interval (PMImin) estimates based on insect activity (Lindgren *et al.*, 2011). Additionally, ants can leave bite marks that can be mistaken for ante- or perimortem injuries, or alter the appearance of pre-existing wounds relevant to a crime (Campobasso *et al.*, 2009). Although ants can alter decomposition rates, they are often not accounted for in PMImin estimation, and the extent of their influence on decomposition processes is rarely quantified (Eubanks; Lin; Tarone, 2019).

While invertebrate carcasses are well-established as a key food source for many ant species (Fellers; Fellers, 1982; Fernandes *et al.*, 2024), the nutritional importance of vertebrate carrion remains overlooked. Although ants are known as predators and necrophages on carrion, their broader ecological roles and community dynamics in the decomposition process are poorly understood (Olea; Mateo-Tomás; Sánchez-Zapata, 2019). The high species richness within the Formicidae family is associated with a wide range of behaviors, morphologies, and life traits that may influence their role and effect on decomposition (Anderson; VanLaerhoven, 1996; Nooten *et al.*, 2022).

Brazil is home to over 1600 ant species (Feitosa; Dias, 2024), and it is also a leader in ant-carrion and forensic entomology research (Eubanks; Lin; Tarone, 2019; Pujol-Luz; Arantes; Constantino, 2008). This chapter provides a systematic review of ant-carrion research in Brazil over the past two decades. We present a list of ant species recorded on vertebrate carcasses and explore their ecological roles, and broader significance in myrmecology. Although ants are hardly considered in forensic investigations, with few exceptions (Richards; Goff, 1997), this review also explores their potential applications in forensic entomology.


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Moreover, we highlight emerging trends in the literature, and knowledge gaps that could help direct future studies. Our overview of ant species exploiting carrion aims to further our understanding of their natural history and trophic ecology.

## METHODS

### Literature search and eligibility criteria

The studies included in this review comprised records of ants sampled on decomposing vertebrate carcasses or tissues (i.e., baits) within Brazilian territory. The goal of this review was not restricted to investigating ant-focused entomological research but rather to gather scattered information regarding the presence of this insect group in the context of carrion breakdown. For this reason, the presence of any data on ants associated with decomposing vertebrate tissues was sufficient for inclusion in our review. The works selected included case studies with either human or animal corpses, diversity lists, ecological experiments, and natural history notes, among others.

We searched Google Scholar, Scopus, and Periódicos Capes for works published up to June 2024, with no lower bound for publication date. Search terms were: ("forensic entomology" OR "vertebrate carrion" OR "vertebrate carcass") AND ("Formicidae" OR "ants") AND ("Brazil" OR "Brasil"). Since major diversity lists were found in theses and dissertations (i.e., gray literature; Yoshida *et al.*, 2024), these sources were included to ensure a more comprehensive and thorough approach. If data were later published and duplicated, only the more detailed source was considered. Literature reviews, books, and honors theses were not included in data collection.

### Data curation and analysis

Data were extracted either from taxonomic tables or the text. Taxonomic names were updated based on the most recent classification (Bolton, 2025). Spelling errors were corrected, and species or genera known not to occur in Brazilian territory (Janicki *et al.*, 2016; Feitosa; Dias, 2024) were assessed as possible historical taxonomical updates. If this verification was not possible, the

record was excluded from the final dataset. To avoid overestimation, all morphospecies within a given genus were grouped and recorded as a single taxon.

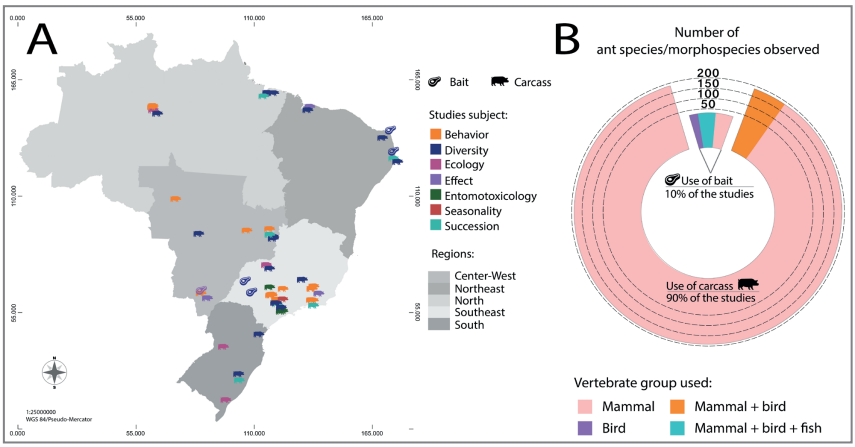
When available, we extracted the following information for each ant occurrence: habitat (e.g., forest, rural, urban), ant presence or abundance in each decomposition stage, role in decomposition (i.g., necrophagous, predator, omnivorous, and incidental), observed behaviors (e.g., tissue removal, infliction of post-mortem injuries), bait attributes (i.e., whole carcass or pieces of carrion, vertebrate species, weight, euthanasia method, sample size), ant collection method, and geographical coordinates. The methods used to euthanize the vertebrates were categorized based on the type of lesions inflicted when it was the case. We also collected metadata, such as year of publication, type of study, main subject, and whether ants were the focus of the study. To standardize decomposition data, we adopted four general stages: fresh, bloated, decay, and dry/remains (Rodriguez; Bass, 1983). When studies referred to alternative decomposition stage terminology (e.g., advanced decay), we reclassified them according to the following criteria: when decomposition was observed from the beginning, the initial stage was classified as 'fresh'; 'bloated' was used when gas accumulation was noted; any subdivisions of the decay process were grouped under 'decay'; and the final stage, marked by the absence of soft tissue, was categorized as 'dry/remains'.

Ant species were assigned trophic, foraging, and nesting ecologies according to Feitosa and Dias (2024), and endemism status (AntWeb, 2025). We also categorized each species, when information was available, based on its observed role in carrion decomposition. For each study, ants were classified as necrophagous if feeding on carrion, predators if preying on other insects, and omnivores if performing both roles. In order to avoid assigning the incidental category to ants from studies that did not observe or report ant behavior, we classified as incidental only if the authors explicitly reported that the ant was not feeding on any of the available resources. Supplementary data is available at https://doi.org/10.6084/m9.figshare.29669132.v2.

## RESULTS

We selected 49 works published between 1997 and 2023, including 30 full articles, seven short communications, and 12 theses or dissertations (Table S1). All five geopolitical regions were represented, with studies from 15 states (Figure 1). More than half of the studies (26) did not have Formicidae as their main focus. Ants were mentioned, and their presence discussed as possibly relevant, but the hypotheses or objectives were related to other groups, mainly Diptera.

**Figure 1 -** (**A**) Geographic distribution of the sampling sites from carrion-visiting ant studies conducted in Brazil. Icons indicate whether the experiment utilized whole carcasses or pieces of carrion (i.e., baits); colors denote the main subject of each study; and gray shading corresponds to the geopolitical regions of the country. (**B**) Total number of ant species collected from carcasses or baits is represented by bar height across concentric dashed-line circles. The longer bar corresponds to studies using whole carcasses, and the shorter to those using baits. Bar colors indicate the vertebrate groups used as carrion or bait.




When considering the main subject of each study, we could observe six categories. The most common category comprised diversity inventories (20 studies), which were focused exclusively on documenting carrion-visiting species and presenting the species list. Although several other studies also presented species lists, their main objectives addressed different topics. These research topics included species behavior on carrion (11 studies); changes in species richness and composition along the decomposition process (i.e., arthropod succession; six studies); the effects of abiotic factors on carrion-visiting communities (five studies); species impact on the decomposition process (four

studies); and entomotoxicology (i.e., how toxins in decomposing tissues affect insects development; three studies).

Nearly all studies sampled whole carcasses (44 studies; Figure 1). Fourteen vertebrate species were utilized, most being mammals (29 studies). The majority of studies used domestic pigs (*Sus scrofa* Linnaeus, 1758) due to their similarity to humans and their potential application in forensic entomology studies (Matuszewski *et al.*, 2020). Other common vertebrates were mice (*Mus musculus* Linnaeus, 1758; seven studies) and rats (*Rattus norvegicus* Berkenhout, 1769; five studies). Bird carcasses were the least common, with five species used in two studies.

In total, 195 ant species and morphospecies (154 species and 41 morphospecies) were found on carcasses, only three, *Camponotus rufipes* (Fabricius, 1775), *C. melanoticus* Emery, 1894, and *Solenopsis saevissima* (Smith, 1855), being observed on both bird and mammal carcasses. Five studies used baits and found in total 42 ant species and morphospecies (29 species and 13 morphospecies; Figure 1). At least 15 species and morphospecies were found in baits from all three vertebrate groups (i.e., bird, fish, and mammal).

The majority of studies (17) collected data with a combination of passive methods and active collections, recording 47 genera, and 123 ant species and morphospecies. Sixteen works sampled solely by active collections and recorded 27 genera and 72 ant species and morphospecies. Nine studies using only passive methods recorded 44 genera and 103 species and morphospecies. Among the passive methods, authors used different types of traps: pitfall traps (12 studies), suspended traps (7), Shannon traps (2), cone traps (1), and unspecified types (3).

**Ant diversity**

In one-quarter (12) of the studies, ants were identified only at the family level. In total, nine subfamilies, 61 genera, and 205 species and morphospecies of ants were recorded (Table S1). When considering only identified species, in total, 50 genera and 162 species were found. The highest species richness was observed in the subfamilies Myrmicinae (95 species and morphospecies) and Formicinae (37 species and morphospecies). *Camponotus* was the most frequently recorded genus, appearing in more than half of the studies, followed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by *Solenopsis* (19 studies), *Crematogaster* (16), *Ectatomma* (15), and *Atta* (12). The most frequent species was *Camponotus rufipes*, present in 14 studies, followed by *Solenopsis saevissima* (eight studies), *Camponotus melanoticus* (seven), *Pachycondyla striata* Smith, 1858 (seven), and *Atta sexdens* (Linnaeus, 1758) (six).

**Ants' role and behavior**

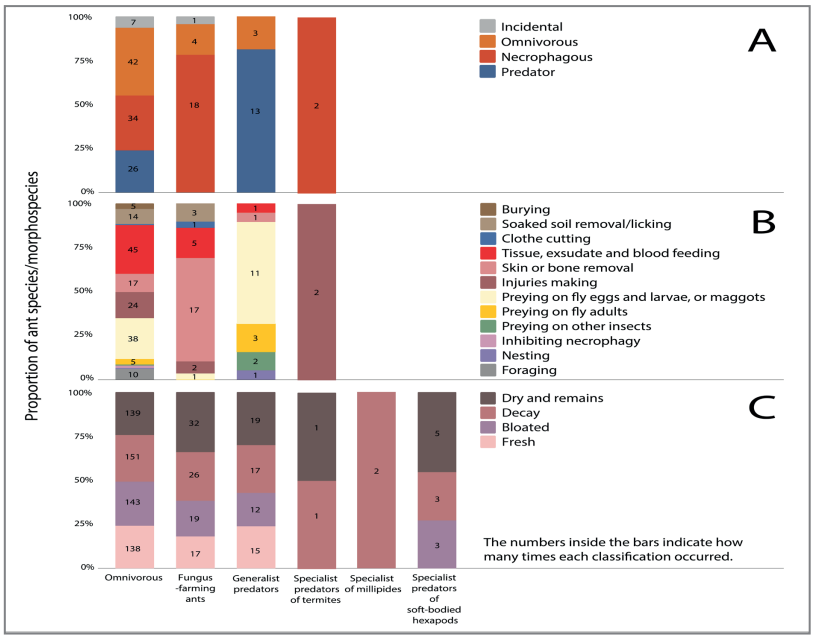
Ants were associated with a functional role in decomposition in 22 studies, covering 53 identified species in 95 records. When morphospecies were included, this number rose to 70 taxa (species and morphospecies), documented in 25 studies and 150 records. Necrophagy included ants taking parts of biological tissues (e.g., bones, skin, and blood) to their nests, and/or causing injuries by feeding directly on the carcass, especially around the nasal and oral areas and other orifices. When acting as predators, ants were observed capturing immature Diptera (eggs, larvae, and pupae), adult Diptera, and other insects (Table S1). In addition, ants fed indirectly or altered the cadaveric environment. These changes included ants covering natural orifices or injuries with soil and sticks, nesting around the carcass, licking and transporting exudate-soaked soil to their colonies, cutting and removing exudate-soaked clothing, causing superficial skin damage, and aggressively preventing other insects from accessing the carcass (Table S1).

Ant species recorded on carrion exhibit diverse trophic, foraging, and nesting ecologies, including generalists (referred to as 'omnivorous' in Feitosa; Dias, 2024, but treated as 'generalists' here to avoid confusion with decomposition roles), specialist predators, army ants, fungus-growers, and both soil- and arboreal-nesting species (Figure 2; according to Feitosa; Dias, 2024). In the matter of trophic ecology, generalist ants were the most frequently reported group, with 27 genera (including species and morphospecies) cited across 40 studies. Of these, 23 studies provided information of 16 genera on their role in the decomposition process (Table S1). Among the generalists, omnivory was the most common role in decomposition (42 records), followed by necrophagy (34) and predation (26; Table S1). Still among the generalists, *Linepithema* was the only genus primarily a predator; however, while not predominantly, *Pheidole* and *Camponotus* were frequently classified as predators in 12 and 5 records,

respectively (Table S1). Two genera were mainly omnivorous, led by *Pheidole* (16 records), followed by *Brachymyrmex* (3). Necrophagy was dominant in three genera: *Camponotus* (15 records), *Solenopsis* (9), and *Cephalotes* (4; Table S1).

Fungus-growing ants were recorded in 18 works, but their role in decomposition was poorly documented. Eleven genera were recorded, with data available for only five. This group was largely necrophagous (Figure 2), especially *Atta* (11 records; Table S1). *Mycocepurus* was categorized as omnivore, while *Acromyrmex* was omnivore and necrophage (Table S1). Predatory ants were represented by 18 genera, in 14 studies, being mostly observed preying on other necrophagous insects. However, only five studies provided decomposition role data. *Neoponera* and *Odontomachus* were recorded as predators. Among five army-ant genera, only *Labidus* had any documented behavior, as omnivorous and as a predator (Table S1). *Tranopelta* was the only specialist predator found and was classified as necrophagous (Figure 2; Table S1).

**Figure 2 -** Proportion of ant species and morphospecies within distinct ecological, foraging, and nesting guilds when classified by Feitosa and Dias (2024), and their roles in carrion decomposition as reported in the studies included in this review (**A**); their specific behaviors when directly or indirectly interacting with carcasses (**B**); and the decomposition stages in which they were recorded (**C**). Numbers overlaid on the bars represent the number of species recorded for each category.



While soil-nesting ants were the most common on carrion, exclusively arboreal ants, represented by *Azteca*, *Cephalotes*, *Dolichoderus*, and *Myrmelachista*, were also recorded (Table S1). They were found along genera with varied nesting strategies, such as *Camponotus*, *Pheidole*, *Pseudomyrmex*, and *Solenopsis*. Since exclusively arboreal ants forage mostly in the canopy, their role in carrion decomposition, which typically occurs on the ground, remains unclear; though *Azteca* was once observed preying on necrophagous insects, *Cephalotes* and *Dolichoderus* were necrophagous, and *Myrmelachista* was incidental.

When sampling on carcasses, only 15 studies specified the decomposition stages in which ants were observed, and just seven quantified their abundance. In total, 111 species from 42 genera were associated with different decomposition stages. Fewer species were recorded in the early stages (59 in fresh, 65 in bloated) compared to the later stages (93 in decay, 91 in remains). Amongst the species found associated with carrion, seven are endemic to Brazil: *Blepharidatta conops* Kempf, 1967, *Camponotus vittatus* Forel, 1904, *Mycetomoellerius iheringi* (Emery, 1888), *Mycetomoellerius oetkeri* (Forel, 1908), *Pachycondyla lenkoi* Kempf, 1962, *Pheidole alienata* Borgmeier, 1929 and *Wasmannia affinis* Santschi, 1929 (Table S1).

**Case studies with human cadavers**

Studies conducted in five different states reported ants in 12 human cadavers. Nine of the corpses were in the fresh stage of decomposition. Ants were identified to the species level in one instance, and in most cases, attributed to a morphospecies. Ants from the genera *Solenopsis*, *Camponotus*, *Pheidole*, *Atta, Cephalotes,* and *Crematogaster* were reported displaying necrophagous behavior. *Solenopsis* sp. and *Camponotus* sp. were responsible for serpentine marks and cigarette burn-like lesions. While *Atta* sp. was associated with circular, irregular-edged skin lesions. The species *Cephalotes atratus* (Linnaeus, 1758), also classified as necrophagous, produced round and brown-colored lesions. Among behaviors not directly related to necrophagy, *Solenopsis* sp. was reported adding plant fragments and small grains to the lesions of two cadavers, and *Atta* sp. was observed cutting the clothing of the deceased at a crime scene. No studies with human cadavers reported ants displaying predatory behavior.

*Solenopsis* was the most frequent genus, present in four corpses, followed by *Camponotus*, found in three. Specimens from the genus *Ectatomma* were found in the initial and advanced stages of decomposition, but no artifacts or other behaviors were reported. Lesions similar to those intra vitam caused by acid or chemical substances were attributed as a result to ants' foraging trail signaling. Other unidentified species caused injuries such as accelerated epidermal detachment, burn-like lesions with dry and serpentine borders, and superficial lesions characterized by yellow abrasions with red margins.

## DISCUSSION

### Ant collection and identification challenges

Little can be said about whether carcass type affects ant diversity and activity, since sample sizes, methods and environments differed between studies. However, morphological characteristics of the decomposing animal likely play a role in ant diversity and activity. Previous research shows that fish carcasses lose 85% of their dry mass after 10 months, compared to 30% for birds under similar circumstances, likely due to different tissue composition (Parmenter; Lamarra, 1991). Larger carcasses can support more diverse assemblages of scavengers (Marais-Werner *et al.*, 2018; Turner *et al.*, 2017) and body cover such as feathers, fur, or dermal plates could restrict access of insects (Matuszewski *et al.*, 2014; Sawyer *et al.*, 2022). These factors could also contribute to variation in decomposition rates among vertebrate groups.

A higher diversity of ant species was found on whole carcasses, compared to when baits (i.e., pieces of carrion) were used. While baits are easier to manage and allow for greater replication, they can be less representative of the carrion decomposition process (LeBlanc; Boudreau; Moreau, 2021; Lutz; Amendt; Moreau, 2025). Baits being a simpler resource, often devoid of dermal cover (e.g., canned sardines), will lose moisture faster and offer a less complex nutrient and microbiological profile (Dáttilo; MacGregor-Fors, 2021; George; Archer; Toop, 2012; LeBlanc; Boudreau; Moreau, 2021; Nene *et al.*, 2016). Nevertheless, controlling bait composition, exposure time, and aging can help address specific questions in carrion ecology (e.g., George; Archer; Toop, 2012; Oliveira; Soares;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Vasconcelos, 2016) as long as the method's limitations are considered. It's also worth noting that tuna is commonly used to attract ants (Brassard *et al.*, 2025; Dáttilo; MacGregor-Fors, 2021; Kirchner *et al.*, 2025). However, studies using this resource typically focus on ant diversity rather than decomposition. As a result, such studies did not appear in our search, likely contributing to the lower diversity observed in bait-based studies.

The most frequent passive collection method was pitfall trapping, which captures a high number of ground-foraging species compared to active collections (Bestelmeyer *et al.*, 2000; Lasmar *et al.*, 2017). While pitfall traps are practical and efficient, caution is needed, as captured ants may not have been attracted to or interacting with the carcass; particularly given that trap distances from baits ranged from 10 cm to 1.5 m. There were several cases in which ants from mass-recruiting species were represented by a sole worker in a pitfall trap, which suggests that the colony was likely not recruiting for that resource. The addition of active collections, especially if combined with standardized observations, helps overcome these limitations by confirming ant interactions with the resource and other organisms.

One-quarter of studies in our survey identified ants only at the family or genus level, despite growing collaborations with taxonomic experts in ant diversity (Feitosa *et al.*, 2023) and in forensic research (Guimarães *et al.*, 2022). Our findings show that such partnerships remain lacking in Brazil, and reflect the taxonomic challenges in biodiversity research and the need for increased investment in the training of taxonomists (Feitosa *et al.*, 2022). Forensic entomology guidelines highlight the need for detailed insect activity records to improve species identification, and to make entomological evidence more useful in investigations (Bambaradeniya; Magni; Dadour, 2023). Accurate identification is crucial in order to confirm ants' activity and role on carrion to further our knowledge in both ecology and forensic science.

**Ant ecology and behavior**

The nine subfamilies observed in the selected studies highlight ants' adaptability in exploiting available resources, and the attractiveness of carrion to generalists. The most frequent and species-rich genera in carrion studies

are also the most common and speciose in other biodiversity studies in Brazil (e.g., *Camponotus*, *Pheidole*, *Solenopsis*, *Crematogaster*; Feitosa *et al.* 2022). Among these species, the effects and dynamics have been explored mainly in the genus *Solenopsis* (Pereira *et al.*, 2017). Aside from *Camponotus*, the most frequent genera comprise ants with mass recruitment (Calcaterra *et al.*, 2008; Ganeshaiah, 2023; Zéphirin *et al.*, 2019), which could monopolize the resource (Czaczkes; Nouvellet; Ratnieks, 2011; de Biseau *et al.*, 1997; Pohl; Ziemen; Witte, 2018) and have implications such as the decrease in the rate of carrion decay and reduced total species richness. At the species level, the most frequent taxa (e.g., *Camponotus rufipes*, *Atta laevigata* (Smith, 1858), *Pachycondyla striata*) have larger body size, which has been suggested as indicative of significant carrion removal (Nooten *et al.*, 2022).

Among the behaviors performed by ants on carcasses, necrophagy was the most representative. Despite the extensive records of these behaviors, we lack studies quantifying ants' contribution to rates of carrion decay through these actions, and implications are largely based on observations of ants removing carrion tissue, creating post-mortem injuries and preying on larvae (Pereira *et al.*, 2017; Ribeiro; Vargas; Lopes, 2018; Santos-Junior *et al.*, 2014). Ants' role as necrophagous seems to be independent of their general diet preferences in other contexts, being a common occurrence in several trophic guilds (De Souza *et al.*, 2020; Leite Junior *et al.*, 2019; Nogueira, 2023; Pinto *et al.*, 2023; Santolin, 2016; Souza, 2020). Most species, if able, will access the resource, and their effect could be more related to morphology than trophic position and nesting habit (Nooten *et al.*, 2022). That is, ants' physical traits might be a more important factor in determining how they interact with carrion and affect decomposition rather than being a generalist, specialist, or arboreal in the ecosystem.

Ants' role as predators appears to be more restricted to a few groups, which could be related to the ants' capacity to capture prey. In the few records of adult flies or third-instar larvae being preyed upon, the predators were mainly larger, stinger-bearing ants such as *Ectatomma* (Gomes; Gomes; Desuó, 2009) and *Neoponera* (Souza, 2020). In contrast, there was one instance of *Atta* trying to capture *Chrysomya albiceps* (Wiedemann, 1819) larvae but being unable to (Souza, 2020).


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Overall, evidence of the effect of ant predatory behavior on decomposition is still scarce, with conflicting results that should be further tested. While a species-specific study suggests that predatory activity may delay decomposition (Pereira *et al.*, 2017), community-level studies show mixed results, with one suggesting a delay in carrion removal (Ribeiro; Vargas; Lopes, 2018) and another finding no effect (Santos-Junior *et al.*, 2014). These findings support the hypothesis that ant impacts on carrion decomposition may be species-specific. Furthermore, groups such as the army ants are still neglected, and could be an interesting avenue of research, given the extreme effect they can have on arthropod communities through predation (Kaspari *et al.*, 2011).

Although we did not directly test this pattern, we noted a higher species richness going further in the decomposition process. The skeletonization stage, characterized by minimal tissue and prey availability, often exhibits a high abundance of ants. During this phase, species have been observed removing remnants of tissue and foraging on soil moistened with decomposition products (Nogueira, 2023; Souza, 2020). At this stage, when other scavengers are less common or have decreased in number (Benbow; Tomberlin; Tarone, 2025; Olea; Mateo-Tomás; Sánchez-Zapata, 2019), ants seem to exploit these remaining resources.

In contrast to the diversity of ecological studies using animal models, the forensic entomology literature focusing on human cadavers and crime scenes is much scarcer. Only three works address this topic, leading to the lack of behavioral records of ants in this context. The type of study is also a factor, as all three works were case studies conducted either at crime scenes (Celino, 2014; Meira *et al.*, 2020) or based solely on photographs of specimens (De Souza *et al.*, 2020). This sampling method is not conducive to the longer and more detailed observations possible in experiments using human cadavers, such as those occasionally conducted in other countries (e.g., Lindgren *et al.*, 2011). For instance, the genus *Ectatomma* has been observed preying on fly larvae in studies with animal models, but in crime scenes, there are no reports of predation or creation of any post-mortem artifacts by this ant. Notably, *Solenopsis* workers' behavior of covering wounds and injuries with soil and other detritus has been observed in both animal models and human cadavers.

In the context of forensic entomology, we found contributions that mostly describe post-mortem artifacts consequence of the necrophagous activity of ants. These alterations ranged from deep punctate marks to superficial patches of dry skin, some similar to those observed in other works (e.g., Byard, 2005; Campobasso *et al.*, 2009; Spitz; Fisher, 1973). These artifacts are considered one of the main impacts of ants on forensic investigations, given that some lesions resemble ante- or peri-mortem injuries relevant to the case, such as cigarette or chemical burns, and may even alter existing wounds (Campobasso *et al.*, 2009). A novel contribution of Brazilian research is the description of tears in clothing, particularly undergarments, caused by leaf-cutting ants (De Souza *et al.*, 2020). While previous works reported ant activity marking the contours of garments (Byard; Heath, 2014), these findings on clothing damage suggest that such activity could lead to erroneous inferences by inexperienced observers, as the resulting alterations may be mistaken for signs of abuse or struggle. Additionally, ants tearing through undergarments can expose natural orifices, which may serve as oviposition sites for Diptera, potentially facilitating colonization by necrophagous flies. The influence of ants on the estimation of PMImin remains speculative, based primarily on observational data, and lacks robust, formal testing. This mirrors a global trend in which such an effect is only briefly addressed in the discussion sections of published studies.

**Implications and future research**

In the last two decades, scientific production on carrion-visiting ants in Brazil has remained steady, while forensic entomology has seen an increase in publications (Guimarães *et al.*, 2022). Despite being one of the most studied insect groups (Noriega *et al.*, 2018), Formicidae is rarely the focus of carrion ecology or forensic entomology studies, presenting potential for new research. Most studies included in our survey were conducted in the Southeast, possibly reflecting the concentration of research centers (Feitosa *et al.*, 2022). Still, this trend could change rapidly, as seen with the geographic expansion of forensic entomology studies in Brazil (Guimarães *et al.*, 2022).

More than half of ant-carrion studies conducted in Brazil consisted of diversity inventories or focused on species richness patterns in distinct environments.


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The results show that a wide diversity of ants, despite their diet preferences, will access vertebrate carrion. Moreover, broader ecological patterns of diversity are likely to be observed despite the presence of vertebrate carcasses, since this does not seem to be the main food source of any ant group. Thus, we suggest a shift in focus, from diversity studies to hypothesis testing more specific to the process of decomposition. There are important gaps regarding the quantification of carrion removal by ants (e.g., Nooten *et al.*, 2022), their effect on fly larvae development (e.g., Sawyer *et al.*, 2022) and their competition with vertebrates (e.g., Turner; Conner; Beasley, 2021). Instead of studies testing for changes in species richness in distinct seasons, we should try to disentangle the effect of climate from ant species richness on the rate of carrion decay, for example.

Moreover, no studies have focused on the nutritional ecology of carrion--visiting ants and the implications of carrion-use for colony fitness along their development. For instance, it remains unclear how fungus-growing ants, such as *Atta laevigata*, utilize carcasses. Hypotheses could range from a conflict between the interests of the fungus and those of the ants, to the possibility that carrion may be post-processed inside the nest and discarded or even retained. In forensic entomology, there are gaps pertaining to the detectability of substances ingested perimortem on ants that are feeding on cadavers, and no Brazilian study systematically compares different patterns of post-mortem injuries caused by distinct ant species (e.g., Pezzi *et al.*, 2020).

There is a tradition of using pig carrion in decomposition studies, due to their similarity to human corpses and consequent importance for forensic studies (Matuszewski *et al.*, 2020). We argue that despite this, most studies we reviewed offer primarily ecological insights and thus could benefit from utilizing carcasses that better represent the natural habitats where they were conducted. Since ants encounter a variety of carcasses in nature, it's important to investigate how different carcass types influence ant behavior and their role in decomposition, extending beyond forensic entomology.

We argue that with the small sample sizes for most of these studies and the high heterogeneity in ants' community, we still do not have enough information to assess the effect of ants in this process. This is a global trend, in which few studies quantify carcass removal by ants (Campobasso *et al.*, 2009; Eubanks; Lin; Tarone, 2019) and the ones that do, focus on a few species, mostly

from the genus *Solenopsis* (e.g., Stoker; Grant; Bradleigh Vinson, 1995; Wells; Greenberg, 1994).

Given the remarkable diversity of Formicidae in Brazil (Feitosa *et al.*, 2022) and the several functional groups of ants recorded on carrion, studies with focal species' traits would help elucidate the outcomes of the ant-carrion interaction, and the mechanisms by which ants can influence carrion breakdown. We suggest studies that quantify carrion removal by frequently found generalist and large ants, such as *Camponotus rufipes* and *Camponotus melanoticus*; small mass recruiting species such as those of the genera *Crematogaster* and *Pheidole*; large predatory ants such as *Pachycondyla striata*; and the abundant large-bodied leaf-cutter ants of the species *Atta sexdens*. While species-focused experiments are useful for understanding how carrion decomposition is affected by ants, in nature, carcasses are exposed to a broad range of species, and carcass fate will be impacted by these interactions in addition to individual species. Therefore, community-level studies are also important for investigating ants' importance for decomposition and should not be neglected.

## CONCLUSION

Myrmecological studies on carrion ecology and forensic entomology have been published at a steady rate for the last 20 years. Ants are present throughout the process of carrion decomposition and can impact directly or indirectly this process. Despite its importance, the information provided by Brazilian literature regarding ants' role in carrion decomposition is scarce. Most of what we know pertains to the high diversity of ant species that are observed on carrion, but precise species identification is lacking. We encourage collaborations with taxonomists, since accurate species identification allows for better inferences of ants' impact in carrion ecology and forensic entomology.

Throughout the whole process of carrion decomposition, generalist widespread species are the most frequent, but a wide breadth of species is present, with no group specialized in this resource. We suggest that future studies should focus on morphological and behavioral traits rather than trophic guilds. A selection from the most frequent ants in carcasses, which are common species with diverse ecologies, could be a viable strategy.


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The quantification of ants' contribution to carrion breakdown is also important. Despite the several species recorded on vertebrate carcasses, few works have measured their effect or even described their actions, mainly focusing on richness and abundance data. In regard to experimental design, we suggest a focus on well-replicated experiments, so that conclusions are more robust. We could also benefit from studies exploring carrion decomposition dynamics with vertebrate carcasses from different species in distinct regions and seasons. These studies could help elucidate the dynamics of ant communities that access an ephemeral resource and could have relevant contributions for criminal investigations. We propose a shift of focus from diversity inventories to hypothesis testing specific to the process of decomposition or forensic entomology.

Overall, with the high diversity of ants, and research groups throughout the country interested in investigating ant-carrion interactions, future studies on the role of ants in carrion decomposition are promising in Brazil.


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# 12

# WHO ARE THE ANTS INTERACTING WITH PLANTS BEARING EXTRAFLORAL NECTARIES IN BRAZIL?

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# ABSTRACT

Ants engage in numerous ecological interactions, including protective mutualisms with plants with extrafloral nectaries (EFNs). In these interactions, plants secrete extrafloral nectar – a carbohydrate-rich solution attractive to ants. Once on plants, ants may deter or consume herbivores, thereby reducing herbivory on plants. Because EFNs morphology does not restrict access to extrafloral nectar, these plants interact with several ant species simultaneously or throughout their lifetime. The lack of broad-scale descriptive information about ant assemblage visiting plants with EFNs and their variation across habitats deeply reduces our understanding about the factors regulating the functioning of this interaction. To address this gap, we conducted a systematic review to describe 1) the ant assemblage interacting with plants with EFNs and 2) how this ant assemblage varies in Brazilian domains. We found 106 studies in 135 locations across Brazil with 2459 observations. These studies described 186 ant species in 44 genera, mostly Formicinae and Myrmicinae, interacting with 155 plant species with EFNs. We also found that the domain with the largest number of ant genera interacting with plants with EFNs was the Amazon Forest, while for ant species Cerrado was the most diverse. Finally, despite the differences among Brazilian domains, the assemblage of ants interacting with plant species with EFNs was similar, both at genera and species levels. This pattern indicates that only a subset of ant species available in each ecosystem interact with plant species with EFNs, highlighting the relevance of some ant species for this mutualistic interaction.

**Keywords:** Ant-plant interaction; bodyguard ants; generalized mutualism; protection mutualisms; systematic review.

## INTRODUCTION

Mutualisms are reciprocal exploitative interactions in which both partners obtain a service or a reward otherwise unattainable (Bronstein, 2015). These interactions vary from highly specialized, with a few species on each side, to generalized, involving multiple species (Afkhami *et al.*, 2014). Although in generalized mutualisms more than one partner can provide the same reward or services, their quality varies due to species-specific differences in morphology, physiology and behavior (Frederickson, 2005; Miller, 2007). Thus, incorporating the composition of mutualistic assemblages might help us predict the outcome of mutualistic interactions across habitats. However, linking assemblage composition to mutualistic outcomes has been hindered by the lack of studies properly describing these assemblages and their assembly rules. Overcoming this gap is a fundamental task, especially under the current scenario of climate change that are expected to deeply modify the assemblages of mutualistic partners, mainly due to species loss (Miller-Struttmann *et al.*, 2015).

In ant-plant protection mutualisms, plants may provide nests (*e.g.*, domatia) or nutritional rewards to ants (Heil, 2010). In most cases, the main nutritional reward is produced in a secretory structure called extrafloral nectaries (EFNs) (but see Heil, 2010 for exceptions). Extrafloral nectaries are found in more than 4000 plant species, and they vary in position, size, and morphology within the plant, as well as in the quantity and quality of nectar secreted (Weber and Keeler, 2013). While consuming extrafloral nectar, ants can reduce herbivory by deterring or consuming herbivores (Rosumek *et al.*, 2009). Plants with EFNs can interact with diverse ant assemblages that differ in protective traits, such as aggressiveness (Leal *et al.*, 2023) and recruitment capacity (Kolay *et al.*, 2020). Therefore, the protective service provided by ants varies according to the taxonomic and functional composition of ants visiting plants with EFNs (Nogueira *et al.*, 2015; Sendoya and Oliveira, 2015; Sendoya and Oliveira, 2017). In addition to composition, the interaction patterns between ants and plants with EFNs is an important component to understanding the dynamic of mutualisms (Guimarães *et al.*, 2006; Juárez-Juárez *et al.*, 2023). Intriguingly, summarized information on ant assemblage interacting with plants with EFNs and their spatial and temporal variation in composition and patterns of interaction remains scarce,


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limiting our understanding of the factors shaping ant composition in different ecological contexts.

Brazil has been a hub for studies on ant-plant mutualistic interactions mediated by EFNs (see geographical distribution of studies in Leal *et al.*, 2023). This pattern could be explained by the ease of finding plants with EFNs. These plants comprise up to 35% of individuals and 58% of plant species in Cerrado savanna (Belchior *et al.*, 2016; Boudouris and Queenborough, 2013), up to 20% of individuals and 10.5% of species on Atlantic Forest (Câmara *et al.*, 2017) and 40% of individuals and 15% of woody species in Caatinga (Leal *et al.*, 2017). Not surprisingly, these studies have been mainly focused on the plant component of the interaction (see Leal *et al.*, 2023; Rosumek *et al.*, 2009; Trager *et al.*, 2010), disregarding the mechanisms underlying ant assemblage composition within and between habitats. In some of these studies, it is possible to find a list of ant species interacting with plants at local study sites, but this information is fragmented across studies and habitats, hindering a comprehensive broad-scale evaluation of ant assemblages visiting plants with EFNs in Brazil both within and between habitats. Interestingly, ants stand out as an exemplary model for biodiversity research in Brazil mainly due to their astonishing diversity in the country (Schmidt *et al.*, 2022). About one-third of the described ant genera (117 out of 345) and one-tenth of the described species of the planet (about 1500 out of 14000) occur in Brazil (Bolton, 2022; Dunn *et al.*, 2007; Feitosa *et al.*, 2022). Most of the biodiversity publications, however, have focused on the factors driving the ant community structure (e.g., Wilker *et al.*, 2024), often assuming that all ants interact equally with plants with EFNs.

In this chapter, we provide the first broad assessment of the ant species associated with plants with EFNs in Brazil. More specifically, we performed a systematic review to answer the following questions: 1) Who are the ant species interacting with plants with EFNs in different Brazilian domains? and 2) how does this ant assemblage and the patterns of ant-plant interaction varies across Brazilian domains? We evaluated the composition of mutualistic ant assemblages into the six vegetation domains officially recognized by Instituto Brasileiro de Geografia e Estatística (2006): Amazon forest (tropical rainforest), Atlantic rainforest (tropical forest across Brazilian coast), Caatinga (seasonal tropical dry forest), Cerrado (savanna), Pantanal (seasonally flooded plain) and

Pampas (subtropical grasslands). Still, to evaluate how the patterns of ant-plant interaction vary across the Brazilian domains, we evaluated the structure of ecological networks formed by the ant-plant interactions observed in each Brazilian domain. By answering these questions, we aim to create the first dataset compiling the ant assemblage associated with plants with EFN in Brazil, highlighting diversity and abundance patterns of this protection mutualism. This dataset will support future research in understudied domains, improving our knowledge about the functioning of these interactions across Brazil — a continental country sheltering some of the most biodiverse habitats worldwide..

## METHODS

### Data search

We searched for studies about the interaction between ants and plants with EFN on ISI Web of Science (main collection) and Scopus. We used the keywords "extrafloral nectar* AND biotic defen*e*". Initially, we considered only studies published in English between 1945 (first year available on Web of Science and Scopus) and June 28th, 2024.To mitigate language and publishing bias, we also searched for unpublished and published studies written in Portuguese on Google Scholar. To accomplish this, we performed one search for each Brazilian domain using the following Portuguese keywords "nectarios extraflorais" (extrafloral nectaries) AND the name of the Brazilian domain. For domain, we used "amazonia" (Amazon rainforest), "caatinga", "cerrado", "mata atlântica" (Atlantic rainforest), "pampa", "pantanal" or "restinga" (Brazilian sand bank). Although restinga is not recognized as a Brazilian domain, the term is widely used in studies conducted on the Brazilian coast. We used Publish or Perish software v. 8.17.4863 (Tarma software research ltda.) to conduct and download our searches on Google Scholar (Harzing, 2007). Finally, because we did not find any studies reporting ants interacting with plants with EFNs on Pantanal, we included a review by Prof. Camila Aoki to be as exhaustive as possible (N = 19). She searched for studies about ants on the Pantanal regardless of the interaction with plants with EFN. We used *litsearchR* v. 0.4.1 package (Grames *et al.*, 2020) in R software v. 4.0.5 (R Core Team, 2022) to help us identify and


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remove duplicates among searches (n = 2074 studies). Additionally, we removed studies that were already published in journals and identified in our search on Web of Science and Scopus. In the end, our database comprised 3422 studies (see Fig S1. PRISMA flowchart and Table S1 PRISMA checklist for details).

**Study selection**

To determine whether studies were suitable for our review, we first inspected the title and abstracts and included studies that mentioned protection mutualism, extrafloral nectaries, or ants. We excluded studies in which plants offered other rewards to ants, such as nesting or nutrition by food bodies. Then, we read the study looking for any taxonomic information about ants and plants with extrafloral nectaries. If the study reported ant taxonomy but not the plant species, we collected only information about ants. In this screening phase, we excluded studies in which data collection was based on baits near to plants unless they specified which ant species feed on extrafloral nectar.

**Data extraction**

To investigate the relationship between ants and plants with EFNs, we registered the ant species, morphospecies or genus, plant species (when available), and location where the study was conducted. To confirm whether ant and plant species names were valid, we checked ant species on AntCat (Bolton, 2024), and plant species on Plants of the World Online (POWO, 2024). We also checked ant species distribution using the Global Ant Biodiversity Informatics (Guénard *et al.*, 2017) available on AntMaps (Janicki *et al.*, 2016). In cases of doubt, we contacted a specialist, who has been working on invasive ant species in Brazil (Vitória Brunetta – MSc student at the Universidade Federal do Paraná). Four independent researchers (AVS, GM, HS, and LL) performed study selection and data extraction, investigating different studies in independent parallel screening.

**Brazilian ecosystem classification**

To determine the Brazilian Domain where ants were observed interacting with EFNs, we mapped the study sites according to the coordinates provided by the authors. If the study did not provide the coordinates but provided the name of the location, we searched for approximated coordinates on Google Maps. After mapping them, we extracted the domain information of each ant-plant occurrence. To accomplish this, we used the official raster layer of Brazilian domains proposed by the Biomes of Brazil of Instituto Brasileiro de Geografia e Estatística (IBGE, 2006). This raster divides Brazil into six domains: Amazon rainforest, Atlantic rainforest, Caatinga, Cerrado, Pampa, and Pantanal, according to vegetation, geology and climate (IBGE, 2006). We mapped the data using *ggmap* v. 4.0.0 (Kahle *et al.*, 2023), *sf* v. *1.0-12* (Pebesma *et al.*, 2023) and *raster* v. 3.6-20 packages (Hijmans, 2021) in R software v. 4.1.3 (R Core Team, 2022).

**Statistical analysis**

To evaluate whether the composition of ant assemblages visiting EFNs differs among Brazilian domains, we performed a Permutational Multivariate Analysis of Variance (PERMANOVA). We performed PERMANOVA at the genus- and at the species-level, separately. For the genus level, we included data about all ants, but for species we subset the data to exclude morphospecies and kept only ants identified to the species level. We used a Jaccard dissimilarity distance matrix since our data is based on the presence/absence of a given ant genus and species visiting EFNs in a given domain. To represent graphically the assemblage dissimilarities, we performed a non-metric multidimensional scale analysis (NMDS), using the PERMANOVA matrix of dissimilarity, grouped by the domain. Because many ant genera and species were found in only one study, we performed the same analyses as described above but excluding genera and species that were observed in only one study.

To evaluate the patterns of interactions among ants and plants with EFN in different Brazilian domains, we used a network approach. To accomplish this, we constructed quantitative matrices of interactions between plants and ant genera for each domain. The strength of each interaction was considered as the number


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of independent observations of each interaction across localities. We analyzed this data by calculating metrics widely used to describe structural properties of bipartite ecological networks: H2' for estimating network specialization (quantifies the degree of exclusive interactions between ants and plants; Bluethgen *et al.*, 2006), wNODF for estimation of nestedness (measures non-random interaction patterns between specialist and generalist ant and plant species; Almeida-Neto *et al.*, 2010) and modularity (identifies subgroups of tightly interacting species; Dorman and Strauss, 2014). For estimating statistical significance, all metrics were compared against the distribution of 1000 values from null models from each domain constructed with the "vaznull" algorithm (that keeps the total number of interactions per species and the total connectance of the network) in the *bipartite* v. 2.20 package. All analyses were done in R using *vegan* v. 2.6-4 (Oksanen *et al.*, 2019) while figures were created using *ggplot2* v. 3.5.1 (Wickham, 2016) and *bipartite* (Dormann *et al.*, 2008)

## RESULTS

Of the 3422 studies, 106 described ants interacting with plants with EFN. From the 106 studies included here, 66 published and 44 unpublished, corresponding to 2459 observations of different ants on plants with EFNs across Brazilian domains (Fig. 1, see S2 for a list of the studies included). These studies described 186 ant species belonging to 44 genera interacting with 155 plant species with EFNs across six Brazilian domains in 135 locations (Fig. 2). Most studies described that ants visiting plants with EFNs belong to Formicinae (N = 103 studies), followed by Myrmicinae (N = 80), Pseudomyrmecinae and Ectatomminae (N = 62 each), Dolichoderinae (N = 48), Ponerinae (N = 30) and Dorylinae and Paraponerinae with one observation each. The number of species and the percentage of unidentified observations per genus are described in Table 1. Regarding ant species, the most common species reported to visit plants with EFNs were *Camponotus crassus* Mayr 1862 (Formicinae) (N = 65 observations), *Cephalotes pusillus* (Klug 1824) (Myrmicinae) (N = 44), *Ectatomma tuberculatum* (Olivier 1792) (Ectatomminae) (N =38), *Camponotus blandus* Smith 1858 (Formicinae) (N = 37) and *Pseudomyrmex gracilis* (Fabricius 1804) (Pseudomyrmecinae) (N = 33), while 90 ant species were observed in only one study. Ants

were identified up to species level in 57.7% of the 2459 observations. In 0.4% and 41.8% of the observations ants were classified up to group (classification below genus, restricting the morphospecies to a group of species) and genus level (morphospecies), respectively. Three ant species were likely misidentified due to their geographical distribution outside the Brazilian range: *Camponotus pallens* Le Guillou 1842 (Italy and Tunisia), *Poneracantha semiferox* Brown 1958 (Ectatomminae) (Haiti and Dominican Republic) and *Pseudomyrmex pallidus* Smith 1855 (North and Central America). For a complete list of ant species visiting the plants and more detail on their occurrence, see the Supplementary material (https://doi.org/10.5281/zenodo.17226318).

Most of the studies included in our database were carried out in the Cerrado domain (N = 68) in 28 different locations, followed by Atlantic Forest (N = 18, locations = 17), Caatinga (N = 11, locations = 7) and Amazon forest (N = 8, locations = 10). Pampa (locations = 2) and Pantanal (location = 1) were the least studied domains, with one study each (Fig. 1). The domain with the largest number of ant genera interacting with EFNs was the Amazon Forest and Cerrado, with 32 and 31 genera, respectively (Fig. 3). *Camponotus* was the predominant genus visiting plants with EFNs across all Brazilian Domains, except in the Amazon Forest, where *Crematogaster* ants were the most frequently observed (Fig. 2). When considering only the records in which ants were classified up to species levels, Cerrado and Atlantic Forest sheltered the richest ant assemblages visiting EFNs (Fig. 3). Although the Amazon Forest, Cerrado and Atlantic Forest had similar number of ant genera visiting plants with EFN, the number of ant species is higher in Cerrado, with almost three-fold more ant species described than Amazon Forest (Fig. 3). In comparison to other ant-plant ecological networks (e.g., Pichon *et al.*, 2024; Schleuning *et al.*, 2012), our networks exhibited low levels of specialization (H2) and modularity, whereas a relatively high level of nestedness (wNODF) (Table 2). However, only nestedness in Amazon Forest and Cerrado were different from null models (Table 2). Finally, we found no difference among the composition of genera ($F_{5, 59} = 1.06$, $p = 0.37$, stress = 0.15, Fig. 4A) or species ($F_{5, 45} = 1.17$, $p = 0.07$, stress = 0.13, Fig. 4B) of ants visiting plants with EFN across domains. The removal of genera ($F_{5, 59} = 0.96$, $p = 0.33$, stress = 0.14, Fig. S2A) and species ($F_{5, 45} = 0.96$,


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p = 0.65, stress = 0.13, Fig. S2B) of ants visiting EFNs that were observed in only one study did not change our results.

**Fig. 1 -** Distribution of sampled areas for interactions between ants and plants with extrafloral nectaries across Brazilian domains. The data was collected from published (circle) or unpublished (triangle) studies. Five studies sampled more than one area and, therefore, are represented by more than one dot. The intensity of the black color of the dots represents the number of times that each site was studied. The darker the color, the larger the number of studies conducted in that region. The size of the dot (n) represents the number of observations within each study and location. The larger the dot, the larger the number of observations from that study in that area.

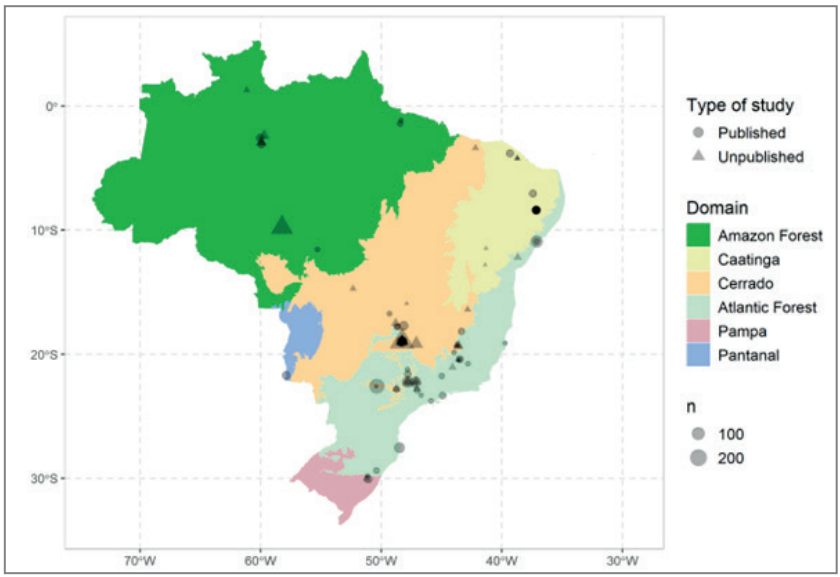
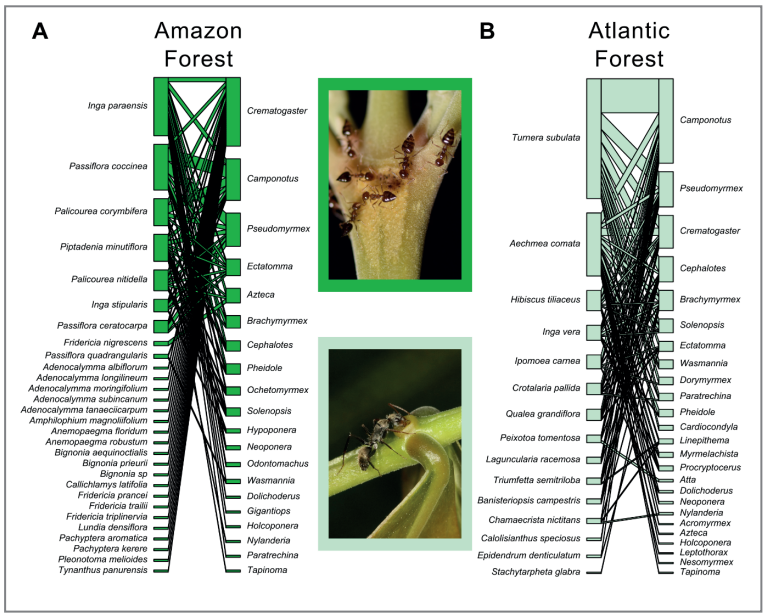


**Fig. 2 -** Patterns of ant genus interaction with plant species with extrafloral nectaries across Brazilian domains. Plant species and ant genera are depicted on the left and right side of the networks, respectively. Lines represent the interaction between the plant species and ants from each genus. The thicker the line, the greater the number of observations between the ant genera and the plant species. (A) Amazon Forest network (picture showing EFNs on the shoot of *Palicourea sp.* visited by *Crematogaster sp.*) ; (B) Atlantic Forest network (picture showing the EFN between leaflets in the compound leaf of *Inga* sp. visited by *Camponotus blandus)*; (C) Cerrado network (picture showing EFN in the stipule at the base of *Ouratea expectabilis* leaf visited by *Cephalotus pusillus)*, (D) Caatinga network (picture showing paired EFNs on the shoot of *Qualea* sp. visited by *Camponotus crassus)*, (E) Pampa network (picture showing EFN on the petiole base of *Erytrina cristagally* leaf visited by *Camponotus cingulatus)* and (F) Pantanal network (picture showing EFN at the base of the leaf blade of *Ipomoea* sp. visited by *Dorymyrmex pyramicus)*. The *Erytrina* species in the image is not in the Pampa network, but it is a common species in this domain, although it was not formally included in any study recovered in our review. Image credits: Sebastian Sendoya.



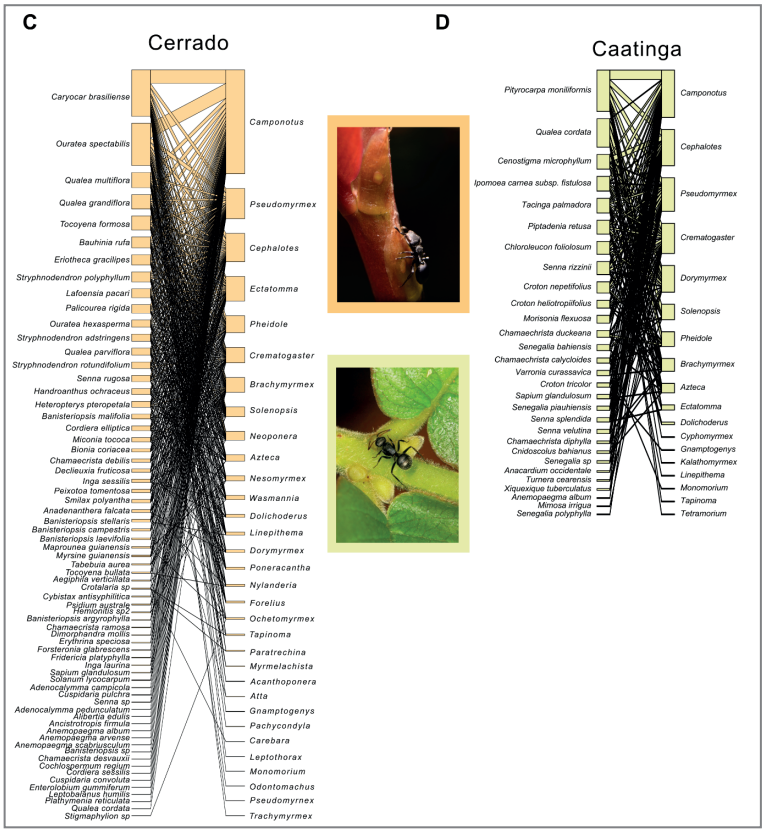

C
Cerrado
Caryocar brasiliense
Ouratea spectabilis
Qualea multiflora
Qualea grandiflora
Tocoyena formosa
Bauhinia rufa
Eriotheca gracilipes
Stryphnodendron polyphyllum
Lafoensia pacari
Palicourea rigida
Ouratea hexasperma
Stryphnodendron adstringens
Qualea parviflora
Stryphnodendron rotundifolium
Senna rugosa
Handroanthus ochraceus
Heteropterys pteropetala
Banisteriopsis malifolia
Cordiera elliptica
Miconia tococa
Bionia coriacea
Chamaecrista debilis
Declieuxia fruticosa
Inga sessilis
Peixotoa tomentosa
Smilax polyantha
Anadenanthera falcata
Banisteriopsis stellaris
Banisteriopsis campestris
Banisteriopsis laevifolia
Maprounea guianensis
Myrsine guianensis
Tabebuia aurea
Tocoyena bullata
Aeigiphila verticillata
Crotalaria sp
Cybistax antisyphilitica
Psidium australe
Hemiorrhiza sp2
Banisteriopsis argyrophylla
Chamaecrista ramosa
Dimorphandra mollis
Erythrina speciosa
Forsteronia glabrescens
Fridericia platyphylla
Inga laurina
Sapium glandulosum
Solanum lycocarpum
Adenocalymma campicola
Cuspidaria pulchra
Senna sp
Adenocalymma peduncularum
Albertia edulis
Ancistrotropis firmula
Anemopaegma album
Anemopaegma arvense
Anemopaegma scabriusculum
Banisteriopsis sp
Chamaecrista desvauxii
Cochlospermum regium
Cordiera sessilis
Cuspidaria convoluta
Enterolobium gummiferum
Leptolobiarus humilis
Platymenia reticulata
Qualea cordata
Stigmaphyllon sp
Camponotus
Pseudomyrmex
Cephalotes
Ectatomma
Pheidole
Crematogaster
Brachymyrmex
Solenopsis
Neoponera
Azteca
Nesomyrmex
Wasmannia
Dolichoderus
Linepithema
Dorymyrmex
Poneracantha
Nylanderia
Forelius
Ochetomyrmex
Tapinoma
Paratrechina
Myrmelachista
Acanthoponera
Atta
Gnamptogenys
Pachycondyla
Carebara
Leptothorax
Monomorium
Odontomachus
Pseudomyrnex
Trachymyrmex
D
Caatinga
Pityrocarpa moniliformis
Qualea cordata
Cenostigma microphyllum
Ipomoea carnea subsp. fistulosa
Tacinga palmadora
Piptadenia retusa
Chloroleucon foliolosum
Senna rizzinii
Croton nepetifolius
Croton heliotropiifolius
Morisonia flexuosa
Chamaechrista duckeana
Senegalia bahiensis
Chamaechrista calycloides
Varronia curassavica
Croton tricolor
Sapium glandulosum
Senegalia piauhiensis
Senna splendida
Senna velutina
Chamaechrista diphylla
Cnidoscolus bahianus
Senegalia sp
Anacardium occidentale
Turnera cearensis
Xiquexique tuberculatus
Anemopaegma album
Mimosa irrigua
Senegalia polyphylla
Camponotus
Cephalotes
Pseudomyrmex
Crematogaster
Dorymyrmex
Solenopsis
Pheidole
Brachymyrmex
Azteca
Ectatomma
Dolichoderus
Cyphomyrmex
Gnamptogenys
Kalathomyrmex
Linepithema
Monomorium
Tapinoma
Tetramorium
E
Pampa
Chamaecrista repens
Passiflora suberosa
Camponotus
Pheidole
Crematogaster
Brachymyrmex
Pseudomyrmex
Solenopsis
Cyphomyrmex
Ochetomyrmex
Paratrechina
Wasmannia
F
Pantanal
Ipomoea alba
Ipomoea amnicola
Neptunia plena
Camponotus
Cephalotes
Crematogaster
Cyphomyrmex
Dorymyrmex
Ectatomma
Linepithema
Nylanderia
Odontomachus
Pheidole
Pseudomyrmex
Solenopsis

**Table 1 -** Diversity of ant genera associated with plants with extrafloral nectaries (EFNs) across Brazilian domains, including number of species, number of observations (N obs.) and percentage of unidentified ants per genera. Data were compiled through a systematic review of published and unpublished studies conducted in Brazil, focusing on ant-plant interaction patterns involving plants with EFNs

| Genera | Species | N obs. | % Unidentified per genera | Domains[1] |
|---|---|---|---|---|
| **Dolichoderinae** | | | | |
| *Azteca* | 1 | 60 | 98.3 | AM, AT, CE, CA |
| *Dolichoderus* | 7 | 39 | 66.7 | AM, AT, CA, CE |
| *Dorymyrmex* | 4 | 56 | 53.6 | AM, AT, CA, CE, PT |
| *Forelius* | 1 | 9 | 0 | CE |
| *Linepithema* | 6 | 28 | 25 | AM, AT, CA, CE, PT |
| *Tapinoma* | 1 | 14 | 92.9 | AM, AT, CA, CE |
| **Dorylinae** | | | | |
| *Eciton* | 0 | 1 | 100 | AM |
| **Ectatomminae** | | | | |
| *Acanthoponera* | 1 | 2 | 0 | CE |
| *Ectatomma* | 8 | 151 | 7.9 | AM, AT, CA, CE, PT |
| *Gnamptogenys* | 1 | 4 | 50 | AT, CA, CE |
| *Holcoponera* | 1 | 2 | 0 | AM, AT |
| *Poneracantha* | 1 | 13 | 0 | CE |
| **Formicinae** | | | | |
| *Brachymyrmex* | 7 | 130 | 79.2 | AM, AT, CA, CE, PP |
| *Camponotus* | 36 | 745 | 27 | AM, AT, CA, CE, PP, PT |
| *Gigantiops* | 1 | 2 | 0 | AM |
| *Myrmelachista* | 2 | 10 | 70 | AT, CE |
| *Nylanderia* | 1 | 25 | 96 | AM, AT, CE, PT |
| *Paratrechina* | 1 | 13 | 61.5 | AM, AT, CE, PP |
| **Myrmicinae** | | | | |
| *Acromyrmex* | 1 | 1 | 0 | AT |
| *Atta* | 1 | 6 | 66.7 | AT, CE |
| *Cephalotes* | 20 | 231 | 20.3 | AM, AT, CA, CE, PT |
| *Cardiocondyla* | 1 | 5 | 20 | AM, AT |
| *Carebara* | 0 | 1 | 100 | CE |
| *Crematogaster* | 22 | 204 | 51.5 | AM, AT, CA, CE, PP, PT |
| *Cyphomyrmex* | 2 | 5 | 40 | AM, CA, PP, PT |
| *Kalathomyrmex* | 0 | 1 | 100 | CA |
| *Megalomyrmex* | 0 | 1 | 100 | AM |
| *Monomorium* | 1 | 2 | 50 | CA, CE |

| Genera | Species | N obs. | % Unidentified per genera | Domains[1] |
|---|---|---|---|---|
| *Nesomyrmex* | 2 | 31 | 51.6 | AM, AT, CE |
| *Ochetomyrmex* | 2 | 16 | 18.7 | AM, CE, PP |
| *Pheidole* | 11 | 156 | 84 | AM, AT, CA, CE, PP, PT |
| *Procryptocerus* | 2 | 4 | 50 | AT |
| *Sericomyrmex* | 0 | 1 | 100 | AM |
| *Solenopsis* | 7 | 100 | 85 | AM, AT, CA, CE, PP, PT |
| *Strumigenys* | 0 | 3 | 100 | AM |
| *Tetramorium* | 0 | 1 | 100 | CA |
| *Trachymyrmex* | 0 | 2 | 100 | AM, CE |
| *Wasmannia* | 2 | 33 | 66.7 | AM, AT, CE, PP |
| **Paraponerinae** | | | | |
| *Paraponera* | 1 | 1 | 0 | AM |
| **Ponerinae** | | | | |
| *Hypoponera* | 0 | 2 | 100 | AM |
| *Neoponera* | 7 | 50 | 0 | AM, AT, CE |
| *Odontomachus* | 3 | 6 | 33.3 | AM, CE, PT |
| *Pachycondyla* | 1 | 16 | 81.2 | AM, CE |
| Pseudomyrmecinae | | | | |
| *Pseudomyrmex* | 20 | 276 | 36.2 | AM, AT, CA, CE, PP, PT |

[1] AM = Amazon Forest, AT = Atlantic Forest, CA = Caatinga, CE = Cerrado, PP = Pampa and PT = Pantanal.

**Table 2 -** Network metrics from the interaction between plants with extrafloral nectaries and ant genus across Brazilian domains. H2' is the overall level of specialization (Blüthgen et al., 2006), wNODF is a weighted estimation of nestedness (Almeida-Neto and Ulrich, 2011) and modularity is a measure of the strength of division of the network into groups (Dormann and Strauss, 2014). * Identify metrics whose values were significantly different from estimation for null models.

| Domain | $H_2'$ | wNODF | Modularity |
|---|---|---|---|
| Amazon Forest | 0.104 | 25.014* | 0.379 |
| Atlantic Forest | 0.147 | 36.266 | 0.236 |
| Cerrado | 0.066 | 54.508* | 0.123 |
| Caatinga | 0.184 | 33.424 | 0.235 |
| Pampa | 0.081 | 27.329 | 0.143 |
| Pantanal | 0.204 | 13.768 | 0.159 |

**Fig. 3 -** Richness of ants visiting plants with extrafloral nectaries across different Brazilian domains. (A) Number of ant genera (including ant species and morphospecies). (B) Number of ant species (including only ants described to species level). Each color represents a different Brazilian domain.

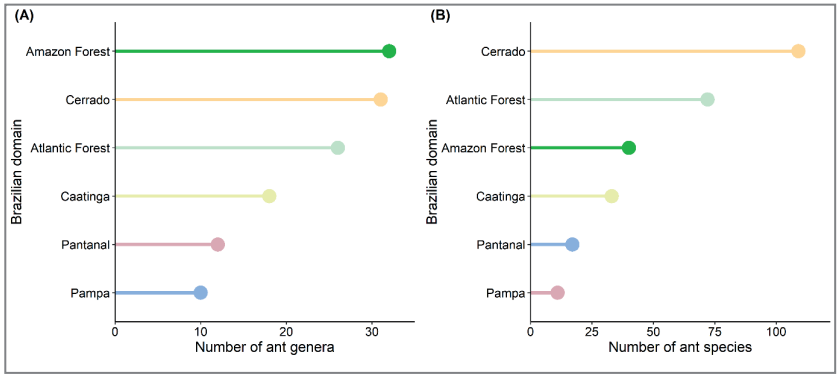
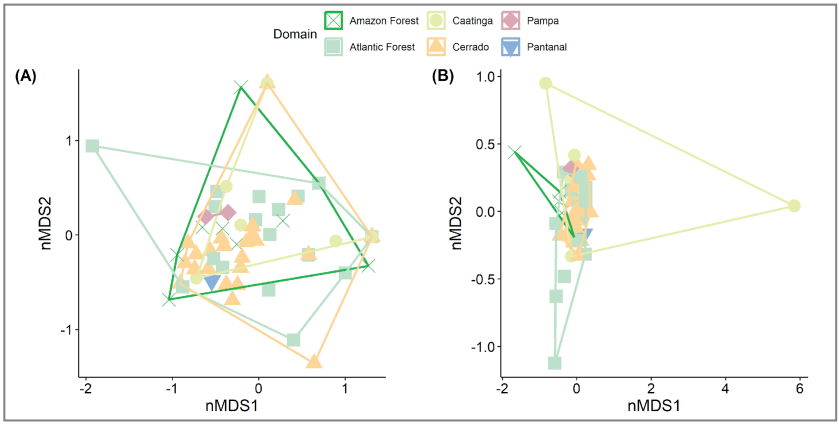



**Fig. 4 -** Variation in the composition of ant assemblages visiting plants with extrafloral nectaries among Brazilian Domains. (A) Composition of ant genera and (B) composition of ant species. Each color and dot type represents different Brazilian domains where the interaction was observed. Non-metric multidimensional scaling (nMDS) was based on the Jaccard similarity index using occurrence data. Polygon area represents the heterogeneity in ant assemblage composition within each Brazilian domain. Overlapping polygons of domains indicate that their ant assemblages share similar species composition..




## DISCUSSION

We provide the first broad assessment of ant diversity associated with plants with EFNs across Brazilian domains. For that, we considered not only published studies, but also unpublished studies whose content is still not available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in international databases (37.7% of our dataset). In total, these studies provided records for 186 ant species interacting with plants with EFNs in Brazil. However, this number is likely higher, since 42.3% of observations were identified only at the genus level. Even though it is still underestimated, the number of ant species described here is 34.4% higher than those from the most recent compilation of ant species visiting EFNs worldwide (Kaur *et al.* 2019). Regarding diversity, plants with EFNs in the Amazon, Cerrado and Atlantic Forest harbored richer ant assemblages. Despite that, most of the interactions observed in all domains were consistently performed by *Camponotus* ant species. The only exception was the Amazonian Forest, where *Crematogaster* species were the main ants associated with EFNs, closely followed by *Camponotus*. This pattern indicates that, although this protective mutualism is a generalized interaction, plants with EFN interact with a recurrent subset of ant species available, with *Camponotus* being a keystone group for plants with EFNs in Brazil. We observed no patterns of specialization, nor clear modules in the ecological networks formed by ant interaction with EFNs in each domain. Indeed, none of the networks from the domains in the module tests differed from the null models. This pattern suggest that ant visitation to EFNs occur as a function of local frequencies. However, in the two of the better studied domains with the larger networks (Cerrado and Amazon Forest), we found the typical nested pattern observed in mutualistic ecological networks (Valdovinos, 2019), in which a core of generalist species interacts with many partners, while rare species interact mainly with generalists. Below, we discuss how these findings advance our understanding of this mutualism and Brazilian biodiversity while highlighting some caveats that must be addressed to broaden our knowledge.

Ants are the most diverse group of social insects, with more than 14,000 species described so far (Bolton, 2024), 1,130 of which occur in Brazil (Feitosa *et al.* 2022). Despite such diversity, we found an astonishing low number of ant species visiting EFNs (less than 17% of Brazilian ant richness), indicating that the EFN-visiting ant assemblage is not a simple reflex of local community. Several studies have proposed that this subset is filtered by traits such as diet (omnivore or predator) and habitat foraging stratum (arboreal, epigaeic or hypogaeic) (Ribeiro *et al.*, 2019). Although, indeed, most of the ant species described here are omnivore and/or arboreal species, they represent only part of the species

exhibiting these traits in each domain. For instance, from the 133 Formicinae species occurring in Brazil (Feitosa *et al.*, 2022), an omnivore subfamily, only 39 were observed on plants with EFN, with *Camponotus* species representing 36 of them (Table 1). Similarly, from the 48 Pseudomyrmecinae species occurring in Brazil (Feitosa *et al.* 2022), a predominantly arboreal subfamily, only 20 of them were observed in plants with EFNs (Table 1). Also, it is important to notice that predatory ponerines, such as *Hypoponera* and *Neoponera* species, and leaf-cutter ants, such as *Atta*, were observed visiting EFNs in different Brazilian domains. These genera are not considered plant bodyguards in studies using a trait-based approach to classify the ant assemblages associated with plants with EFNs – something undermining the relevance of trait-based approaches to classify ant assemblage visiting EFNs, especially at the large scales.

Nutrient requirements and ant morphology may explain why some ant genera are more frequently observed in plants with EFNs than others. Formicinae and Dolichoderinae ant species, such as those from *Camponotus*, *Azteca*, *Dolichoderus* and *Crematogaster* genera, exhibit a specialized proventriculus that allow them to ingest liquid faster than species without this specialized structure (Davidson *et al.*, 2004) and store larger amounts of liquid for nutrition (Cook and Davidson, 2006; Davidson, 1997). For this reason, ant species with this specialized proventriculus heavily rely on carbohydrate-rich liquids for nutrition (Davidson, 1997; Ribeiro *et al.*, 2019). Although liquid-food specialization explains the importance of *Camponotus* ants for plants with EFNs across Brazilian domains, it is not the sole filter structuring the ant assemblages visiting EFNs. For instance, Dolichoderinae ants, which exhibits a proventriculus and can be ecologically dominant in Brazilian ecosystems (Baccaro *et al.*, 2015), was not a common subfamily observed on plants with EFNs in Brazil. Conversely, predatory species, such as ponerines and ectatomines, which lack a specialized proventriculus and do not rely exclusively on sugar-rich exudates, were also common partners of plants with EFNS in all domains. These ants carry extrafloral nectar drops externally on their mandibles (Davidson *et al.*, 2004) and use this resource for balancing carbohydrate-protein intake in their diets (Ribeiro *et al.*, 2019). In such case, competitive interactions among exudate-consuming ants can act as a second filter structuring ant assemblages visiting EFNs. If so, ant species more dependent on nectar ingestion and exhibiting higher competitive


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ability would competitively exclude other ants' species from EFNs. In fact, dominant ant species have been reported as the most common partners of plants with EFNs worldwide (Dáttilo *et al.*, 2014; Souza *et al.*, 2024). The jointly effect of competitive ability and nutrition requirements in structuring the ant assemblage interacting EFNs have never been evaluated, being a fruitful avenue of investigation in Brazilian domains.

Despite marked climatic and ecological differences among Brazilian vegetation domains, ant assemblage composition associated with EFNs did not vary substantially across them. This is notable given that both ant richness and composition vary substantially across these domains (Feitosa *et al.* 2022). While plant species with EFN also vary across domains, suggesting potential variations in ant-plant interactions (Barbosa *et al.*, 2025), our data does not reveal such divergence. Instead, EFN plants consistently rely on a core subset of ants across habitats. Network analysis shows that interactions are mostly performed by the same ant genera throughout all domains: *Camponotus, Crematogaster, Pseudomyrmex* and *Cephalotes.* These genera interact with most of plant species with EFNs in all domains, strongly influencing the mutualistic networks structure (for instance, by increasing nestedness). Less common ant genera interact with a subset of plants that also engage with dominant ants. Therefore, *Camponotus, Crematogaster, Pseudomyrmex* and *Cephalotes* act as keystone species for the dynamics of this ant-plant mutualistic interactions in Brazil, especially due to their diets based on carbohydrate-rich liquid food resources. It is important to note that *Camponotus* ants have been pointed out as the main partner of plants with EFNs worldwide (see Leal and Peixoto, 2017; Leal *et al.*, 2023 , and references therein), suggesting that the relevance of these ant groups for plants with EFNs is not restricted to Brazil. The protective consequences of interacting with *Camponotus* ants for plants with EFNs can be highly variable, since this genus varies in aggressiveness and monopolizing behaviors (Law and Parr, 2020).

So far, we have emphasized the biological relevance of our results. However, a key caveat must be considered when interpreting our findings: the strong asymmetry in study numbers across vegetation domains. While Cerrado and Atlantic Forest are relatively well sampled when compared to other domains, Pantanal and Pampa remain severely neglected, with only one study conducted

in each. This likely explains ant richness found in each domain. For example, the higher number of ant species in Cerrado when compared to forested domains, as Amazon and Atlantic Forest, contradicts the findings of ant diversity in Brazil (Feitosa *et al.*, 2022). This contradiction might be an artifact of the larger number of studies investigating the protection mutualism in Cerrado. We also found some bias in the distribution of studies within each domain. In Cerrado, the sampling efforts are concentrated near the Atlantic Forest border, whereas in Amazon the area sampled is probably near research centers. Not surprisingly, a similar sampling pattern was also found in other studies investigating ant biodiversity in Brazil (Divieso *et al.*, 2020; Feitosa *et al.*, 2022; Schmidt *et al.*, 2022). This asymmetry in study numbers and spatial sampling biases likely stem from multiple factors. Historically, socioeconomic development—and research funding—has been uneven across Brazil, concentrating along the Southern coast before expanding inland, a pattern that remarkably persists today (De Marques *et al.*, 2016; Stegmann *et al.*, 2024). Although research centers have expanded in recent years (Schmidt *et al.*, 2022), efforts in remote areas still face logistical challenges, particularly in hard-to-access regions like the Pantanal, where seasonal floods and fire regimes hinder fieldwork (Oliveira *et al.*, 2016). Given the rapid loss of species and interactions due to habitat destruction (Souza *et al.*, 2020), these geographical biases highlight priority areas for future biodiversity and ecological interaction studies (Divieso *et al.*, 2020).

A second important caveat is the low taxonomic resolution. In 42% of observations, ants were identified only to genus – similar to patterns in broader Brazilian ant surveys (Feitosa *et al.* 2022). This represents an important source of uncertainty in compositions comparisons and hence may lead to diluting possible differences among domains at the species level. Identifying ants to species-level is challenging, especially for ecologists unfamiliar with taxonomic complexities. Many genera lack comprehensive taxonomic revisions (e.g., *Pheidole, Solenopsis, Azteca*), and some species are easily misidentified (*e.g.*, *Carebara*, a non-arboreal genus, was recorded visiting EFNs; Baccaro *et al.*, 2015). Additionally, commonly recorded species might exhibit phenotypic plasticity, allowing them to occupy multiple habitats, which can affect plant interactions (Azevedo-Silva *et al.*, 2025). This is extremely worrisome since this low taxonomic resolution weakens our predictive power about the forces driving ant assemblages involved in these


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interactions and, consequently, the role of extrafloral nectar into ants' population dynamics and community structure. Pointing out solutions is out of scope, however, there is no doubt that establishing partnerships with taxonomists is a first step to overcoming this limitation (Feitosa *et al.*, 2022). Fortunately, Brazil offers an exciting scenario for these collaborations since we shelter one of the most productive and numerous myrmecological communities worldwide, including several of the most prominent ant taxonomists worldwide (Schmidt *et al.*, 2022).

## CONCLUSION

Here, we provided the first compilation of ant species interacting with plants with extrafloral nectaries across Brazilian domains. Although restricted to Brazil, this compilation is a valuable source of information for future studies on the factors shaping these assemblages, since Brazil is a hotbed of studies on interactions between plants and ants (see map available in Leal *et al.*, 2023). In the face of the alarming rate of habitat loss and biodiversity decline, it is an urgent task to know the species and, consequently, interactions we are losing to then understand the consequences of such losses for ecological processes occurring at different levels of biological organization. In this context, our study sheds light on critical issues in Brazilian studies focused on this ant-plant mutualism which still limits our full understanding of the ant assemblages relying on extrafloral nectar. For instance, the ants interacting with plants with EFNs were not identified to the species level in almost half of the observations. This can be explained by the historical phytocentric perspective of studies on ant-plant interactions (Alencar *et al.*, 2023; Byk and Del-Claro, 2010; Chinarelli *et al.*, 2022; Souza *et al.*, 2024). However, this issue could be easily solved by establishing collaboration with ant taxonomists – which are not a limiting resource in Brazil. By not identifying these ants up to species level, we are missing important information about their function in the ecosystem and their role in protective mutualisms. Only by refining our knowledge of species composition can we assess the ecological significance of these mutualisms for both plants and ants and their vulnerability to ongoing environmental change.

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# 13

# ANTS AS FLAGSHIP SPECIES: WHICH ONES AND WHY? A STUDY CASE WITH BRAZILIAN ANTS

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# ABSTRACT

The fragmentation and loss of habitats, pollution, and climatic change are the main drivers leading to an unprecedented decline in insect populations. A strategy to generate public engagement and funding for conservation action is using flagship species. Large mammals and top predators are often used as flagship species, but this does not ensure that insects also might benefit from this strategy. A solution to this bias is to select insects as flagship species directly. Three categories of flagship insects are proposed: ecosystem service providers, threatened species, and charismatic species. Unfortunately, ants are popularly known as pests or unbeloved species making it difficult to discuss conservation strategies for them. Hence, selecting ants as flagship species would require direct attention and conservation efforts straight to them. Our aim is to select ants as flagship species, considering the species' ecological importance and charismatic appeal using species occurring in Brazil as a study case. Using the list of officially threatened species in Brazil and the non-human charisma concept, we selected two species as potential flagship species with ecological relevance and charisma: *Dinoponera lucida* for the Atlantic Forest and *Atta robusta* for restinga. In addition, we discuss the use of species with cultural relevance as flagship species and *Eciton burchellii* as an umbrella species used as flagship species too. We hope this study stimulates ant researchers to work with conservation biologists, social studies researchers, politicians, grassroots organizations, and other stakeholders in projects using ants as flagship species for conservation.

**Keywords:** Formicidae; conservation; charismatic species; endangered species; umbrella species.

## INTRODUCTION

Recent analyses have highlighted a worrying global decline in insect populations (SÁNCHEZ-BAYO and WYCKHUYS, 2019. SEIBOLD *et al.*, 2020). Despite their vast diversity and importance for ecosystems and human societies, insects are seen by most people as pests that need to be managed. Consequently, they are seldom considered when conservation decisions are made (KIM, 1993). They are important ecosystem service providers acting in processes like pollination, seed dispersal, or even soil fertilization (ELIZALDE *et al.*, 2020). This means that, beyond their intrinsic importance, insects are essential to human society and therefore must be preserved.

The scientific community has paid less attention to insects compared to the greater number of extinction studies on large animals or vascular plants (DUNN, 2005). Given high insect diversity, species monitoring and managing is a laborious and difficult task. Data deficiency is one of the main limitations against biodiversity loss, thus monitoring neglected fauna is required to fill these gaps (HOCHKIRCH *et al.*, 2020). According to Hochkirch *et al.* (2020), a key goal for the next decades is to provide funding mechanisms for these monitoring programs. A conservation strategy to address this biodiversity issue is the use of focal species, also referred as surrogate species (DUCARME; LUQUE; COURCHAMP, 2013). Among surrogate species, flagship species are specifically used as symbols for conservation efforts in fundraising campaigns (DIETZ J.; DIETZ L.; NAGAGATA 1994; CARO and O'DOHERTY, 1999; Figure 1).


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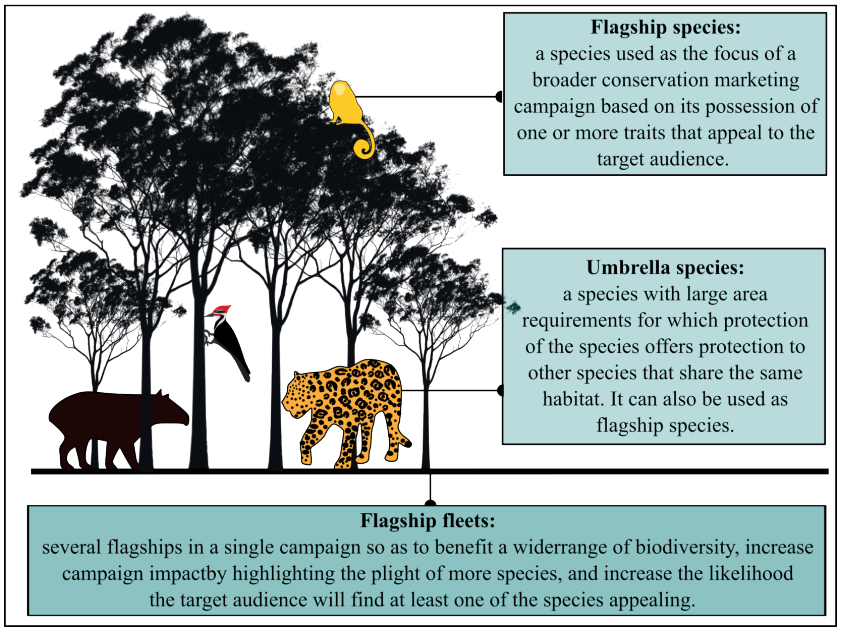
**Figure 1 -** Definitions of different surrogate species with conservation appeal. The scheme illustrates the Atlantic Rain Forest and some different species. Animal illustrations do not correspond to the original scale. Flagship species definition from Verissimo, MacMillan and Smith (2011). Umbrella species definition from Ozaki *et al.* (2006). Flagship fleets definition from Verissimo *et al.* (2014).




The conservation appeal exerted by flagship species is exploited using very charismatic species like large mammals or top predators as umbrella species (ALBERT; LUQUE; and COURCHAMP, 2018. Figure 1). However, this strategy does not ensure the conservation of insects and other invertebrates (DIETZ J.; DIETZ L.; NAGAGATA 1994; GUINEY and OBERHAUSER, 2008). This can be explained by two reasons: conservation efforts are concentrated in a single flagship species; and biased conservation campaigns or policies by the teams or individuals who work with these species (VERISSIMO; MACMILLAN; SMITH, 2011). Verissimo *et al.* (2014) also point out that choosing charismatic or umbrella species as flagship species causes saturation of flagship species, weakening the effectiveness of this approach to attract efforts or funding for conservation. In other words, if large mammals compete with each other for funding of their respective campaigns, this competition reduces their effectiveness in attracting funding for their organizations. A suggested solution is focusing

on uncommon species for conservation because they do not suffer from this saturation. This strategy can be reinforced by using species never considered charismatic historically and culturally (DUCARME; LUQUE; COURCHAMP, 2013).

In general, insects suffer from a "charisma challenge" due to stereotyping as pests and disease vectors, leading them to be neglected when discussing conservation strategies (BERENBAUM, 2008). For this reason, insects are unusual options as flagship species and therefore have better chances of standing out from the more typical ones and attracting attention. Attempting to solve this problem, Guiney and Oberhauser (2008) proposed yet to use insects directly as flagship species. Three categories for potential flagship species were proposed: ecosystem service providers, endangered species, and charismatic species. This strategy can be used for direct insect conservation and more broadly to attract attention to general conservation issues. Some insects have already been used as flagship species: butterflies, because of their aesthetical charisma, (BARUA; AHMED; TAMULY, 2012) and bees due to their services as pollinators and honey producers (SUMNER; LAW; CINI, 2018).

Among insects, ants stand out due to their diversity, abundance, huge biomass and eusocial organization (HÖLLDOBLER and WILSON, 1990). Ants are also globally noteworthy as ecosystem service providers and essential to terrestrial ecosystems (DEL TORO; RIBBONS; PELINI, 2012; ELIZALDE *et al.*, 2020). Ants can be a food resource in some cultures or provide substances with potential medical or biotechnology applications. They also act directly as biological controllers of other organisms. Lastly, ants can inspire or be personified in movies, literature, or sacred symbols for some New World indigenous cultures (SLEIGH, 2003). They also have already been used as surrogate species with ecological relevance, like keystone species (Sanders and Van Veen 2011) and bioindicators of ecological restoration (CASIMIRO; SANSEVERO; QUEIROZ, 2019). However, their use as surrogate species with conservation appeal is uncommon (VAN ITTERBEECK *et al.*, 2014).

Brazil has the highest ant species diversity in the Neotropics with thousands of possible new species (BACCARO *et al.*, 2015). There are officially 11 endangered ant species on the Brazilian Red List, threatened mainly by habitat loss, and all of them are endemic to the Atlantic Rainforest (BRASIL, 2022, Table 1). Because of the scarcity of studies monitoring ant populations in Brazil and the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growing rates of deforestation, more species are probably at risk. Considering these factors, the conservation of ants is necessary to ensure their existence, and consequently, the ecosystem services provided by them. There are currently no ants used as flagship species in the Neotropics. Beyond the Neotropics, *Formica rufa* has been proposed as an effective flagship species in Europe (BALZANI *et al.*, 2022). Considering the rich diversity of ants, the extensive habitat loss (BRASIL, 2022), the scarcity of population monitoring studies, and their importance to human societies and terrestrial ecosystems, conservation strategies focused on ants are needed (ALONSO, 2010). Our aim with this study is to select ants as flagship species *per se* in Brazil and for the conservation of their ecosystems, considering the species' ecological importance and charismatic appeal.

## METHODS

From the three insect flagship species categories, namely *ecosystem service providers*, endangered, and *charismatic species* (GUINEY and OBERHAUSER, 2008), we focus on threatened species due to the urgency of conservation actions. In addition, we filtered the charismatic ones according to the non-human charisma concept proposed by Lorimer (2007) (Figure 2). This way, we combine conservation priorities (threatened status) and charismatic features that can be used with the flagship species selected. We performed bibliographic research about studies published in Brazil from 1945 to 2019 with ants with cultural importance using SCIELO (All Databases) and SCOPUS (Elsevier). Given the traditional practice of consuming *Atta* queens by human populations in Brazil, the following keywords were individually paired with "Formicidae" during the literature search: *entomophagy, Atta*; *biotechnology*; *biological control*; *ethnobiology/ethnoentomology*. The species with cultural importance were not filtered through the non-human charisma concept because they were already considered charismatic to the cultures in which they are used (BOWEN-JONES and ENTWISTLE, 2002, Table 2).

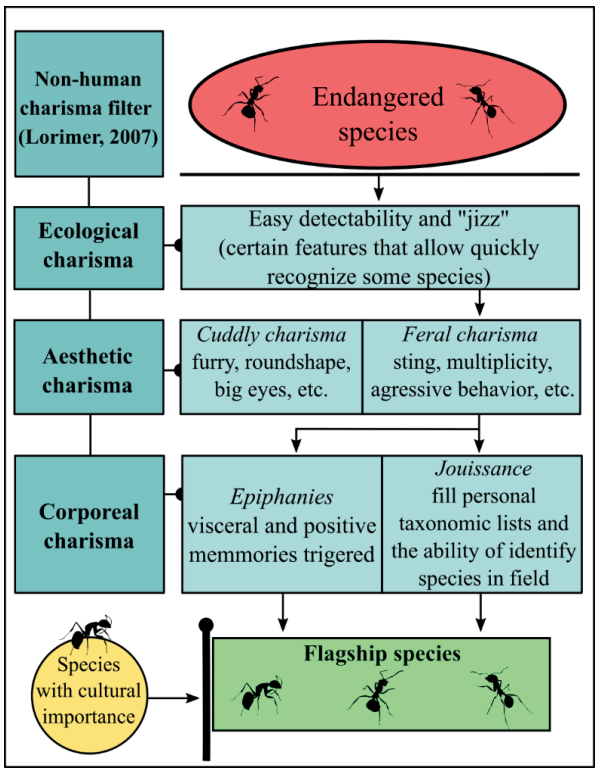
**Table 1 -** List of endangered ant species in Brazil (Brasil, 2022). All the threat categories follow the IUCN Red List pattern. VU=Vulnerable; EN=Endangered; Critically Endangered (CR); Protected areas: PE=Parque Estadual; APA=Área de Proteção Ambiental; PARNA: Parque Nacional; RPPN: Reserva Particular do Patrimônio Natural; REBIO: Reserva Biológica; FLONA: Floresta Nacional.

| Ant species | Threat category | Habitat | Occurrence at protected areas |
|---|---|---|---|
| *Atta robusta* (Borgmeier, 1939) | VU | Restinga on the coast of Rio de Janeiro (RJ) and Espírito Santo (ES) states. | PE de Itaúnas, REBIO de Comboios, PE de Setibas, APA Costa das Algas (ES); Parque Natural Municipal do Grumari, PM Ecológico de Marapendi (RJ) |
| *Brachymyrmex micromegas* Santschi, 1923 | VU | City of Agudos, Anhembi, Mogi das Cruzes and São Paulo, in São Paulo (SP) State. | APA Estadual Várzea do Rio Tietê (SP) |
| *Diaphoromyrma sofiae* Fernández, Delabie & Nascimento, 2009 | EN | Natural reserves between eucalyptus plantations in the south of Bahia (BA) state in the cities of Porto Seguro and Santa Cruz Cabrália. | PARNA do Pau-Brasil, RPPN Estação Veracel (BA) |
| *Dinoponera lucida* Emery, 1901 | EN | Atlantic Forest from southern Bahia (BA) to Espírito Santo (ES) states and in small isolated forest areas in the east of Minas Gerais state. | PARNA e Histórico do Monte Pascoal, PARNA do Pau Brasil (BA); REBIO de Sooretama, FLONA de Goytacazes, PE de Fonte Grande, REBIO de Duas Bocas (ES). |
| *Fulakora cleae* (Lacau & Delabie, 2002) | CR | Known only by type locality in a fragment of semi-deciduous forest on top of a hill in Itororó city, southern of Bahia (BA) state. | Unknown |
| *Gnamptogenys wilsoni* Lattke, 2007 | EN | Known by a few registers in Ilhéus city, Bahia (BA). | Unknown |
| *Monomorium delabiei* Fernández, 2007 | VU | Known only by three registers at seasonal deciduous forest in Barra do Chiça, Guaratinga and Boa Nova cities in Bahia (BA) state. | PARNA de Boa Nova (BA) |
| *Mycetagroicus urbanus* Brandão & Mayhé-Nunes, 2001 | CR | Known only by type locality in the Ibirapuera Park in São Paulo (SP) state. | Does not occur at conservation units |
| *Mycetomoellerius atlanticus* (Mayhé-Nunes & Brandão, 2007) | VU | Restinga areas in the coasts of Rio de Janeiro (RJ), Espírito Santo (ES) and Bahia (BA) states. | RPPN São João Farm, RPPN Arte Verde Farm, RPPN Salto Apepique (BA); APA Municipal da Orla Marítima da Baía de Sepetiba, REBIO Estadual de Guaratiba (RJ) |
| *Mycetophylax simplex* (Emery, 1888) | VU | Restinga areas in the coast of Santa Catarina (SC) and Rio Grande do Sul (RS) states. | Unknown |
| *Rhopalothrix plaumanni* Brown & Kempf, 1960 | EN | Known only by type locality in Araucária forest in Seara city, west of Santa Catarina (SC) state. | Unknown |

## SELECTING ANTS AS FLAGHIP SPECIES

According to Lorimer (2007) "Nonhuman charisma can be best defined as the distinguishing properties of a non-human entity or process that determine its perception by humans and its subsequent evaluation". The author defines three types of non-human charisma: *ecological*, *aesthetic* and *corporeal* (Figure 2). Ecological charisma is related to ethological resemblance to humans, like diurnal lifestyle, social behaviour, or parental care. These features also need to be easily recognizable, which means, the ecological charismatic species must be recognizable. The facility to find and recognize the flagship species is also mentioned by Dietz *et al.* (1994) as a relevant trait for them. In the case of ants, this implies that rare or even too small or cryptic species are not good choices. Considering this, large-sized species are the best candidates.

**Figure 2 -** Diagram representing the selection of ants as flagship species through the non-human charisma. Squares represent non-human charisma categories.



The second non-human charisma proposed by Lorimer (2007) is aesthetic charisma, subdivided into "feral charisma" and "cuddly charisma". The first one best applies to insects: organisms and places that have wild or chaotic features that are considered admirable. This kind of ecological charisma is possessed by the 20 most charismatic species for conservation and the authors pointed out that being terrifying is an important trait to be considered charismatic (ALBERT; LUQUE; COURCHAMP, 2018). Another characteristic that is common between these feral species is their large size. When it comes to insects the size scale is completely different from the vertebrates, so relatively large insects would be considered feral charismatics. Even though ants are much smaller than the typical charismatic mammals, among ants some species are relatively larger. Cuddly is a mostly mammalian-associated feature that is not readily applicable to ants or insects in a general way. Due to this, all the ant species were filtered only through the feral charisma (Figure 2), which means that species with a sting, aggressive behaviour, and/or multiplicity are good choices.

Corporeal charisma is more related to individual experiences and abilities than species features. The term "epiphanies", coined by Lorimer (2007), is related to visceral memories of positive experiences with some species. For example, the sound of birds and crickets during a vacation trip, a colourful butterfly in our garden or even the smell of some plants or the taste of its fruits. In this case, ant species that can be related to some specific places or positive situations are good options, like those with cultural relevance. The satisfaction feeling related to the desire of some people to complete personal taxonomic lists or the ability to identify them in the field was called by Lorimer (2007) as "jouissance". It is common among bird- and butterfly-watchers. In this case, endangered species are good examples considering their vulnerable status or rarity.

**Brazilian ants with cultural importance**

The search for papers regarding the cultural importance of ants in Brazil points to *Atta* Fabricius, 1804 species used as food by indigenous people (Table 2). Another culturally important species is *Paraponera clavata* (Fabricius, 1775), also known as the bullet ant or locally as *Tocandira* or *Tucandeira*.

**Table 2 -** Ant species used in Brazilian indigenous traditions.

| Ant species | Indiginous community | How ants are used | References |
|---|---|---|---|
| *Atta cephalotes* (Linnaeus, 1758) | Several Amazonian tribes | Winged queens are consumed with a kind of manioc cake and the eggs are considered delicacies. | Posey (1978) |
| *Atta sexdens* (Linnaeus, 1758) | Mave and Arapium | Winged queens' gasters are roasted, grinded and added to manioc flour | |
| | Tukano | Workers are used as flavoring because of their lemon odor. | Dufour (1987) |
| *Atta laevigata* (Smith, 1858) | Tukano | Major workers and winged queens are consumed as food resources. | |
| *Paraponera clavata* (Fabricius, 1775) | Sateré-Mawé | Essential element at Waumat's rite of passage | Alvarez (2005) |

For New World indigenous people, ants are ecosystem service providers in two different ways: as a food resource or as an important cultural ritualistic element (SILVESTRE and NETO, 2020). The custom of eating winged queens, captured during nuptial flights is widespread in Latin America (COSTA-NETO, 2015), and in Brazil, generally, some populations consume queens of *Atta* as delicacies. The consumption of winged queens of *Atta*, popularly called *Tanajura* or *Içá*, and of workers collected from nests or ground have been described since the nineteenth century by explorer-naturalists in Brazil (DUFOUR, 1987). Additionally, indigenous people can use them for medicinal purposes (SILVESTRE and NETO, 2020). Besides this importance as a food resource, curiously, people do not associate the *Tanajuras*, with their workers, popularly called *Saúvas*, also known as leaf-cutter ants. This can be perceived in the contrast between considering the reproductive caste as a delicacy and the sterile caste as a crop pest. Similarly, some people do not associate caterpillars with butterflies, considering the larval and adult stages as different species with different conservation views associated with them (BARUA; AHMED; TAMULY, 2012). Even though leaf-cutter ants are highly social, easy to recognize in the field, and relatively big, choosing a leaf-cutter ant as a flagship species initially seems a bad strategy due to their image as farm pests. However, thanks to the cultural importance of these ants, they could become good options in regional projects that include local people. Leaf-cutter ants consumed as a food resource

have considerable nutritional value (DUFOUR, 1987) suggesting they may also be exploited for ecotourism in Brazil's northern states as unique gastronomic delicacies. Entomophagy is widely recommended by FAO (Van Huis 2013) and, if adopted, may change the image of leaf-cutter ants as farm pests by converting them into a food resource worthy of being conserved. An example of this approach is the use of *Atta sexdens* (Linnaeus, 1778) workers, as a flavouring in artisanal chocolate (CASA LASEVICIUS©, 2020).

Species used by traditional populations and with popular names are good choices for flagship species on the local or regional scale (BOWEN-JONES and ENTWISTLE, 2002). Charisma depends on cultural factors (DUCARME; LUQUE; COURCHAMP, 2013), and the fact that some ant species are already used by indigenous people shows their acceptance. Even though leaf-cutter ants are considered farm pests, they can trigger memories of observing, collecting, or even eating the *Tanajuras,* responsible for a corporeal charisma called "epiphanic affections" (LORIMER, 2007). The visual appeal of *Atta* nuptial flights is a feature that can be considered charismatic and used to captivate public attention. Leaf-cutter ants also inspired the name of a group of indigenous women called Yarang, which means "leaf-cutter ants" in their language (IKPENG, 2019). The Yarang women collect seeds from the forest floor in the Indigenous Territory of Xingu in Brazil to reforest it. The name Yarang was chosen because the ants work collectively, walking in line, each with a piece of leaf or a seed. This example shows how different cultures and target audiences can offer several interpretations of the same species. This is also a good example of how an ant species can be used as a flagship species that inspires the local community in ecosystem restoration.

*Paraponera clavata* (Fabricius, 1755) has one of the most painful stings (SCHMIDT, 2016) and can be considered an ecosystem service provider of cultural importance. This species is a relevant ritualistic symbol for the *Waumat* coming-of-age ceremony among members of the Sateré-Mawé people, attracting fascination because of its mysticism (ALVAREZ, 2005) and association with sexual arousal. Some cultures use this painful sting, compared to a gunshot, as a treatment for sexual impotence (SILVESTRE and NETO, 2020). This species can be easily recognized in the field. These factors can trigger jouissance in tourists and the relatively large size and painful sting make this species ecological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and feral charismatic. These peculiarities can be highlighted with marketing strategies to attract attention to indigenous people and their cultures, needing attention and more effective protection too. Beyond their cultural importance, the *Tocandiras* are also capable of triggering epiphanic affections in the indigenous men who have experienced their sting. That means, local people also interpret them as charismatic and can be included in conservation actions without interest conflicts (VAN ITTERBEECK *et al.*, 2014). Approaches that use this species to attract attention to the conservation of Amazonia associated with the conservation and protection of indigenous people are promissory because they can reach more people and act like a flagship fleet (VERISSIMO; MACMILLAN; SMITH, 2011; Figure 1).

**Endangered Brazilian ant species**

Although species officially listed as endangered tend to be more successful as flagship species (DIETZ J.; DIETZ L.; NAGAGATA 1994 *apud* GUINEY and OBERHAUSER, 2008), few threatened insect species have been suggested as flagship in comparison to vertebrates (BARUA; AHMED; TAMULY, 2012). The reasons are mainly explained by the difficulty of observing insects due to their generally small size, the relative rarity of threatened species, and lack of visual appeal. Regarding endangered Brazilian ants, most of them are small and rare (Table 1), however, advertising campaigns can make them more known and attractive for use as flagship species (VERISSIMO; MACMILLAN; SMITH, 2011). Therefore, these ants could be used to promote the protection of areas where they occur (Table 1). This proposal can be used to inform the public about threats to biodiversity and how protected areas can act as a refuge for threatened species, or even engage people in volunteer work. Curiously, *Mycetagroicus urbanus* Brandão & Mayhé-Nunes, 2001 besides its small size, has a peculiar fact regarding its discovery: its type-locality is the Ibirapuera Park, located in São Paulo city, the largest city in Brazil. *Mycetagroicus urbanus* could become a symbol of the importance of urban green areas for insect conservation (SANTOS, DELABIE; QUEIROZ, 2019). The critical threaten status can be a warning of how urbanization can negatively affect biodiversity.

Finding and recognizing endangered ant species can provoke jouissance (Figure 1), but the rarity and small size do not make most of these species ecological and aesthetically charismatic. However, two endangered Brazilian ants have great potential as flagship species: *Atta robusta* (Borgmeier, 1939) and *Dinoponera lucida* Emery, 1901. Thanks to their relatively large size they are easy to observe, thus ecological and feral charisma can be evoked. The restricted distribution of both species helps to recognize them in the field with certainty and this is a good trait for flagship species (BOWEN-JONES and ENTWISTLE, 2002; GUINEY and OBERHAUSER, 2008). Easy observation is one trait of ecological charisma (LORIMER, 2007) and is important since the people who donate or act in conservation programs expect to observe these species when visiting their habitats (DIETZ J.; DIETZ L.; NAGAGATA 1994).

*Atta robusta* has traits that evoke some empathy through ecological charisma (LORIMER, 2007). The complex social organization with task labour division (HÖLLDOBLER and WILSON, 1990) can be compared to professions in human society, including agriculture. Leaf-cutter ants can process impressive amounts of vegetable mass to feed the fungus that they cultivate (LEAL; WIRTH; TABARELLI, 2014), an agricultural activity exercised long before humans (HÖLLDOBLER and WILSON, 2010). The easily identifiable trails formed due to foraging activity can be compared to streets or avenues and so be of interest to people. These characteristics associated with the endangered status enhance the conservational appeal. Meetings with *A. robusta* provoke epiphanic affections among people who frequent the beaches due to their distribution along littoral areas and their nests established in sandy soil (GONÇALVES, 1945; TEIXEIRA; SCHOEREDER; MAYHÉ-NUNES, 2003; QUEIROZ 2018). All the forms of charisma that *A. robusta* has can be used to engage people to keep beaches clean or even in citizen science programs monitoring nuptial flights since the population trend of this species is unknown (QUEIROZ, 2018). *Atta robusta* occurs in urban areas in Rio de Janeiro city (GOMES; ELIZALDE; QUEIROZ, 2013), which has a high flux of tourists, as well as in the areas of the state of Espírito Santo, it would be interesting to use it as flagship species in touristic campaigns.

*Dinoponera lucida* belongs one of the genera with the largest ants in the world, with the workers of some species longer than three centimetres long (DIAS and LATTKE, 2022). This species occurs in the Atlantic Rain Forest, a


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conservation hotspot biome decimated by historic and ongoing deforestation (DIAS and LATTKE, 2022; Table 1). The restricted distribution of *D. lucida,* its large size, and its smooth and shining integument make it easy to recognize and evoke both ecological and feral charisma (LORIMER, 2007). This ant could become a symbol for the areas where it occurs and engage people in Atlantic Forest conservation. People encountering this species probably will have some jouissance upon recognizing it. Hence, its ecological, feral and corporeal charisma makes this species a great candidate as a flagship species.

**Ants as umbrella species**

Flagship species with ecological relevance (i.e., umbrella species), are frequent as well as charismatic species (DIETZ J.; DIETZ L.; NAGAGATA 1994; VERISSIMO; MACMILLAN; SMITH, 2011; DUCARME; LUQUE; COURCHAMP, 2013). There is a keystone species that is proposed as an umbrella, and in this case also as a flagship species: *Eciton burchellii* (Westwood, 1842) (PÉREZ-ESPONA, 2021). It needs large areas to live (BOSWELL *et al.* 1998; BRADY 2003) and is affected by habitat fragmentation (KUMAR and O'DONNELL, 2007). Further being a key species, *E. burchellii* is the animal with more known associations with other species (RETTENMEYER *et al.* 2011). A total of 557 species were counted, mostly arthropods, associated with *E. burchellii*, with up to 300 depending on it. These associations occur in three ways: in the swarm raids, on the ant's refuse deposits, and inquilines that live in the bivouacs and columns. Some birds are very or even totally dependent on the swarm raids, which makes this species even more relevant as an umbrella species (PÉREZ-ESPONA, 2021). This is an important trait because of the importance that birds have for conservation through people interested in bird-watching (Steven and Morrison 2016). *Eciton burchellii*, and birds associated with it, can act together as flagship fleets (Figure 1; VERISSIMO; MACMILLAN; SMITH, 2011).

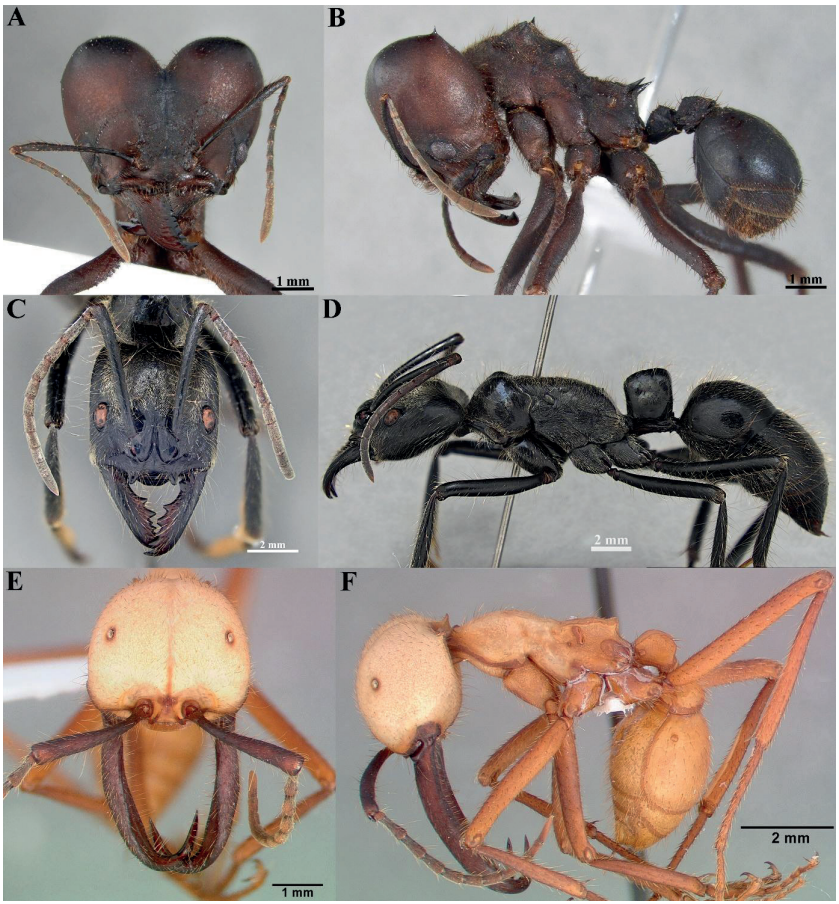
Beyond a keystone and umbrella species, *E. burchelli* can be considered charismatic too. It is easy to recognize it in the field due to its epigeic raids. The large mandibles of major workers and painful sting evoke feral charisma. The magnitude of their raids can trigger epiphanies in bird-watchers. For this reason, this species has great potential as a charismatic flagship species with

an ecological appeal. Taking into account that insects as flagship species can be used in campaigns beyond their own (GUINEY and OBERHAUSER, 2008), *E. burchelli* could be used for projects that stimulate the conservation and restoration of the Atlantic Forest. This way, it is possible to raise funds and encourage commitment to reforestation or even monitoring programs that benefit many other invertebrate species under its conservation umbrella.

**Why ants as flagship-species**

How to select a flagship species is an issue that has been discussed often (BOWEN-JONES and ENTWISTLE, 2002; VERISSIMO; MACMILLAN; SMITH, 2011; BARUA; AHMED; TAMULY, 2012; DUCARME; LUQUE; COURCHAMP, 2013; JEPSON and BARUA, 2015). Two factors are essential for the choice to be successful: how the species are already seen by society and how they can be promoted in marketing campaigns. Verissimo *et al.* (2011) propose that any species could become a flagship species with marketing campaigns. Jepson and Barua (2015) warn that the complexity of pre-existing cultural frames should be considered for the species chosen to be efficient and lasting. Similarly, Bowen-Jones and Entwistle (2002) make clear the importance of cultural factors over the choice of a flagship species. The approach proposed by Guiney and Oberhauser (2008) uses ecological relevance criteria (i.e. ecosystem services and endangered status) as well as marketing aspects (i.e. aesthetical charisma). This approach was made thinking specifically of insects, different from the other authors. Hence, combining the ecological relevance and charismatic features, the ant species chosen in this study are promising candidates (Figure 2). Together, both criteria can be used in marketing campaigns for conservation programs calling attention via ecological appeal and charisma.

**Figure 3 -** Ant species selected as flagship species with ecological relevance and charisma. *Atta robusta* in frontal view (A) and lateral view (B), imaged by Eder França. *Dinoponera lucida* in frontal view (C) and lateral view (D), imaged by Amanda Nunes (DZUP549807, Source: AntWeb.org/); *Eciton burchellii* in frontal view (E) and lateral view (F), imaged by April Nobile (CASENT0009218, Source AntWeb.org/).




Insects may have some characteristics that can cause phobia in humans such as multiplicity, monstrosity, autonomy, and parasitism (LORIMER, 2007). Specifically, the fact that ants are eusocial insects (HÖLLDOBLER and WILSON, 1990), contradicts the concept of subjectiveness that, for humans, is something important (LORIMER, 2007). However, species with social behaviours are also interesting options to become flagship species, because they share this feature with human societies (DIETZ J.; DIETZ L.; NAGAGATA 1994). Eusocialism when approached in ways that do not neglect the importance of individuality, can be a

powerful tool to positively enhance the image of ants, as shown in the movies "A Bug's Life" and "AntZ". Cultural factors are trivial for how these traits would be perceived among different people in different cultural frameworks (DUCARME; LUQUE; COURCHAMP, 2013). *Oecophylla smaragdina* (Fabricius, 1775) is an example of it that would not be accepted by local people as a flagship species because it is seen as a food resource that does not need to be protected (VAN ITTERBEECK *et al.*, 2014).

An example of ants as a Flagship fleet is the book "Formigas do Alto Tietê" (SUGUITURU *et al.*, 2015), which aims to attract people's attention to the biodiversity in remnants of the Atlantic Forest in the Tietê river basin. The charismatic challenge faced by insects is an important issue when it comes to conservation (KIM, 1993). Macroscopic photos associated with natural history are an efficient strategy against their image as disgusting or worthy of hate (BERENBAUM, 2008). In the case of "Formigas do Alto Tietê", the ants can raise awareness in the readers of the importance that place has on the maintenance of biodiversity and ecosystem service provision. Recently, Brazilian myrmecologists have worked on new books about ant biology available for the general public and scientific divulgation actions (FRANÇA and QUEIROZ, 2021). These efforts are good starting points for overcoming the charismatic challenge and attracting people to the ants' natural history. With society sensitized the acceptance of ants as flagship species can be easier.

Considering that all of the species selected here (Figure 2) have ecological and charismatic appeal, they stand out from the other categories of insects proposed by Guiney and Oberhauser (2008). All of these species are attached to other contexts of conservation and can be used as flagship fleets in their own biomes (VERISSIMO; MACMILLAN; SMITH, 2011) warranting that different people can be reached and engaged in the conservation of their habitats.

## First steps about ants as flagship species

Ants are among the insects neglected in monitoring surveys (SÁNCHEZ-BAYO and WYCKHUYS, 2019). This factor is alarming considering that they are great ecosystem service providers (ELIZALDE *et al.*, 2020) and diverse (HÖLLDOBLER and WILSON, 1990), especially in tropical regions. Fundings are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necessary to fill these gaps (HOCHKIRCH *et al.*, 2020), and flagship species can promote the image of themselves and their habitats. Most of the hotspots for conservation are in tropical regions, where ants are diverse with some species threatened by extinction (MYERS, 2000). A massive amount of ant species is associated with these priority areas and their ecosystem service provisioning. It would be interesting if other regions could choose their flagship ants. The methodology proposed here ensures that these species have ecological and charismatic traits to be exploited in marketing campaigns for conservation. However, to select a flagship species is just the first step in a long way to solid conservation campaigns and it requires interdisciplinarity (VERÍSSIMO *et al.*, 2011).

Media streaming associated with extension projects has a fundamental role in the way people look ecosystem services (SUMNER; LAW; CINI, 2018). Bringing it to the flagship species means that scientists need to be closer to people who work with social communication. It needs to be done in ways that do not create misconceptions about the roles of each species (MELERO, 2017) and make clear the benefits that human society receives from ecosystem services. This way, people can create affection or respect for the importance of each ant species because they can disperse seeds, prey on pests, display wildness or even be endangered due to deforestation. Even though ecosystem service valuation of eusocial insects needs more advances (ELIZALDE *et al.*, 2020), some simple strategies can be applied. For example, when someone questions a myrmecologist about reasons for studying ants, instead of quickly answering about ecosystem services, a good alternative is to simply respond "Why not?". This makes it possible to identify factors that cause displeasure or estrangement so the arguments in favour of ants can be given objectively and misunderstandings corrected assertively.

Using ant species as flagships will depend on local factors, the target audience, and the short and long-term goals (BOWEN-JONES and ENTWISTLE, 2002; VERISSIMO; MACMILLAN; SMITH, 2011; BARUA; AHMED; TAMULY, 2012). As leaf-cutter ants inspired Yarang indigenous women (IKPENG, 2019), we hope that the species chosen in this study can inspire conservation projects in Brazil that mitigate or reduce their respective habitat loss. Beyond their benefit, insects as flagship species act to inspire people to take more sustainable attitudes, or even create future naturalists (NEW, 2011 *apud* BARUA; AHMED;

TAMULY, 2012). Social media are good alternatives to stimulate engagement from audiences previously sensitized. Groups interested in ant breeding could be the target audiences for which campaigns about ant conservation could start. Even so, it is necessary to be careful with charismatic appeals because the attention raised by flagship species does not outshine the other sympatric species that need to be conserved too (DUCARME; LUQUE; COURCHAMP, 2013).

Even though we can find charismatic and ecological ants that can be used as flagship species, it is still necessary to address how it could be applied. Studies about people's perceptions regarding ants are also necessary. Using their results, the flagship species strategy might be refined and applied on different scales, with specific goals and target audiences. Sumner *et al.* (2018) already asked, "Why do we love bees and hate wasps", and what about ants? Maybe the answer would be positive if we could measure the benefits of their ecosystem services like their disservices. Data deficiency also can reinforce the negative perception of hymenopterans by society (SUMNER; LAW; CINI, 2018). This gap and the farm pest stereotype also reinforce the neglect of ants in conservation projects. Two strategies suggested by Hochkirk *et al.* (2020) to address data deficiency in neglected biodiversity are to create monitoring programs for lesser-known taxa, and funding mechanisms. The flagship species strategy can act in both strategies with any species chosen. The data and funding gathered by them also could be applied to projects involving local people and the conservation of their habitats. Once again, marketing strategies and interdisciplinary efforts are necessary to achieve short and long-term goals.

## CONCLUSION

Selecting flagship species is a hard task and it is necessary to take into consideration ecological, cultural, and marketing aspects. Species with cultural importance can be used at a local scale with specific target audiences. *Dinoponera lucida, A. robusta* and *E. burchellii* have ecological and charismatic appeal, being good options as flagship species for their respective habitats.

We hope this study stimulates myrmecologists to work with conservation biologists, social studies researchers, politicians, grassroots organizations, and other stakeholders on ant conservation projects. Our qualitative approach can


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be applied to other places with their ant fauna or other insect groups. Ecological and charismatic species can boost the flagship strategy making them even more appealing. Based on the criteria of insects as flagship species and non-human charisma, we advise selecting species that are ecosystem service providers (in this case species with cultural relevance), that are relatively large, easily recognizable in the field, with feral features, and species that can evoke epiphanies or jouissance.


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# Ant Diversity

# 14

# BRAZILIAN AMAZONIA MYRMECOFAUNA IN THE CONTEXT OF BIODIVERSITY RESEARCH

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# ABSTRACT

In Amazonia, one of the largest and most biodiverse tropical rainforests on the planet, the main natural laboratories comprise its forests, rivers, and caves, as well as the wide range of interactions found across urban, rural, riverine, and traditional territories. These ecosystems, rich in both biological and cultural diversity, serve as sources of ecological and ethnobiological data. They provide insights into a highly complex region and offer directions for conservation efforts with global relevance. Ants are also diverse in Amazonia, though enormous knowledge gaps remain. This chapter presents an overview of the 1,140 species, 106 genera, and 12 subfamilies currently recorded for the Brazilian Amazonia. These records represent more than two centuries of scientific investigation, alongside the millennia of traditional knowledge that exists in the region. Due to the large scale and complexity of the region, data on Amazonian ants remain fragmented and often inconsistently documented. Despite these limitations, this chapter compiles recent database information to present the current state of knowledge and highlight the ecological importance of Amazonian ant diversity. Furthermore, we examine Amazonia from an ant-centered perspective, emphasizing how the diversity of this group and the development of collaborative research networks advance myrmecology and regional conservation.

**Keywords:** Entomology; filling biodiversity gaps; formicidae; tropical forest.

## THE BRAZILIAN AMAZONIA IN CONTEXT

Amazonia, the largest continuous tropical rainforest on Earth, encompasses diverse climates, water flows, geomorphology, and soils, which together form a complex mosaic of terrestrial and aquatic ecosystems sustained by intricate biogeophysical interactions and representing a key part of the world's biological and sociocultural heritage (Nobre *et al.*, 2021). Home to some of the highest recorded levels of biodiversity, the region harbors unique genetic resources and performs essential ecological functions that sustain ecosystem services globally (Guayasamin *et al.*, 2024). This richness stems from the long evolutionary history of several Amazonian lineages, placing the forest at the heart of the origin and maintenance of Neotropical biodiversity (Antonelli *et al.*, 2018). Biological diversification in the Amazonia results from complex interactions between biotic and abiotic factors (Hughes *et al.*, 2013), making it one of the most biodiverse regions for many taxonomic groups (Mittermeier *et al.*, 2003; Zapata-Ríos *et al.*, 2021), though a significant portion of its biodiversity remains unexplored (Zapata-Ríos *et al.*, 2021).

In addition to its ecological importance, the Amazonia supports diverse ways of life and is a pivotal territory for Indigenous peoples, traditional communities, and a growing urban and rural population (Ellwanger *et al.*, 2020). Brazil contains the largest portion of the Amazonia Rainforest, covering about 59% of the national territory (IBGE, 2022), encompassing 52% of the country's protected areas (Qin *et al.*, 2023) and around 60% of recognized Indigenous lands (ISA, 2025). The Brazilian Amazonia is home to nearly 28 million people, including over half of the country's Indigenous population (IBGE, 2022). The region's cultural diversity is equally remarkable, with the Amazonia being a global hotspot of sociocultural diversity, reflected in the plurality of languages, worldviews, and social structures (Neves; Rostain, 2012). In many well-preserved areas, Indigenous languages coexist with biodiversity hotspots, revealing a deep interdependence between biological and linguistic diversity (Hamans *et al.*, 2024).

Despite its global importance, the Amazonia faces persistent challenges, including chronic underfunding, unstable investments, and resource concentration in a few consolidated centers (Stegmann *et al.*, 2024), combined with logistical barriers to remote areas. These factors limit knowledge production


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and practical application. The scenario is worsened by knowledge gaps across various biological groups, hindering understanding of regional biodiversity and its responses to environmental change (Carvalho *et al.*, 2023). Accelerated land-use changes, driven by logging, mining, dam construction, and road building, have led to social conflicts and affected species distribution, abundance, and ecology, even interfering with evolutionary processes (Celentano *et al.*, 2018). Also, climate change, has emerged as a threat on par with land-use changes, with studies forecasting impacts on key taxa such as ants. Monitoring shows varied biological responses to these climate extremes, highlighting challenges in predicting and conserving Amazonian biodiversity (Rodrigues-Filho *et al.*, 2024).

As the future of the Amazonia resonates globally, deepening knowledge about the organisms that structure its ecosystems has become a priority. Among them, ants play a particularly prominent role. Extremely abundant in Amazonian fauna, these insects perform numerous ecological functions. One example is how their eusocial behavior allows them to dominate forest soils, contributing to soil aeration and mediating interactions (King *et al.*, 2016). They maintain symbiotic relationships with fungi, inspiring human agricultural systems (Schultz *et al.*, 2024). They act as predators in regulating populations and modulate biotic interactions (Dáttilo; Dyer, 2014; Dejean *et al.*, 2025) but can also cause negative impacts on a smaller scale in agriculture, public health, and the environment, emphasizing the need to understand their ecological roles (e.g., Albuquerque; Prado, 2017). In addition to their ecological roles, ants are also deeply woven into the culture, cuisine, and everyday life of many Amazonian peoples (Lenko; Papavero, 1979).

This chapter provides an overview of the ants of the Brazilian Amazonia, based on a dataset (Andrade-Silva *et al.*, 2022) compiling information from publications, field expeditions, and biological collections. The aim is to highlight research on ants and demonstrate how their diversity and collaborative initiatives have strengthened myrmecology in Amazonia.

## ON SOME MILESTONES IN AMAZONIAN MYRMECOLOGY

Understanding scientific development requires considering regional specificities, including environmental, cultural, historical, political, and institutional

contexts. In Amazonia, reconstructing science relies on historical, administrative, and technical data, as well as records from collections and oral histories (Leite, 1993). Using the dataset compiled by Andrade-Silva *et al.* (2022), which includes published and unpublished data and ant collection records, we analyze how myrmecology became established, marking the region as a key player in the early development of the field in Brazil.

### *Early Steps Toward Myrmecology in the Amazonia*

Amazonia's biological and cultural diversity has long attracted interest for many different purposes. Even though ants were not the subject, the first recorded mention of a Brazilian animal occurred precisely in the Amazonia, in 1500, just a few months before the official discovery of Brazil, made by the Spanish commander Vicente Yáñez Pinzón, probably in the Marajó Bay (Papavero *et al.*, 2000). Since then, the region has served numerous explorations and scientific expeditions (Papavero *et al.*, 2000; Vanzolini, 2004). The first references to ants in the Amazonian literature began appearing mainly from the 17th century onwards, that is, even before these insects were formally described in science. These early accounts usually referred to species that had a strong presence in the daily lives of local communities, such as the bullet ant/tocandira (*Paraponera clavata* (Fabricius, 1775)), leaf-cutter ants/saúva, fire ants/formiga de fogo (*Solenopsis* spp.) and certain *Camponotus* species, though not exclusively. Among the earliest records is the work of Maurício de Heriarte, who in 1662 mentioned ants in the Madeira River region. A few decades later, between 1694 and 1698, Father João Felipe Bettendorff made important observations in what are now the states of Maranhão and Pará. Then, between 1761 and 1763, Dom Frei João de São Joseph Queiroz also referenced ants in the Alter do Chão area along the Tapajós River, in present-day Pará. Still, in the 18th century, Father João Daniel provided detailed descriptions of the fauna along the Amazon River; his writings were later published at various points throughout the 19th century (Papavero *et al.*, 2000). These early mentions of ants were often cultural or folkloric, tied to daily life, pests, and local traditions. As Lenko & Papavero (1979) noted, ants were generally regarded with aversion for the harm or nuisance they could


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cause, but there is no evidence of systematic extermination, as they were mostly avoided or driven away.

### *Myrmecology in Amazonia: trajectories, challenges and scientific protagonism*

Myrmecological research in the Amazon basin has been key to establishing the field in Brazil. The historical development of myrmecology in the region remains partially understood, and the knowledge produced has never been fully organized. This overview summarizes its history in three phases:

#### 1. *The Establishment of Myrmecology in Amazonia*

The first phase began in the late 19th century, with the founding of the Museu Paraense Emílio Goeldi (MPEG). Key factors in its early prominence included the coordination of expeditions throughout Amazonia and other regions of Brazil, the creation of its scientific journal, contact with leading international researchers, and the leadership of Emílio Goeldi and later Emília Snethlage. A notable example was the collaboration between Goeldi and Auguste Forel, who published the first compilation of Brazilian ant species, including distribution and natural history data (Forel, 1895). Forel also published several works based on material collected during MPEG expeditions from Amazonia and other Brazilian biomes. Emília Snethlage, one of the first women to lead a natural history museum in Brazil, collected and sent material to specialists and organized expeditions, including the myrmecologist William Mann's (Stanford Expedition to Brazil, 1911), resulting in the publication *The Stanford Expedition to Brazil, 1911, John C. Branner, Director* (Mann, 1916). Following the rubber crisis and political setbacks starting in 1914, scientific activity declined, and MPEG experienced a long period of inactivity. Recovery began only in the second half of the 20th century (Leite, 1993). Despite recurring instability and chronic underfunding, MPEG established itself as a leading institution for myrmecology in Amazonia and the Neotropics, with research encompassing ecology, taxonomy and natural history (Prado *et al.*, 2020).

## 2. *Institutional Expansion and the Consolidation of Collections*

The second phase marks the growing role of the Instituto Nacional de Pesquisas da Amazônia (INPA) in establishing research groups focused on ecology, taxonomy, and the strengthening of scientific collections. The INPA's myrmecological collection began in the second half of the 20th century and has been enriched by contributions from researchers conducting expeditions across the Brazilian Amazonia. In the 1990s, INPA established the Programa de Coleções Científicas Biológicas (PCCB) to integrate and coordinate collection initiatives. Research groups dedicated to ecology, biodiversity, monitoring, taxonomy and faunal surveys further reinforced their role in expanding collections. The INPA's collections now reflect transformations in Amazonian biota, including impacts from large hydroelectric dams (Fernandes; Oliveira, 2020). Ecological studies under the Programa de Pesquisa em Biodiversidade (PPBio) using standardized sampling across Amazonian states also expanded myrmecological data (Rosa *et al.*, 2021). The INPA and MPEG played complementary roles, with INPA primarily responsible for western Amazonia and MPEG for the eastern portion, each conducting expeditions, coordinating projects, and participating in biodiversity and sociobiodiversity networks.

## 3. *The Current Phase: Decentralization and Research Protagonism in Amazonia*

Currently, new research groups have been established across nearly all Amazonian states, extending beyond capitals and creating new centers. Network-based projects such as PPBio have contributed to decentralizing scientific production (Magnusson *et al.*, 2008; Rosa *et al.*, 2021). Despite challenges, Amazonian research has strengthened collaborative networks, increasing the visibility and impact of myrmecology. Initiatives such as the Guia para os Gêneros de Formigas do Brasil (Baccaro *et al.*, 2015), the Formigas do Brasil course, and projects including ABC Expeditions, SCIANTS Amazônia, Plataforma Taoca, and Rede BIA demonstrate regional leadership. Institutions such as (but not restricted) INPA, MPEG, UFAM, UFAC, UFMT, UEMA, UFMA, UFOPA, UNIFESSPA have


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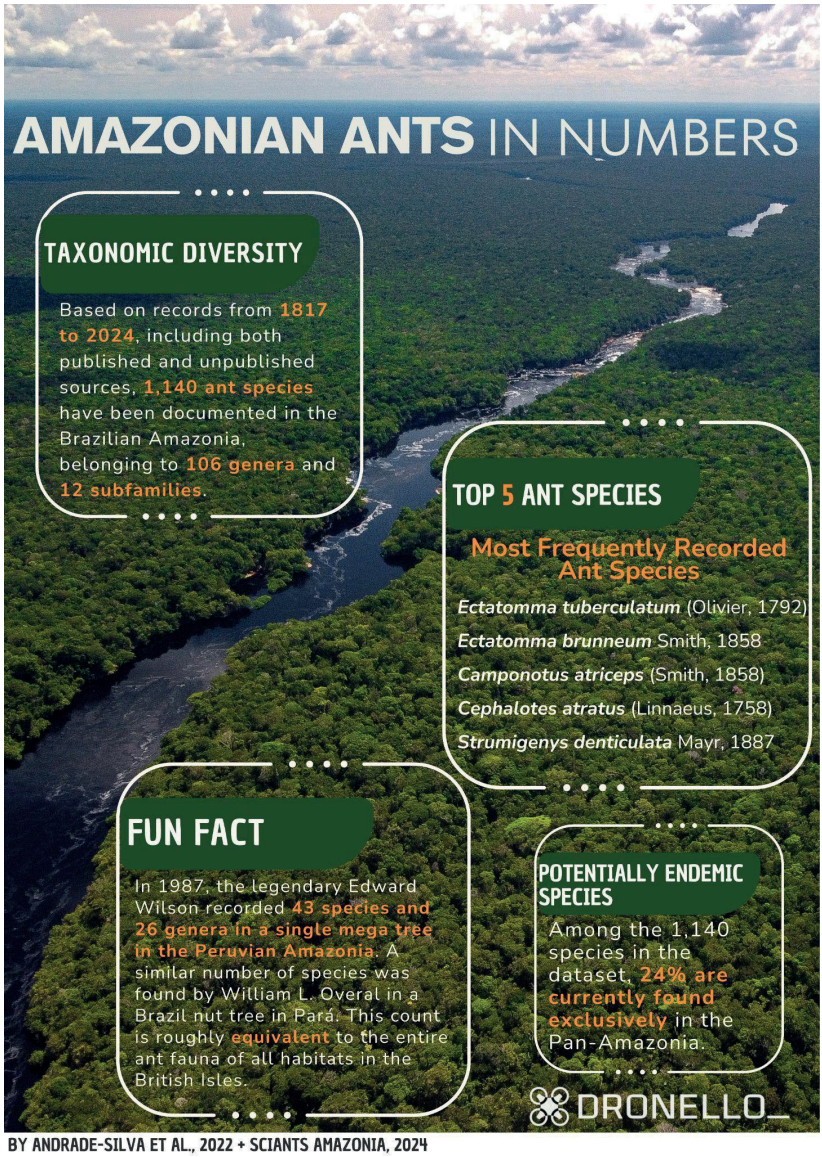
positioned Amazonia as a protagonist, addressing local needs and building the foundations for a stronger and more inclusive myrmecology.

## ANTS OF THE BRAZILIAN AMAZONIA

The Brazilian Amazonia harbors one of the most diverse ant faunas on Earth, representing a critical component of the region's biodiversity (Fig. 1). Recent findings indicate that the Amazonia basin records over 1,140 ant species across 106 genera and 12 subfamilies (Fig. 1), though the full extent of their diversity remains incompletely understood, largely due to the biome's vastness, logistical challenges in sampling, sample processing and taxonomic complexities (Fig. 2; see also Andrade-Silva *et al.*, 2022; SCIANTS, 2024). This remarkable diversity emerges from complex ecological gradients, habitat heterogeneity, ranging from dense lowland rainforests to seasonally flooded *várzea* and transitional savanna-forest ecotones, and evolutionary processes that have shaped ant communities across the basin. Amazonian ants exhibit extraordinary niche partitioning, occupying distinct strata from the forest floor to the canopy and specializing in various microhabitats, thereby creating intricate patterns of biodiversity.

**Figure 1 -** Data extracted from our datasets by Andrade-Silva *et al*., 2022, and SCIANTS, 2024, highlighting the diversity of ant species in the Amazon.




**Source:** Andrade-Silva *et al*., 2022; SciAnts Amazonia, 2024. **Photo by** Raffaello Di Ponzio (@ dronello_).

The current understanding of ant diversity in the Brazilian Amazonia reveals several key patterns. **First**, species richness shows significant spatial variation across the basin, with exceptionally high richness in the eastern, central,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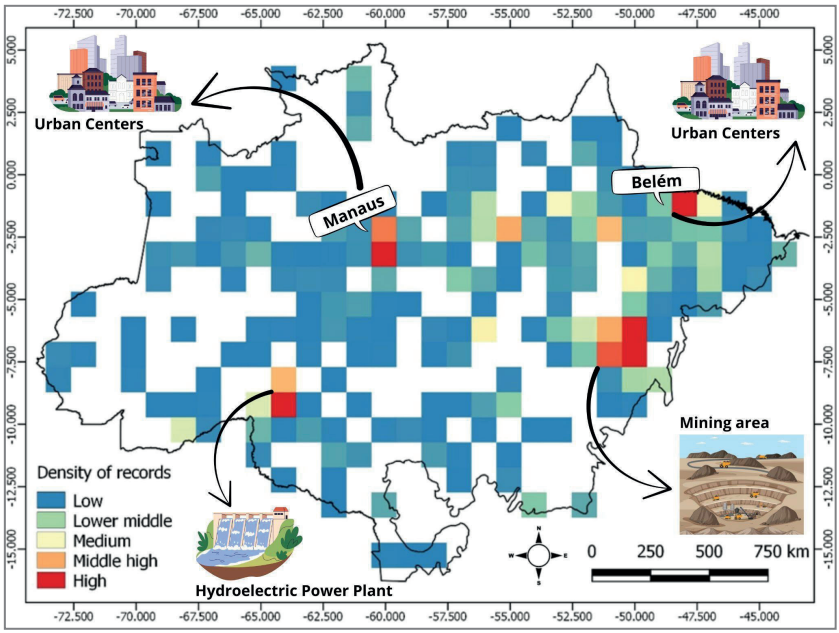
southern, and Madeira-Tapajós interfluvial (Andrade-Silva *et al.*, 2022). This gradient appears to be influenced by multiple factors, including precipitation patterns, habitat heterogeneity, and historical biogeographic processes (Dantas; Fonseca, 2023; Oliveira *et al.*, 2025). **Second**, vertical stratification gives rise to distinct communities across forest strata, with canopy and understory assemblages differing substantially from ground-dwelling communities (Fowler *et al.*, 2000; Vasconcelos; Vilhena, 2006). **Third**, habitat specialization is pronounced, with many species exhibiting strong associations with specific microhabitats such as dead wood, leaf litter, soil moisture, or epiphytic mats, highlighting the role of fine-scale environmental filtering in structuring assemblages.

Ant species composition also varies across different forest types. Floodplain (várzea) forests support assemblages distinct from adjacent terra firme forests, while white-sand campinas harbor specialized communities adapted to nutrient-poor conditions (Siqueira; Silva, 2021; Oliveira *et al.*, 2025). These habitat specialists often exhibit unique morphological and behavioral adaptations, reflecting how morphological diversity is structured across Amazonian ant communities. Common species tend to dominate morphological space in the Brazilian Amazonia Basin, suggesting that widespread taxa exhibit greater phenotypic variability than rare species (Andrade-Silva *et al.*, 2024). These findings challenge conventional assumptions about niche specialization and highlight how dominant species may exploit broader ecological opportunities through morphological plasticity. A largely underexplored dimension of Amazonian ant diversity lies in their intricate mutualistic relationships with plants, fungi, and other arthropods, interactions that promote niche specialization and facilitate coexistence. Such symbioses create microhabitat-specific dependencies, providing resources and protection in exchange for ant-mediated defense or other ecological services (Rico-Gray; Oliveira, 2007). These mutualistic relationships can also structure vegetation food webs and influence nutrient dynamics (Sánchez-Peña *et al.*, 2005).

Amazonian ant diversity is shaped by the region's deep phylogenetic history, influencing species distributions and community assembly. Molecular phylogenies show contrasts in diversification rates across clades (Moreau; Bell, 2013), illustrating how evolutionary processes create areas that act as "museums" of ancient diversity or "cradles" of recent radiation. The Brazilian

Amazon's ant diversity results from a complex interplay of ecological and evolutionary forces. Macroecological gradients, habitat stratification, and mutualistic networks shape spatial niche partitioning, while edaphic specialization further refines community assembly. Crucially, the region's phylogenetic legacy explains why certain lineages dominate specific habitats and how historical processes underpin modern richness patterns. This evolutionary perspective complements the ecological view, revealing that Amazonian ants are not only ecologically versatile but also embody a living archive of ancient diversification. However, accelerating deforestation and climate change now threaten to erase both species and the evolutionary histories they represent. Effective conservation must therefore prioritize not only areas of high species richness, but also regions of high phylogenetic distinctiveness, safeguarding the Amazon's dual role as both a cradle and a museum of ant biodiversity.

**Figure 2 -** Map of the Brazilian Amazon, showing nearly 50,000 records since 1817. The density of records highlights data accumulation driven by factors such as concentration in major urban centers (due to accessibility and lower research costs) and large-scale projects (e.g., hydropower plants and mining), which often require environmental impact studies and, in some cases, ant surveys.



## HIGHLIGHTING AMAZONIAN ANT DIVERSITY

### *Ants × Forest: Diversity of Ecological Interactions*

Ants play a key role in numerous ecological processes in the Amazonia, including nutrient recycling, seed dispersal, population control of other invertebrates, soil formation, and aeration, and forming associations with plants, fungi, and other animals. Although most species forage on the soil surface, the vertical complexity of the Amazonia Forest supports ant communities across multiple strata, including the canopy and understory (Andrade-Silva *et al.*, 2022). Each stratum presents distinct resources and ecological pressures, resulting in diversified interactions. For example, many ants feed on sugary substances produced by extrafloral nectaries in the canopy (Fig.3A; B). These nectaries function as a strategy by which plants attract ants; in return, ants tend to attack any intruder approaching the food source due to their aggressive behavior. By attracting ants, the plant thus reduces herbivory (Dáttilo; Dyer, 2014; Dejean *et al.*, 2025). A similar mutualistic relationship occurs with hemipterans that secrete sugary substances known as honeydew. Ants protect these insects and, consequently, defend the host plants on which the hemipterans feed (Fig.3C) (Delabie, 2001; Pringle, 2021).

Amazonia stands out for the specialization and complexity of its ant-plant mutualistic networks, particularly those involving myrmecophytes, plants that have evolved specialized structures called domatia, hollow cavities that house ant colonies. In exchange for shelter and, in many cases, food (such as extrafloral nectar and nutrient bodies), ants provide protection against herbivores, competitors, and pathogens, while also contributing nutrients through waste and prey remains (Dáttilo *et al.*, 2009; Dejean *et al.*, 2025). Approximately 80% of *Cecropia* species, for instance, are myrmecophytic, housing *Azteca* ants that prune vines, manage Müllerian bodies, and reduce herbivory from leaf-cutting ants such as *Atta laevigata* (Smith, 1858) in restoration areas (Dejean *et al.*, 2025; Vasconcelos; Casimiro, 1997).

Another classic example involves highly aggressive ants *Pseudomyrmex*, which establish colonies in the domatia of *Tachigali* spp. (Fabaceae: Caesalpinioideae) (Pacheco; Del-Claro, 2018). However, *Tachigali paniculata* Aubl. has also been recorded in association with other, non-*Pseudomyrmex* ants that

opportunistically occupy the domatia (Dejean *et al.*, 2025), indicating a less specialized and more flexible ant-plant interaction in some cases. In contrast, some associations are highly specific, such as *Myrcidris epicharis* Ward, 1990, found exclusively in association with *Myrcia madida* McVaugh (Myrtaceae) along riverbanks in the Amazonia. These ants inhabit the plant's hollow branches and defend it against herbivores (Ward, 1990; Vicente *et al.*, 2018).

These mutualisms are not only taxonomically diverse but also structurally modular, organized into discrete clusters of species that interact more strongly with each other than with species outside their group (Dáttilo *et al.*, 2013). This modular organization is likely maintained by evolutionary filters, such as domatia morphology, chemical cues, and behavioral specificity, which restrict generalist ants from colonizing specialized host plants (Dáttilo *et al.*, 2013; Dejean *et al.*, 2025). In addition to mutualistic plant-ant interactions, the well-known symbiosis between ants and fungi is also noteworthy. Leaf-cutting ants of the genus *Atta* Fabricius, 1804 cultivate fungal gardens within their nests using plant material, thereby functioning as important soil engineers in the Amazonia (Verchot *et al.*, 2003). Their populations tend to be more concentrated at forest edges, where they preferentially harvest leaves of pioneer plants, increasing herbivory pressure and influencing forest regeneration dynamics (Crist, 2009). Fungus-growing ants are particularly frequent in fragmented or drier environments (Baccaro *et al.*, 2013), and some species, such as *Kalathomyrmex emeryi* (Forel, 1907), exhibit remarkable adaptations by constructing nests that can endure prolonged flooding during the rainy season (Klingenberg; Brandão, 2009).

Conversely, army ants such as *Eciton burchellii* (Westwood, 1842) are more sensitive to forest fragmentation than leaf-cutting ants, avoiding areas with low vegetation cover due to their low tolerance to heat (Crist, 2009). Army ants play a key role in regulating invertebrate populations. Although some animals, like birds, benefit from these ant raids by capturing fleeing prey, the ants do not receive any direct benefit in this relationship. Nevertheless, the diversity and abundance of ant-following birds in the Amazonia are closely linked to the availability and distribution of army ant colonies, making these ants indirectly important for maintaining avian biodiversity in forest ecosystems (Crist, 2009). Altogether, the resilience and specialization observed in these relationships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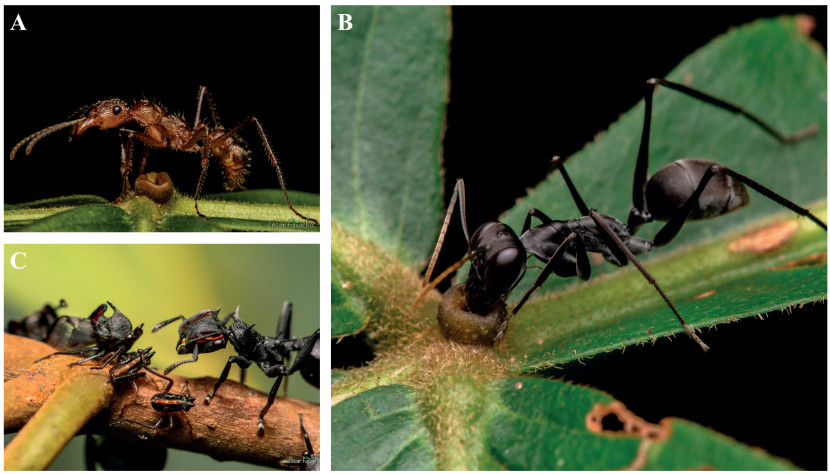
underscore the importance of conserving Amazonian habitats, not only for the ants themselves but for the intricate web of species that depend on their presence.

**Figure 3 -** Ants and mutualistic relationships. A. *Ectatomma tuberculatum* (Olivier, 1792) visiting an extrafloral nectary; B. *Gigantiops destructor* (Fabricius, 1804) feeding on an extrafloral nectary; C. *Cephalotes atratus* (Linnaeus, 1758) tending hemipterans.




**Photos by** Cesar Favacho.

### *Ants × Humans: Environmental and Cultural Impacts*

The relationship between humans and ants in the Amazonia is multifaceted, shaped by the ecological consequences of human activity on ant populations and the impact these insects have on urban and natural environments. Habitat degradation, forest fragmentation, and urbanization have facilitated the spread of invasive species, which have invaded ecologically areas and urban spaces. This phenomenon not only threatens local biodiversity but also disrupts human communities (Albuquerque; Prado, 2017).

In the northern region of Brazil, fire ants (*Solenopsis* spp.) (Fig. 4A) invasions have long been a problem, particularly in urban areas, where they are often involved in incidents of severe allergic reactions due to their stings. In Novo Airão (AM), an infestation of *Solenopsis invicta* Buren, 1972 was so intense that residents were relocated (Baccaro *et al.*, 2015). In Eirunepé (AM), *S. saevissima* (Smith, 1855) infestations reached densities of up to 40 nests per hectare, prompting a control plan involving both chemical insecticides and natural products

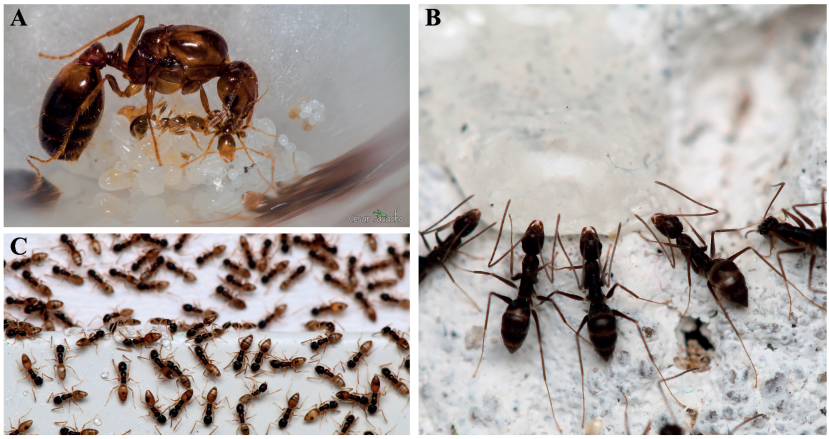
(Albuquerque; Prado, 2017). While these species are native to Brazil, *Solenopsis* ants are highly aggressive, often outcompeting native species and negatively impacting local biodiversity.

Additionally, *Solenopsis* species are also a significant concern in hospital environments. These ants, along with other invasive species like *Monomorium pharaonis* (Linnaeus, 1758), *Paratrechina longicornis* (Latreille, 1802) (Fig. 4B) and *Tapinoma melanocephalum* (Fabricius, 1793) (Fig. 4C), are commonly found in such environments, where they can act as vectors of pathogens (Albuquerque; Prado, 2017). For example, *Monomorium pharaonis* has been frequently found carrying *Pseudomonas aeruginosa*, a harmful bacterium, in a hospital in Eastern Amazonia (Nascimento *et al.*, 2020).

The relationship between humans and ants in the Amazonia extends beyond urban invasions. Both ant consumption and medicinal use have been documented among Indigenous communities (Silvestre; Neto, 2020). The most well-known example is the initiation ritual of the Sateré-Mawé people involving *Paraponera clavate,* known internationally as the bullet ant and in Brazil as *Tocandira***,** considered to have the most painful sting of any insect (Alvarez, 2011). During the rite of passage to adulthood, young boys must place their hands into woven gloves filled with dozens of these ants, ensuring that the ants' gasters face inward. They then endure the painful stings as part of this challenging tradition. Additionally, Indigenous groups have been reported to temporarily abandon their homes when army ant raids approach, returning later once undesirable invertebrates have been eliminated (Baccaro *et al.*, 2015).

These long-standing relationships between humans and ants reflect an understanding and coexistence with native ant fauna. However, environmental degradation and urban expansion have disrupted these relationships, creating conditions for opportunistic and invasive species to thrive. These ants now pose ecological and public health challenges, requiring control measures and further research on their impacts.

**Figure 4 -** Ants from urban and hospital environments. A. *Solenopsis* sp., fire ant queen with workers and immatures; B. *Paratrechina longicornis* workers feeding on sugar in a residence in Belém, Pará; C. *Tapinoma melanocephalum* in a residence in Belém, Pará, Brazil.




**Photos by** Cesar Favacho.

### *Little-Known Predatory Ant Species*

The immense biodiversity of the Amazonia region, combined with the elusive nature of certain species and the challenges of conducting research in such a vast environment, has resulted in significant gaps in our knowledge about their biology and ecological roles. Among these, several predatory ant species stand out as particularly enigmatic and understudied.

Among the most intriguing and least known species in the Amazonia is *Martialis heureka* Rabeling and Verhaagh, 2008, discovered in the region of Manaus, Brazil. Studies suggest that *Martialis heureka* is the most basal member of the Formicidae, providing insights into the early evolution of ants. The species has unique characteristics, including a pale exoskeleton, lack (or absence) of eyes, and a narrow body adapted for a hypogean or nocturnal lifestyle. *Martialis heureka* has only been sporadically recorded, making it one of the rarest and most enigmatic ant species (Rabeling *et al.*, 2008). Similar to *Martialis*, species of the genus *Leptanilloides* Mann, 1923 exhibit pale coloration, lack of eyes, and morphological traits indicative of hypogeic habits. Only two species have been recorded in dense central Amazonian forests, *L. manauara* (Brandão *et al.*, 1999) and *L. amazonus* (Brandão *et al.*, 1999). Due to the scarcity

of collected specimens, studying these ants remains particularly challenging, and their biology and ecological roles are still largely unknown (Baccaro *et al.*, 2015; Brandão *et al.*, 1999).

Another interesting genus is *Tatuidris* Brown and Kempf, 1968, which includes the single species *Tatuidris tatusia* Brown and Kempf, 1968. Although its distribution spans the Neotropical region, from the Brazilian Amazonia to Mexico, collections from lowland Amazonia are few. Very little is known about the biology of these ants. The only colony discovered to date contained just three workers and four queens, suggesting that colonies may be small and potentially fragile (Donoso, 2012). Other poorly studied genera include *Sphinctomyrmex* Mayr, 1866, and *Cheliomyrmex* Mayr, 1870. *Sphinctomyrmex*, a genus of predatory ants with a single specimen found in the Amazon, *Sphinctomyrmex marcoyi* Feitosa *et al.*, 2011, is known only from the holotype and nothing is known about its biology. *Cheliomyrmex* species are subterranean and found in the Brazilian Amazon Basin. Two species have been recorded: *C. andicola* Emery, 1894, from the state of Acre, and *C. megalonyx* Wheeler, 1921, with a few specimens collected from Amazonas, Rondônia, and Pará. The lack of studies on subterranean ants means that of their ecology and behavior remains a mystery (Albuquerque *et al.*, 2021).

In contrast to these subterranean predator species, *Dinoponera hispida* Lenhart *et al.*, 2013 is one of the largest ant species in the world, can reach a body length exceeding 3.5 cm, and is found in the humid forests of the Brazilian Amazon, particularly in the state of Pará. While *Dinoponera hispida* is not subterranean, it faces similar threats due to habitat destruction from mining and deforestation. The species is relatively rare, with a restricted distribution, and is likely to be at risk. Some specimens in collections have been misidentified as *Dinoponera gigantea* (Perty, 1833), which occurs in different parts of the Amazon. Additionally, *Dinoponera nicinha* Dias and Lattke, 2021 has been recorded in the Brazilian states of Amazonas and Rondônia. This species is large and potentially faces threats from habitat destruction as well (Dias; Lattke, 2021). Continued research on predatory ants is essential to understand their biology, behavior, and conservation needs, especially as habitat destruction and environmental changes threaten the Amazonia and its ecosystems.

## FUTURE DIRECTIONS IN AMAZONIAN MYRMECOLOGY

After briefly outlining the historical context and current state of knowledge on Amazonian ant fauna, we further provide perspectives for advancing research specifically within the Amazon basin. The huge geographical scale of the Amazonia basin requires different approaches to enhance our knowledge of the ant fauna in this biome. As global change accelerates, accurate predictions of species distributions and biodiversity patterns in the basin become critical to mitigating biodiversity loss. Although detailed local site information remains important for improving fine-grain species distribution models (e.g., Cohen; Jetz, 2024), a basin-wide perspective for myrmecology in Amazonia is presented here, based on the research line and ongoing projects.

### *Making Knowledge Accessible through Collections*

Scientific collections are widely recognized as essential for understanding biodiversity (Winker, 2004). Given the importance of taxonomic accuracy in biodiversity research, we suggested that taxonomic work on Amazonian ants from material deposited in collections is crucial to advance the knowledge gaps and analyses from a macroecological perspective. Collections frequently hold a large volume of unsorted material and today the majority of newly described species are discovered within existing collections (Meineke *et al.*, 2018). With the huge gaps in our understanding of Amazonia biodiversity, it is critical to identify ant taxa at risk and prioritize conservation efforts. Material from Amazonia housed in museums should be constantly examined and updated to correct misidentifications and fill knowledge gaps. Further, strong support to human resources and infrastructure is crucial for maintaining the extensive databases of Amazonian species compiled to date (Guayasamin *et al.*, 2024).

### *Addressing Knowledge Gaps through Species Distribution Modeling*

Considering the huge gaps in ant sampling (Andrade-Silva *et al.*, 2022), we understand that, currently, a comprehensive range maps for most ant species in Amazonia are unfeasible. Further, given the worrying degradation across the

entire basin (Matricardi *et al.*, 2020), alongside the emerging loss of high-integrity native forests historically subject to minimal anthropogenic influence (high-integrity forests; Pillay *et al.*, 2024), extensive spatial analyses are also needed. We have pursued that based on updated databases on ant species occurrences in the Amazonia (Andrade-Silva *et al.*, 2022; 2024). To address these biodiversity shortfalls, synthesizing information from literature, museum collections, and specimen datasets, through computational approaches, can aid in overcoming the challenges of creating comprehensive biome maps of ant diversity in the Amazon basin (see a global analysis by Kass *et al.*, 2022). Predicting the spatial distribution of species assemblages remains a significant challenge in the Amazonia. However, achieving this can lead to better understanding of the geographical patterns of ant species richness and composition of local communities across the Amazon Forest. Most importantly, given the current scenario of climate change and anthropogenic impacts, temporal and spatial predictions of biodiversity are fundamental to support conservation and restoration actions.

### *Networked Initiatives in Large-Scale Research*

Recent network initiatives funded by national and international agencies are focused on gathering primary data on biodiversity in tropical forests (e.g., PPBio program, Amazon +10 initiative). As a result, research groups studying ant biodiversity now have the opportunity to gather standardized data on a large scale in Amazonia, which has been lacking in the past. Over the next few years, we expect that valuable data will be generated by various research groups throughout the Amazon basin, allowing for the sharing and integration of numerous digitized records. This is expected to contribute to ongoing large-scale analyses across the basin and facilitate comparisons among morphospecies.

### *Assessing Endemism Centers as a Critical Need*

The subdivision of Amazonia in large interfluvial areas of endemism, as delimited by major rivers, has been an important starting point for understanding the biome's megadiversity (Laranjeiras *et al.*, 2024). This regionalization is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grounded mainly on the distributions of birds and primates, which often have ranges delimited by major rivers (Rego *et al.*, 2024; Laranjeiras *et al.*, 2024). Although the validity of this approach has been recently questioned, including for ants (Dambros *et al.*, 2020), it remains a recurrent background for studies on evolution, conservation, and species discoveries (see Laranjeiras *et al.*, 2024). Effective conservation strategies depend on understanding the evolutionary and ecological processes that generate and maintain local species diversity in the numerous unique biological communities present across Amazonia (Guayasamin *et al.*, 2024). Therefore, there is an urgent need for studies that assess the compartmentalization of ant diversity in the Amazonia and explore the unique characteristics of each region and habitat type.

### *Integrating Regional Scenarios with Macroecology, Biogeography and Phylogeography*

Amazonian biodiversity is the outcome of tens of millions of years of evolution, in a unique and unrepeatable combination of geological history, climatic, and biological processes over broad spatial and temporal scales. This includes taxa distributed across the entire South American continent and evolving over a period of tens of millions of years (Antonelli, 2021; reviewed by Guayasamin *et al.*, 2024). Although abiotic changes and shifts in the distribution and connectivity of different habitats over space and time were responsible for the accumulation of the mega diversity in the Amazonia basin (and described in the literature; see review by Guayasamin *et al.* 2024), historical patterns of Amazonian ant taxa are largely lacking. Indeed, information on biogeography, phylogeography, and areas of endemism was poor or not explored in ant literature and there is no wide-biome data (i.e., the Amazonia biogeographic province).

### *Ant Communities and Their Contribution to Ecological Resilience*

Empirical evidence indicates that the Amazonia rainforest has been losing resilience since the early 2000s, likely driven by drier conditions and increased human land-use activity (Boulton *et al.*, 2022). To maintain the resilience of Amazonia rainforest we must combine local efforts to end deforestation and degradation

with initiatives to expand restoration (Flores *et al.*, 2024). Specifically, restoring at least 5% of the biome is crucial to establishing safe boundaries that define a viable operating space for rainforest resilience (Flores *et al.*, 2024). In signing the Paris Agreement and the Kunming-Montreal Global Biodiversity Framework, most Amazonian countries have committed to achieve zero deforestation and restore 30% of degraded ecosystems by 2030 (UNFCCC, 2015; COP26, 2021; CBD, 2022). However, dedicated regional studies evaluating ecosystem recovery from various restoration strategies particularly concerning the Amazon's biodiversity are still incipient. Natural forest regeneration in deforested and degraded areas, resulting in secondary forests, has been studied in a few regions of Amazonia (e.g., Solar *et al.*, 2016), but without a long-term monitoring of successional stages at regional scales (but see Nunes *et al.*, 2022). Agroforestry is often employed as a strategy of forest landscape regeneration, linking economic interests and conservation efforts during the recovering of degraded areas (Perfecto *et al.*, 1996; Shakur *et al.*, 2025). Nevertheless, the current information available is insufficient to quantify what has already been recovered in terms of ecological processes and biodiversity (Cruz *et al.*, 2021).

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# 15

# THE ANT FAUNA OF THE CERRADO: DIVERSITY, ECOLOGICAL DRIVERS, AND HUMAN PRESSURES IN A GLOBAL BIODIVERSITY HOTSPOT

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# ABSTRACT

As in many other terrestrial ecosystems, ants are a dominant insect group in the savannas, forests and grasslands that together compose the Brazilian Cerrado. Myrmecological research in this biome started more than one century ago and here we show that the scientific knowledge about this insect group and the representativeness of Cerrado ants in Brazilian entomological collections has grown enormously during the past few decades. Based on diverse sources we estimate that total ant diversity in the Cerrado may reach 700-900 species, many of which remain unnamed. Yet, local diversity can be quite high, with intensive surveys showing the presence of over 200 species in a single locality. Both variation in tree cover and vertical stratification can help to explain the high number of species coexisting locally, given that different species tend to be associated with different vegetation types or with different nesting and/or foraging strata (arboreal or ground). Species turnover is particularly high between adjacent forest and savanna habitats. Fire suppression can transform open savanna areas into dense savannas or forests, thereby reducing ant diversity at the landscape level. However, reintroducing fire allows the return of open savanna specialists. The rapid conversion of the Cerrado native vegetation has a negative impact on ant diversity, but the magnitude of this effect is much higher in lands devoted to intensive agriculture (rather than to pastoralism or plantation forestry), as it affects not only the richness of species but also the functional and phylogenetic diversity of ant communities. Maintaining habitat heterogeneity and integrating ants into biodiversity-friendly agriculture are key to safeguarding ecosystem functions and services in the Cerrado.

**Keywords:** Ant diversity**;** fire disturbances; Neotropical savanna; vegetation heterogeneity; vertical stratification.

## INTRODUCTION

Located in central Brazil, and originally covering an area of ca. 2 million km2, the Cerrado is the largest and most threatened tropical savanna and a biodiversity hotspot. This chapter is about the Cerrado mirmecofauna. We begin by describing when myrmecological research started in this region and the extent to which it grew in recent years, including a description of how well Cerrado ants are represented in entomological collections and how this is important for the future development of Neotropical myrmecology. Then we present estimates of how diverse the Cerrado ant fauna is and summarize the available information on which factors influence this diversity at both local and regional scales. Finally, we seek to synthetize the current information about the influence of fire and the effects of land use change on the different levels and dimensions of Cerrado ant diversity, and on ant ecosystem functions.

## MYRMECOLOGICAL RESEARCH IN THE CERRADO: ROOTS AND TRAJECTORIES

The first formal observations of ants associated with this biome can be attributed to the Danish naturalist Peter Wilhelm Lund (1801–1880), who provided observations on the life habits of Brazilian ants, including species from the Cerrado (Lund, 1831a,b). In addition, he described two ant genera, *Crematogaster* and *Dolichoderus*, highly represented in the Cerrado.

Until relatively recently, the representation of Cerrado ants in myrmecological collections was significantly lower compared to specimens from other Brazilian biomes. This is mainly due to the historical concentration of collecting efforts in the country's forested environments, especially the Atlantic Forest (Schmidt *et al.*, 2022). From the 1970s onwards, however, expeditions and standardized surveys began to increase the number of Cerrado ant specimens in these collections. Among the most important initiatives were the expeditions of Colonel Moacyr Alvarenga (1915–2010) to the Sinop region, Mato Grosso, between 1973 and 1976. Alvarenga, an officer of the Brazilian Air Force and an enthusiastic amateur entomologist, was able to travel extensively through Brazil and collect insects in numerous localities. A large portion of the ants he


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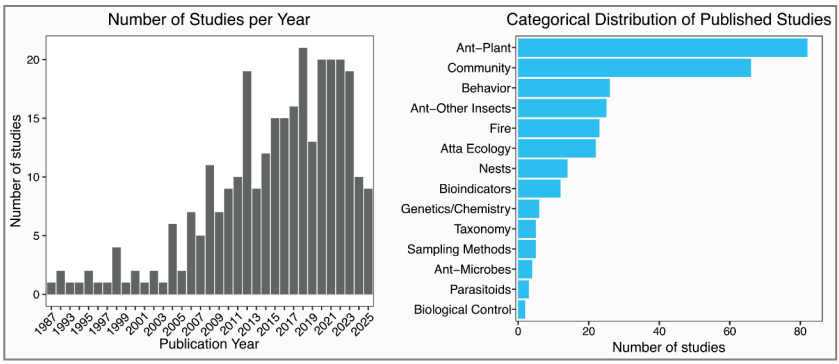
collected in Cerrado areas of Mato Grosso are now deposited in the *Museu de Zoologia da Universidade de São Paulo* and in the *Padre Jesus Santiago Moure* Entomological Collection of the *Universidade Federal do Paraná* in Curitiba (Andrade & Feitosa, 2020). In the 1980s, the Federal Government launched the "*Polonoroeste Project*" (Northwest Brazil Integrated Development Program), which promoted agricultural expansion and included the construction of the BR-364 highway crossing the states of Rondônia, Mato Grosso, southern Goiás, and northern São Paulo. Insect surveys were carried out (as requested for the project's environmental licensing) and many ants collected during *Polonoroeste* Project are now deposited in the Entomological Collection of the *Universidade Federal do Paraná*.

In 1990, the project "Social Insects of the Northeastern Brazilian Vegetation Formations" (led by Dr. Carlos Roberto F. Brandão, Eliana Marques, and Paulo Oliveira) resulted in the most extensive standardized inventory of Brazilian savanna ants at the time. In addition, this study was the first to indicate that the ant fauna of the Cerrado is vertically stratified, and that there are marked differences between the diurnal and nocturnal faunas (Brandão, 1995). Based on the material collected in this extensive survey, a series of studies followed, which greatly advanced our understanding about diversity patterns and the functional ecology of ants in the Cerrado (Silvestre *et al.*, 2003; Silva *et al.*, 2004). As head of the Frei Walter W. Kempf Myrmecology Laboratory, at the *Universidade Federal de Goiás* in Jataí, Dr. Jorge Luís Machado Diniz played a major role in collecting and assembling an impressive collection of Cerrado ants, especially from Goiás and northern São Paulo. Upon retirement in 2016, Dr. Diniz donated his collection of about 50,000 specimens to the *Universidade Federal do Paraná* Entomological Collection (Andrade & Feitosa, 2020). This material continues to fuel taxonomic and biogeographic studies, underscoring his invaluable contribution to Cerrado myrmecology.

Significant advances in knowledge about Cerrado ants came after the establishment, between 1990 and 2010, of important ant ecology research groups at federal universities in Minas Gerais state, -- including those in Belo Horizonte, Lavras, Uberlândia and Viçosa -- , and which have made major contributions to different areas of myrmecology. A literature search in the Web of Science using the keywords "Ants" and "Cerrado", or "Ants" and "Neotropical savanna"

initially resulted in 472 papers. We then refined our search, looking at the title and abstract of each paper, to include only papers in which ants were the focus of the study, and that actually were conducted in the Cerrado even when also involving other biomes. This resulted in a total of 295 papers published between 1987 and 2025 (Figure 1). Of these, about half (49.15%) were published during the last 15 years. There is a strong bias towards the study of mutualistic interactions between ants and plants or between ants and other insects, totaling 107 papers (36.3%), and those interested in the subject should consult the excellent reviews by Oliveira & Freitas (2004) and Rico-Gray & Oliveira (2007). Papers involving different aspects of ant community ecology or the use of ants as bioindicators represent 26.4% of those published so far. There are also several papers involving different aspects of the behavior of Cerrado ants, their responses to fire, characteristics of the nests (e.g., structure, inquilines), or the ecology of leaf-cutter ants (*Atta*) (Figure 1). Studies about the genetics or chemistry (e.g., cuticular hydrocarbons) of Cerrado ants, their taxonomy (or new distributional records), about the efficiency of different sampling methods, about the interaction of Cerrado ants with microorganisms, about ant parasitoids, or the use of ants as agents of biological control are comparatively scarce (Figure 1).

**Figure 1 -** Number of papers published during the past 38 years, and the main study topic of each paper. The list only includes papers whose main subject of the study where Cerrado ants.




**Source:** Web of Science.

## DIVERSITY AND ENDEMISM

The Cerrado is surrounded by two large tropical forest biomes, the Amazon and the Atlantic Forest. It is regarded as a relatively young biome, given that most of the modern Cerrado flora originated only about 10 million years ago (Simon *et al.* 2009). However, most Neotropical ant lineages originated much earlier, during the Eocene (>30 Ma), coinciding with the expansion of tropical forests (Moreau & Bell, 2013). Much of the ant fauna of the savannas of central Brazil appear to have a forest origin, given that the two faunas share many lineages (Vasconcelos *et al.* 2018, Andersen & Vasconcelos 2022). This is also evidenced by phylogenetic analyses of two prominent Cerrado ant groups, the turtle ants (*Cephalotes*) (Price *et al.*, 2014) and the fungus-growing ants (Branstetter *et al.*, 2017), which indicate that both originated in rainforest and only later expanded and diversified into drier habitats.

Many Cerrado ants are widespread forest species that extend into the semi-arid Caatinga as well (Leal *et al.*, 2018). In the most extensive standardized survey of Brazilian savanna ants, Vasconcelos *et al.* (2018) sampled 29 Cerrado sites across the biome, covering ca. 20° of latitude and 18° of longitude. Species richness per site ranged from 59 to 144, totaling 455 species. In addition, a recent synthesis of ant diversity across the Brazilian biomes (Feitosa *et al.*, 2022) ranked the Cerrado as the third most diverse biome, after Amazonia and the Atlantic Forest, with ~4,500 ant records (over the last 50 years) and 389 nominally identified species. Combining the two datasets, the total number of named species recorded for the Cerrado is 442. Arboreal ants are partially responsible for this remarkable diversity, particularly *Cephalotes*, *Pseudomyrmex*, and *Crematogaster*, along with numerous arboreal specialist species in the genus *Camponotus* (Vasconcelos *et al.*, 2018). Epigaeic ants also contribute substantially, with fungus-growing Attina ants (especially *Acromyrmex* and *Mycetomoellerius*) and *Pheidole* being especially diverse (Feitosa *et al.*, 2022).

A notable pattern in Neotropical savannas is the relatively low endemism of ant species, especially compared to the highly endemic Australian savanna ant fauna (Andersen *et al.*, 2018). This discrepancy likely reflects both the younger age of the Cerrado and its strong derivation from adjacent forests, which limited the time available for diversification. Indeed, only a few ant taxa are endemic to

the Cerrado (excluding other South American savannas), including *Anochetus vexator* Kempf, 1964; *Cephalotes betoi* De Andrade, 1999; *Cephalotes gabicamacho* Oliveira, Powell & Feitosa, 2021; *Cephalotes marycorn* Oliveira, Powell & Feitosa, 2021; *Cephalotes specularis* Brandão, Feitosa, Powell & Del-Claro, 2014; *Ectatomma planidens* Borgmeier, 1939; *Ectatomma vizottoi* Almeida-Filho, 1987; *Leptomyrmex relictus* Boudinot *et al.*, 2016; *Mycetagroicus cerradensis* Brandão & Mayhé-Nunes, 2001; *Mycetagroicus triangularis* Brandão & Mayhé-Nunes, 2001; *Mycetomoellerius agudensis* (Kempf, 1967); *Mycetomoellerius dichrous* (Kempf, 1967); *Rogeria sicaria* Kempf, 1962; and *Sericomyrmex maravalhas* Ješovnik & Schultz, 2017.

Despite its relatively low endemism rates, many Cerrado areas host remarkably high local richness, often exceeding 200 species in relatively small areas (Camacho & Vasconcelos, 2015; Oliveira & Feitosa, 2021; Vasconcelos *et al.*, 2022). In addition, it is also well known that a large portion of ants recorded in Brazilian diversity studies are not identified to species level, due to the taxonomic complexity of hyperdiverse and morphologically challenging genera (Feitosa *et al.*, 2023). In such cases, researchers classify ants as morphospecies, usually employing their own coding systems, sometimes unique to individual projects. This is the case for most Cerrado surveys.

Considering the ~450 named species currently recorded for the Cerrado, and the fact that 56% of Cerrado ant records in the literature are associated with morphospecies codes (Vasconcelos *et al.*, 2018; Feitosa *et al.*, 2022), it is reasonable to estimate that Cerrado ant diversity may in fact reach 700–900 species. In this scenario, the large number of unidentified species in diversity studies may prove fundamental for advancing our taxonomic knowledge of Cerrado ants. Much of this undescribed diversity is likely already sitting in myrmecological collections under morphospecies codes, underscoring the urgent need for investment in taxonomist training and integrative approaches to species delimitation, especially for genera that currently represent the greatest taxonomic barriers in the study of both Cerrado and broader Brazilian ant faunas.

## VEGETATION HETEROGENEITY AS A PROMOTER OF ANT DIVERSITY

As other tropical savannas, the Cerrado biome is composed of a mosaic of vegetation types, including grasslands, savannas (the dominant vegetation type), and forests (Figure 1). Local scale variation in vegetation structure and composition in the Cerrado is associated primarily with local-scale variation in soil chemical and physical features, and the occurrence of fires (Oliveira & Ratter 2002).

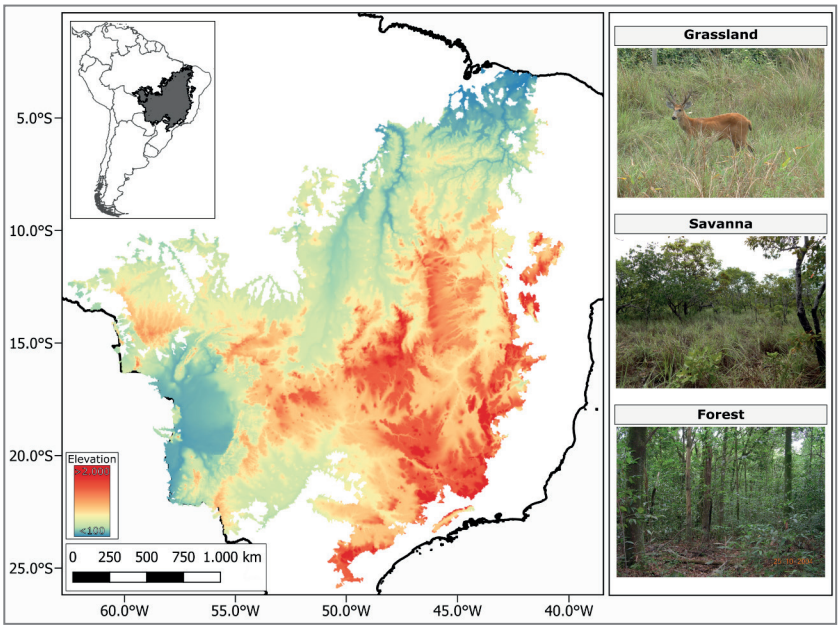
Ant diversity tends to be high in most of these vegetation types. Studies that have compared ant diversity between Cerrado savannas and forests have found either greater species richness in savanna (Marques & Del-Claro 2006, Vasconcelos *et al.* 2008), in forest (Vasconcelos & Vilhena 2006), or no difference between the two habitats (Lopes & Vasconcelos 2008, Vasconcelos *et al.* 2023a). Similarly, studies that have analyzed the relationship between ant species richness and tree cover (or tree density) have also produced contrasting results as both positive (Ribas *et al.* 2003, Pacheco & Vasconcelos 2012), negative (Neves *et al.* 2013, Neves *et al.* 2023), linear (Ribas *et al.* 2003, Neves *et al.* 2013), and non-linear (Neves *et al.* 2023) relationships were detected. It is not clear which factors are behind such contrasting results, but differences in sampling design and the sampling methods employed in the different studies may well be involved. This is because the effectiveness of different ant sampling methods can vary with the structure of the vegetation (Parr & Chown 2001, Lopes & Vasconcelos 2008) and so studies using different methods may produce results that are not fully comparable.

Despite that, all the existing studies converge in showing that tree cover has a major influence on ant species composition. For instance, an intensive inventory of the ground-dwelling ant faunas of the open savannas (*campo sujo*), dense savannas (*cerrado sensu stricto*), and forests (*cerradão*) from a Cerrado reserve in southern Brazil, showed that most (60.1%) of the species analyzed were significant "indicator" species due to their strong association with a given vegetation type (Vasconcelos *et al.* 2023a). This and other studies strongly suggest that habitat heterogeneity enhances ant diversity in the Cerrado, and that the mosaic of vegetation types that characterizes this biome is a key

factor explaining the elevated number of species that can be found at relatively small spatial scales.

In fact, two independent studies showed that beta diversity due to the turnover of species between different Cerrado vegetation types is higher than the random expectation, whereas alpha diversity and beta diversity due to species turnover between plots of the same habitat type are both smaller than expected (Pacheco & Vasconcelos 2012, Neves *et al.* 2013). As a result, as much as 50% of the overall species richness found in a given Cerrado landscape (i.e., its gamma diversity) can be attributed to the differences in species composition between vegetation types.

**Figure 2 -** (left) Elevational variation and location of the Cerrado in South America. (right) The three major types of vegetation found in the biome.




## VERTICAL STRATIFICATION

As indicated earlier, the savannas of the Cerrado support a relatively high diversity of arboreal nesting species. These species usually use pre-formed cavities to nest in trees, and specialization on different types of cavities seems to be

a mechanism enhancing species coexistence (Powell *et al.* 2011, Camarota *et al.* 2016). The high diversity of arboreal ants appears also to be associated with the high abundance and diversity of plants (especially trees) that produce extrafloral nectaries (EFNs) in the Cerrado (Oliveira & Leitão-Filho 1987, Schoereder *et al.* 2010). The nectar produced by these trees has positive effects on the fitness of arboreal ant colonies (Byk & Del-Claro 2011), and more ant species are found in trees with than without extrafloral nectaries (Camarota *et al.* 2015).

Arboreal and ground species present differences in morphology, which in turn are associated with differences in physiology and in the functional ecology of species (Almeida *et al.* 2013). Arboreal savanna ants have comparatively smaller mandibles, but larger eyes and eyes that are positioned more dorsally than ants living on the ground (Almeida *et al.* 2023, Vieira *et al.* 2025). Larger and more dorsally positioned eyes are potentially an advantage for arboreal species because they rely more on visual navigation than those that forage on the ground (Almeida *et al.* 2023). Differences in mandible length, in turn, likely reflect differences in the diet of ants from different vertical strata. Many arboreal species have a predominantly liquid diet of insect and plant exudates (such as the nectar produced in EFNs), whereas those on the ground act more as scavengers or predators of invertebrates (Vieira *et al.* 2021, Vieira *et al.* 2025), and this largely reflects the differences in the availability of different food resources between vertical strata. Consequently, when confronted with alternative food sources, arboreal and ground ants tend to prefer those that are rare where they live (but see Lasmar *et al.* 2023). For instance, a baiting experiment in both savanna and forest habitats of the Cerrado showed that arboreal ants are two times more frequent on sodium (NaCl) than on sugar baits, whereas on ground the frequency of ants on NaCl baits is about 20 % lower than on sugar baits (Vieira & Vasconcelos 2015). While sugar is relatively abundant in tree foliage, that is not the case for sodium (a vital element to maintain the osmotic balance and the neuromuscular activities of animals), as the concentration of sodium is much smaller in plant than in animal tissues (Kaspari *et al.* 2008).

Typical arboreal genera in the Cerrado are *Azteca*, *Cephalotes*, *Myrmelachysta*, as well as most *Camponotus* and nearly all *Pseudomyrmex* (Vasconcelos *et al.* 2023b). In contrast, on the ground, the most abundant genera are *Atta*, *Brachymyrmex*, *Dorymyrmex*, *Ectatomma*, *Forelius*, *Linepithema*, *Pheidole* and

*Solenopsis* (Vasconcelos *et al.* 2023b). The number of ant species foraging on the ground is about 2.3 times greater than the number of species foraging in trees (Vasconcelos *et al.* 2023b). However, not all the species foraging in a given stratum at a given time are necessarily typical of that stratum. In fact, about one-quarter of the species collected in arboreal pitfall traps are ground-nesting species, while 9% of those found on the ground actually nest in trees (Vasconcelos *et al.* 2023b). Yet, these two nesting/foraging strata present clear cut differences in species composition (Vasconcelos & Vilhena 2006, Vasconcelos *et al.* 2023b), indicating that vertical stratification, similarly as found for habitat heterogeneity, is a promoter of local and landscape scale ant diversity in the Cerrado.

## MACROECOLOGICAL PATTERNS OF DIVERSITY

The Cerrado is a climatic and environmentally heterogeneous biome, and as such the diversity and composition of its biota tend to be geographically variable (e.g., Ratter *et al.* 2003). The mean annual temperature varies nearly 10°C, from ~27 °C in the extreme north of the Cerrado and in the isolated savannas of the Amazon, to ~18°C in the southern limit of the Cerrado in the north of Paraná state (Oliveira & Feitosa 2021). The altitudinal variation is also high, with some sites located near sea level while others at elevations > 1,000 m a.s.l. (Figure 2). Less than 1,000 mm of rain falls annually in some Cerrado areas, notably those in the northeast, while in others annual rainfall can be nearly twice as high.

Ant sampling across the biome revealed that ant species richness patterns in the Cerrado do not follow the classical diversity pattern of increasing diversity as latitude decreases and thus temperatures increase. Rather, ant species richness shows a strong and positive relationship with latitude (Vasconcelos *et al.* 2018). This pattern is best explained by the latitudinal variation in rainfall, more specifically, by the latitudinal increase in the total amount of rainfall during the warmest quarter of the year (Vasconcelos *et al.* 2018). Rainfall during the warmest quarter is strongly correlated with net primary productivity, indicating that ant alpha diversity in the Cerrado follows a gradient of plant productivity (Vasconcelos *et al.* 2019). Indeed, ant diversity patterns in the Cerrado -- including patterns of alpha and beta diversity -- correlate with patterns of tree diversity, as revealed by a concomitant survey of the ant and tree communities in over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30 sites (Vasconcelos *et al.* 2019). About 45% of the variation in ant species richness and 22% of the variation in ant species composition were associated, respectively, with the variation in tree species richness and composition. However, there is little evidence that the observed congruence in diversity patterns between ants and trees results from direct interactions between the two taxa, as they both share the same environmental correlates of species richness and turnover (Vasconcelos *et al.* 2019).

Along the latitudinal gradient in the Cerrado, the proportion of arboreal species and the proportion of ground species in the total fauna remains relatively invariant (Vasconcelos *et al.* 2023b), so that the relationship between latitude and species richness is quite similar for ants typical of each vertical stratum (Vasconcelos *et al.* 2018). However, when considering the total number of species found within each stratum (regardless of its main vertical-stratum association), one finds that ant species richness on the ground increases at a much faster rate with latitude than ant species richness in trees (Vasconcelos *et al.* 2023b). Moreover, and interestingly, it is more likely to find a typical ground-nesting species foraging in trees at lower than at higher latitudes. Due to these factors, the similarity in ant species composition between vertical strata increases as latitude decreases (Vasconcelos *et al.* 2023b). In other words, there is less vertical stratification of the fauna as one moves from the colder to the hotter areas of the Cerrado.

Although some metrics of functional and phylogenetic diversity are positively correlated with taxonomic diversity, there is evidence that, overall, the latitudinal pattern of ant species richness described above does not adequately represent other dimensions of ant diversity in the Cerrado. Furthermore, there is also evidence that such representativeness varies between vertical strata (Neves *et al.* 2024). This is notably the case when one looks at the mean pairwise functional distance (MFD) and the mean pairwise phylogenetic distance (MPD) among all species from the sampled community. These diversity metrics represent the degree of functional or phylogenetic divergence among community members, whereas their standardized effect sizes provide evidence of the relative importance of competition versus environmental filtering in structuring the community (Webb 2000, Swenson & Weiser 2014). Neves *et al.* (2004) analyzed the relative influence of latitude and elevation as predictors of different

dimensions of ant diversity in the Cerrado, and found that while latitude was the only significant correlate of taxonomic diversity, both on the ground and in trees, and the only correlate of phylogenetic diversity on the ground, both the phylogenetic and the functional diversity (MPD and MFD) of arboreal ant assemblages were influenced only (and negatively) by elevation (Neves *et al.* 2024). This was also the case for the standardized effect sizes of the functional and phylogenetic diversity metrics, suggesting that as temperatures decrease with elevation, the importance of competition and niche partitioning in structuring arboreal communities decreases, while the role of habitat filtering becomes increasingly important.

## FIRE DISTURBANCES

Although the Cerrado is a fire-dependent biome, human activities and misleading fire-suppression policies have largely changed the timing, frequency, and/or intensity of savanna fires (Durigan & Ratter 2016). Studies to date indicate that ant responses to fire in the Cerrado can be dependent on all these parameters. In addition, responses can be different between ants from different vertical strata. Savanna fires have a limited direct effect on the survival of ground-nesting ants, as temperature rises are negligible below 5 cm of depth (Miranda *et al.* 1993). Similarly, arboreal ants that nest on relatively large trees are likely to survive if flames do not reach and thus consume the branches of these trees, as is often the case during low-intensity fires (Vasconcelos *et al.* 2009). However, high-intensity fires, which often occur as a result of very dry conditions and the accumulation of inflammable biomass (as usually happens in fire-suppressed savannas), can have marked effects on arboreal nesting ants (Morais & Benson 1988, Rosa *et al.* 2021). Therefore, while the effects of fires on savanna ground-ant communities are usually indirect, mediated by changes in the structure of the vegetation (Andersen 2019), that on arboreal communities are more contingent on the extent to which fires directly affect their nests.

In fact, studies that evaluated the effects of a single fire of low to moderate intensity on the arboreal ant community found no change in species richness and composition one to two years after the fire (Frizzo *et al.* 2012, Anjos *et al.* 2017). In contrast, a study that analyzed the arboreal communities of the same


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individual trees, before and after two consecutive fires of high severity, found a strong decline in species richness and marked changes in species composition, which became even more pronounced after the second fire (Rosa *et al.* 2021). After the fires, some species become more prevalent in the community, while many others, notably those with strictly arboreal nesting habits (and therefore more susceptible to the direct effects of fire), became rare or even disappeared from the focal trees (Rosa *et al.* 2021).

Short-term studies about the effects of fire on the structure of ground-dwelling ant communities have produced somewhat contrasting results. Durigan *et al* (2020) detected no effect on species richness or composition after a single prescribed fire, while others have reported an increase in species richness (Frizzo *et al.* 2012) or a weak effect on species composition (Anjos *et al.* 2017) one to two years after a wildfire. On the other hand, longer-term experimental studies have been consistent in showing that ant species composition (but usually not richness) is affected, and that these effects are mediated by changes in vegetation structure.

Annual or biennial prescribed-fires in a fire-suppressed savanna resulted in an increase in the richness and occurrence of open savanna specialists, and a decrease in the richness of species most typical of dense savanna or dry forests (Leão *et al.* 2025). However, these effects were noted only ~8 years after the beginning of the experiment, when differences in grass cover, in leaf-litter depth, and in the amount of bare ground between the burned and unburned plots became significant (Leão *et al.* 2025). Similarly, marked differences in ant species composition, related to fire-induced changes in vegetation structure, were detected in another fire experiment in the Cerrado (Maravalhas & Vasconcelos 2014). Ant species composition, both on ground and in trees, was different between plots that were burned biannually, quadrennially, or that remained unburned for 16 years. In addition, there were differences in species composition among plots burned at the beginning, at the middle, or at the end of the dry season every two years. However, these differences were less marked than those between plots burned at different time intervals and were restricted to the ground-dwelling fauna (Maravalhas & Vasconcelos 2014). Although these two studies presented different results regarding the validity of the pyrodiversity–biodiversity hypothesis (Parr & Brockett 1999) for the Cerrado, they both

show that fire is important for the maintenance of open-habitat specialists and thus can promote ant diversity at the landscape scale.

## LAND-USE CHANGES

Although conversion of the native Cerrado vegetation for agriculture and ranching started more than two centuries ago, it was not until the 1970´s, when government incentives and the development of techniques to deal with soil acidity and high concentrations of aluminum took place, that large-scale commercial agriculture became a reality. The Cerrado is now the major producer of soybeans and other agricultural commodities (Santana *et al.* 2020). As a result, the biome has witnessed very rapid transformation over the past few decades, losing over 50% of its original vegetation (Parente *et al.* 2021).

Studies about the effects of land-use change on Cerrado ant communities indicate that the conversion of the native vegetation into anthropogenic land uses inevitably causes a decline in species diversity and eventually also biotic homogenization. However, effects on species richness and composition often vary in magnitude depending upon the structural differences between the original and converted habitats (Dalle Laste *et al.* 2019, Queiroz *et al.* 2020, Carvalho *et al.* 2022). For instance, conversion of open grasslands into cattle pastures had a comparatively smaller impact on ant species richness than did the conversion of grasslands into eucalypt plantations (Queiroz *et al.* 2020), whereas the conversion of open or dense savannas into any of these two land--uses presented comparable results on species richness (Queiroz *et al.* 2020). Similarly, Carvalho *et al.* (2022) showed that the effects of land-use change on ant species composition are comparatively greater for the forest than for the savanna-associated ant faunas.

While the conversion of native habitats into areas devoted to pastoralism or to forestry causes marked changes in the taxonomic structure of ant communities, the effects on functional diversity and composition are much less severe (Rabello *et al.* 2021, Carvalho *et al.* 2022), indicating that different aspects (dimensions) of ant diversity can respond differentially to changes in land-use in the Cerrado. However, this is not the case in areas used for large-scale production of agricultural commodities (soybean mainly), and which are rapidly


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expanding both into natural areas and areas previously devoted to other land uses. This is of concern given that ant species richness in soy fields is typically very low – even when compared to cattle pastures or tree plantations (Frizzo & Vasconcelos 2013, Carvalho *et al.* 2022) – and the species found in the soy fields tend to represent a nested subset of the species found in the other land uses or in the native habitats (Pacheco *et al.* 2013, Vasconcelos *et al.* 2024). In addition, the functional and phylogenetic diversity of the soy field communities is much lower than that of Cerrado forest and savanna communities (Vasconcelos *et al.* 2024). Furthermore, there is strong evidence of biotic homogenization when comparing different soy fields both from a functional and a phylogenetic perspective (Vasconcelos *et al.* 2024).

One possible way to minimize the effects of land-use change on Cerrado ant communities is through the maintenance of trees in agricultural landscapes, given that such trees can increase ant diversity locally. It was found that the number of ground-dwelling ant species found beneath isolated trees in cattle pastures and soy fields was 8 and 55% greater, respectively, than the number found only 30 m away from these trees (Frizzo & Vasconcelos 2013). Unfortunately, although isolated trees are relatively common in cattle pastures, they are not in the soy fields, except when former pasturelands are leased by soybean producers. In this sense, compliance with the Brazilian Forest Code is of uppermost importance. This law requires that, in the Cerrado, landowners keep 20 to 35% of their properties with native vegetation (as "legal reserves"). As one study revealed, the maintenance of these small patches of natural Cerrado vegetation can increase ant diversity within a rural property by as much as 76% (Pacheco *et al.* 2013).

## ECOSYSTEM SERVICES

Changes in land use have implications for the delivery of ant services by ants. Ants play a variety of ecosystem services and that is no different in the Cerrado. One of the most important of these services is the predation of other insects, which contributes to biological control. One study showed that ant predation rates are positively associated with ant species richness (Frizzo *et al.* 2020), while another indicates higher predation rates in native Cerrado vegetation

than in coffee plantations (Wilker *et al.* 2024). Aboveground ant predation rates did not differ between crop (soybean) and non-crop (savanna) habitats, but belowground predation rates were much smaller in the agricultural areas largely due to the scarcity of army ants (Dorylinae) in these areas (Pacheco *et al.* 2017).

Many ant species also act as seed predators and/or as secondary seed dispersers. They transport both myrmecochorous and non-myrmecochorous seeds, with a preference for lipid-rich diaspores (Christianini *et al.* 2007). Although seed dispersal distances are generally shorter than those mediated by vertebrates, larger-bodied ant-species can move seeds beyond parent plants (Wilker *et al.* 2023). Moreover, in post-fire or in degraded areas, ants frequently surpass vertebrates in seed removal rates (Alcolea *et al.* 2022, Coelho *et al.* 2023). Seed removal rates by ants can be affected by land use changes in the Cerrado. For instance, removal rates were much smaller in eucalypt plantations than in native vegetation, but differences were much less marked when comparing cattle pastures with native vegetation (Rabello *et al.* 2018).

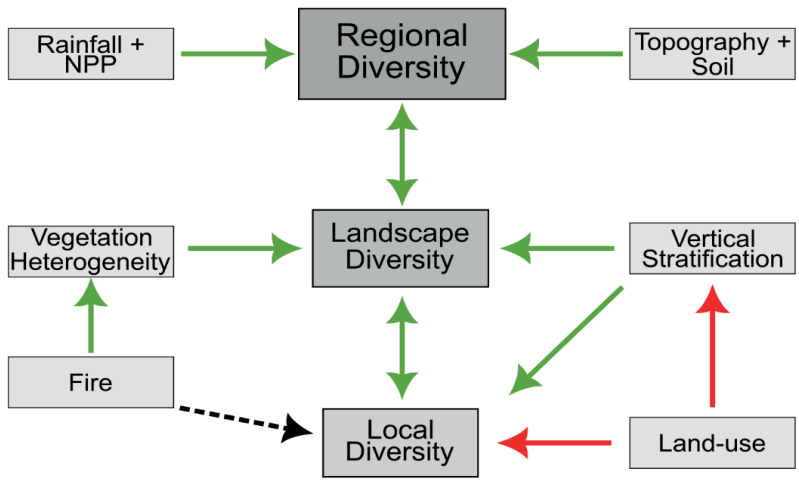
Ants also visit flowers, and in some cases act as non-specialist visitors and contribute to pollination, as observed in two Cerrado species *Microstachys serrulata* and *Paepalanthus lundii* (de Faria *et al.* 2022, Del-Claro *et al.* 2019). Nevertheless, negative effects are also reported, since ants can deter pollinators or compete for floral resources, reducing seed set (Calixto *et al.* 2024, de Sousa-Lopes *et al.* 2020). Thus, ant–plant interactions on Cerrado plants may reduce herbivory while simultaneously affecting pollination.

Another key function played by ants is the cycling of nutrients. Many species act as scavengers removing dead insects, animal carcasses, or bird droppings Others, as the leaf-cutting of the genus *Atta*, which are notably abundant in many Cerrado native and non-habitats, transport large amounts of fresh vegetation to their belowground chambers (Costa *et al.* 2008), thus increasing soil fertility and root density around their nests (Sousa-Souto *et al.*, 2008). In this sense, the conservation of ant-mediated functions should be viewed as essential for maintaining both the biodiversity and the long-term sustainability of the Cerrado.

## CONCLUDING REMARKS

In Figure 3, we attempted to summarize the available information about the influence of different factors on Cerrado ant diversity at various spatial scales. Climate seems to play a key role in explaining the observed variation in ant diversity across the Cerrado. In addition, there is evidence that ant diversity at the regional scale is also influenced by the geographic variation in elevation, and thus in temperature, soils, and topography. Vertical stratification helps to increase ant diversity at the local scale, and local-scale diversity can increase, decrease, or remain unchanged due to fire disturbances. On the other hand, the conversion of the native Cerrado vegetation into anthropogenic land-uses, notably the conversion into areas devoted to production of agricultural commodities, has severe and negative impacts on multiple dimensions of ant diversity. At the landscape scale, ant diversity is often enhanced by the diversity of native vegetation types, given that different ant species tend to be associated with different vegetation types. Fire helps to maintain this mosaic of vegetation types and thus indirectly can increase ant diversity at the landscape scale. However, severe fires and fire suppression usually have negative impacts on ant diversity at both the local and landscape scales.

**Figure 3 -** The influence of physical factors, fire, land-use changes, vegetation structure and vertical stratification on Cerrado ant diversity at various spatial scales. Green arrows represent positive effects, red arrows negative effects, whereas the black-dashed arrow represent variable effects.



Research on Cerrado ants now spans nearly a century, growing notably over the past few decades thanks to the increasing number of research groups working in the region. By linking species-level data to their various ecological roles and ecosystem services, efforts to survey and document the Cerrado ant fauna undoubtedly helped to reveal the ecological significance of these ants and their responses to environmental change. The representativeness of Cerrado ant specimens in Brazilian myrmecological collections has also grown enormously. Much of this material forms the foundation of our current knowledge about the diversity of ants in the Brazilian savanna biome, and provide support to conservation planning, molecular research and, importantly, the training of new ant specialists. Together, these efforts are key for better understanding and preserving the "little things that run the Cerrado".

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# 16

# ENDEMISM AND VULNERABILITY OF ANTS IN THE PHYTOPHYSIOGNOMIES OF THE BRAZILIAN ATLANTIC FOREST

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# ABSTRACT

The Brazilian Atlantic Forest encompasses a diversity of formations composed of a vast forest mosaic with remarkably distinct phytophysiognomies. This forest has historically experienced extensive habitat loss, leading to the urgent need for effective conservation measures. However, the lack of information on taxonomic diversity within the phytophysiognomies of the Atlantic Forest, particularly concerning invertebrates, hinders the development of efficient conservation strategies. We present here a systematic review of publications on ants across the different phytophysiognomies of the Brazilian Atlantic Forest over the past 105 years (1918–2023). In parallel, we indicated potentially endemic species for the forest and its phytophysiognomies. We compiled species occurrence records and spatial distribution data using on two ant databases and indicated potentially endemic species for the Brazilian Atlantic Forest and its phytophysiognomies. In total, we recorded 383 publications, with a significant increase beginning in the 2000s. Four phytophysiognomies were mentioned in the publications, with Ombrophilous Forest being the most studied (20.74% of publications). About 4% of the 1,109 analyzed species were classified as endemic to the Atlantic Forest, representing nine subfamilies and 30 genera, with most species belonging to *Pheidole* (22.45% of all species). A total of 38.78% of all species occurred in only one phytophysiognomy. According to the "Brazil Red Book of Threatened Species of Fauna" (Red Book), nine analyzed species are listed, of these five of which are threatened with extinction. Additionally, we identified potential biases and knowledge gaps in the available data.

**Keywords:** Formicidae; geographic distribution; Hymenoptera; tropical forests.

## INTRODUCTION

Insects provide a variety of essential ecosystem services (DINIZ-FILHO *et al.*, 2010; COWIE *et al.*, 2022). However, recent studies have indicated a drastic decline in their abundance (CHOWDHURY *et al.*, 2023; RABITSCH and ZULKA, 2024), and many may become extinct before their species is even described (DIVIESO *et al.*, 2020). This could lead to significant losses of the ecosystem services they provide (CARDOSO *et al.*, 2011). Despite their ecological importance, insects are underrepresented in official lists of threatened fauna (e.g., "International Union for Conservation of Nature and Natural Resources" - IUCN) due to a lack of experts and/or information available about the species (DINIZ-FILHO *et al.*, 2010; COWIE *et al.*, 2022). As a result, they tend to be underrepresented in conservation planning, management, monitoring, and decision-making policies (CARDOSO *et al.*, 2011; CHOWDHURY *et al.*, 2023).

This scenario is particularly concerning because the Atlantic Forest is the Brazilian biome with the highest number of endangered terrestrial invertebrate species (ICMBIO, 2018a,b). Yet, only 11.4–16% of its original vegetation remains, and this is highly fragmented (RIBEIRO *et al.*, 2009; SOLÓRZANO *et al.*, 2021). Though, 30% of the existing vegetation cover is located within protected areas (REZENDE *et al.*, 2018).

The Atlantic Forest is recognized as one of the world's biodiversity hotspots (MITTERMEIER *et al.*, 2004; HIROTA, 2019; MARQUES and GRELLE, 2021). Despite the lack of data for most invertebrate groups (MITTERMEIER *et al.*, 2004), the Brazilian Atlantic Forest harbors high ant diversity, with 1,114 described species and 2,235 morphospecies recorded to date (SILVA *et al.*, 2022). Up to 30 species can be found in just 1 m2 of leaf litter (SILVA and BRANDÃO, 2010). However, despite this richness, only three genera are considered as restricted to this biome: *Anillidris* Santschi, 1936; *Phalacromyrmex* Kempf, 1960; and *Diaphoromyrma* Fernández *et al.* 2009 (FEITOSA *et al.*, 2021). At the species level, thirteen are endemic to the Atlantic Forest, and all are listed in the "Brazil Red Book of Threatened Species of Fauna" (ICMBIO, 2018b; FEITOSA *et al.*, 2021).

Some of these species have records restricted to specific phytophysiognomies: (*i*) Pioneer Formation (Restinga) - *Atta robusta* Borgmeier, 1939, *Mycetophylax simplex* (Emery, 1888) and *Mycetomoellerius atlanticus* (Mayhé-Nunes


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& Brandão, 2007); (*ii*) Semideciduous Forest - *Fulakora cleae* (Lacau & Delabie, 2002); and (*iii*) Seasonal Deciduous Forest - *Monomorium delabiei* Fernández, 2007 (ICMBIO, 2018b). Despite this, knowledge about endemic ants of the Atlantic Forest, or their phytophysiognomies, remains limited for most species (FEITOSA *et al.*, 2021). This lack of consolidated information is concerning, as it compromises the assessment of extinction risk and implementation of targeted conservation measures (BRITO, 2008), given that habitat fragmentation and loss are among the main drivers of species extinction (SÁNCHEZ-BAYO and WYCKHUYS, 2019).

In this context, this study aimed to analyze publications on ants in the Brazilian Atlantic Forest quantitatively. Specifically, we determined: (1) the areas of knowledge and sampled regions; (2) the studied phytophysiognomies; and (3) the strata and collection techniques used in each phytophysiognomy. Additionally, we indicate: (4) species potentially endemic to the Atlantic Forest; (5) the phytophysiognomies where endemic species occur; and (6) consult the extinction risk classification of these species to extinction.

## METHODS

### Bibliographic review

A systematic review was conducted using records from the "Scielo", "Web of Science", and "Scopus" databases. The search terms included "Formicidae", "Atlantic Forest", and "Mata Atlântica"; combined as "Formicidae + Atlantic Forest" and "Formicidae + Mata Atlântica", covering a time frame from 1950 to 2024. To complement the review, data were also obtained from the "ATLANTIC ANTS: a dataset of ants in Atlantic Forest" (Silva *et al.*, 2022) and the "Global Ant Biodiversity Informatics - GABI" database (Guénard *et al.*, 2017). These sources include publications before 1950, which were also incorporated in the review, thereby extending the time range.

Publications were excluded if: (*i*) they did not mention the biome; and (*ii*) the research was conducted outside the Brazilian Atlantic Forest. The selected publications were categorized by "Region", "Area of knowledge", "Phytophysiognomy", "Strata", and "Collection technique" (Table 1). Multiple subcategories

in a publication were separated, and each was counted for once. Thus, the publications that fit into more than one subcategory were counted according to the number of subcategories. The individual count for each subcategory is presented as absolute values, and the total percentage considers this count in relation to the total number of publications analyzed (n = 383).

**Table 1 -** Description of categories and subcategories addressed in the analyzed papers.

| Category | Subcategory | Description |
|---|---|---|
| Region[1,2] | Central-West | Goiás, Mato Grosso do Sul. |
| | Northeast | Alagoas, Bahia, Ceará, Paraíba, Pernambuco, Piauí, Rio Grande do Sul, Sergipe. |
| | Southeast | Espírito Santo, Minas Gerais, Rio de Janeiro, São Paulo. |
| | South | Paraná, Rio Grande do Sul, Santa Catarina. |
| Knowledge areas[3] | Diversity | Taxonomic, genetic, and functional diversity; occurrence and/or geographic distribution of species. |
| | Ecology | Biology and natural history (e.g., ecological interactions). |
| | Ethology | Animal behaviour. |
| | Phylogeny | Evolutionary studies. |
| | Genetics | Cytogenetics. |
| | Taxonomy | Species inventory and description. |
| Phytophysiognomies[4] | High-Altitude Fields | High-Altitude Fields. |
| | Seasonal Forest | Grouped vegetational classes: Seasonal Semideciduous Forest and Seasonal Deciduous Forest. |
| | Ombrophilous Forest | Grouped vegetational classes: Dense Ombrophilous Forest, Mixed Ombrophilous Forest, and Open Ombrophilous Forest. |
| | Pioneer Formation | Grouped vegetational classes: mangroves, restingas, saline fields, and alluvial areas. |
| Stratum | Leaf litter | Ants collected in leaf litter. |
| | Soil | Ants collected on the soil. |
| | Vegetation | Ants collected in herbaceous, shrubby, and tree species. |
| Collection technique[5] | Field picking | Active search for ants (collection on the soil, leaf litter, twig, fruits, and vegetation). |

[1]Only the States covering the Brazilian Atlantic Forest; [2]In articles without specification of the region, but with mention of the State, the respective region was recorded; [3]The predominant area of knowledge in the publication was considered; [4]The name mentioned in the publication was used, and the phytophysiognomies were categorized according to Law No. 11,428/2006, Decree No. 6,660/2008; [5]Description of grouped collection techniques only.

## Endemic species

The list of potentially endemic ant species in the Brazilian Atlantic Forest was compiled following three steps: (*i*) selection of target species; (*ii*) Selection of species occurrences (geographic distribution); and (*iii*) compilation of the list of endemic ants based on their distribution.

## Target species

The endemic ants were identified by compiling and updating species names using Bolton (2025), drawing on three data sources: (*i*) publications from this study (see Section 2.1 Bibliographic review), which mentioned or assessed 13 species restricted to the Atlantic Forest (Table 2); (*ii*) Silva *et al.* (2022), who reported 1,114 species from studies conducted in the Atlantic Forest. Selection criteria included: (a) occurrence within the Atlantic Forest (field "ma.lmt"); (b) records in Brazil (field "Country"); and (c) taxonomically validated occurrences (field "Exclude"). Morphospecies (field "Morphospecies") or exotic species (field "Exotic") were excluded. This process yielded 1,057 species occurring within the Brazilian Atlantic Forest; and (*iii*) Feitosa *et al.* (2023), who reported 1,130 species (657 occurring in the Brazilian Atlantic Forest) based on studies of ant diversity in Brazil over the past 50 years. Species were selected using the same criteria (occurrence within the Brazilian Atlantic Forest; records in Brazil, and validated occurrences). Morphospecies and exotic species were again excluded, resulting in 635 species recorded in the Brazilian Atlantic Forest. After compiling all records from these three data sources, a total of 1,112 ant species were recorded in the Brazilian Atlantic Forest.

**Table 2 -** Titles of publications on the bibliographic survey evaluating or mentioning species restricted to the Atlantic Forest.

| Publications |
|---|
| 1. Clemes Cardoso e Schoereder, 2014 - Biotic and abiotic factors shaping ant (Hymenoptera: Formicidae) assemblages in Brazilian coastal sand dunes: the case of restinga in Santa Catarina. |
| 2. Datillo et al., 2012 - Predictive model of distribution of *Atta robusta* Borgmeier 1939 (Hymenoptera: Formicidae): subsidies for conservation of a Brazilian leaf-cutting ant endangered species. |
| 3. Delabie et al., 2007 - Contribution of cocoa plantations to the conservation of native ants (Insecta: Hymenoptera: Formicidae) with a special emphasis on the Atlantic Forest fauna of southern Bahia, Brazil. |
| 4. Mariano et al., 2008 - A biogeographical study of the threatened ant *Dinoponera lucida* Emery (Hymenoptera: Formicidae: Ponerinae) using a cytogenetic approach. |
| 5. Fernandes et al., 2017 - Análise filogenética de *Anochetus* Mayr, 1961 e *Odontomachus* Latreille, 1804 (Hymenoptera: Formicidae: Ponerinae) e revisão taxonômica de *Anochetus* para a região Neotropical. |
| 6. Fowler et al., 1996 - The endemic Brazilian leaf-cutting ants, *Atta silvai* and *Atta robusta* (Hymenoptera, Formicidae): population status. |
| 7. Micolino et al., 2019 - Chromosomal dynamics in space and time: evolutionary history of *Mycetophylax* ants across past climatic changes in the Brazilian Atlantic coast. |
| 8. Peixoto et al., 2008 - Comportamento e estrutura reprodutiva da formiga *Dinoponera lucida* Emery (Hymenoptera, Formicidae). |
| 9. Santos et al., 2017 - An assessment of leaf-litter and epigaeic ants (Hymenoptera: Formicidae) living in different landscapes of the Atlantic Forest Biome in the State of Bahia, Brazil. |
| 10. Silva et al., 2020 - Diversity of the ant genus *Neoponera* Emery, 1901 (Formicidae: Ponerinae) in the north of the Brazilian Atlantic Forest, with new records of occurrence. |
| 11. Simon et al., 2020 - Environmental response of *Dinoponera lucida* Emery 1901 (Hymenoptera: Formicidae), an endemic threatened species of the Atlantic Forest Central Corridor. |
| 12. Teixeira et al., 2004 - Occurrence of *Atta robusta* Borgmeier (Hymenoptera: Formicidae) in the North of Espírito Santo State, Brazil. |
| 13. Vicente et al., 2023 - The Capixaba ant species inventory is far from complete: A local scale assessment of the ants (Formicidae) reveals the importance of diversity studies and entomological collections. |

## Endemic species

Occurrence data were extracted from Silva *et al.* (2022) and Kass *et al.* (2022a,b) for each target species (see Section 2.2.1 Target species). These publications provide validated datasets on ant occurrences. The selection of records included those with: (*i*) complete geographic coordinates (latitude and longitude); (*ii*) validated records; and (*iii*) target species. Initially, we used the valid species names to extract the information. No results were returned, for some species; however, they were found in the databases with obsolete names. Data extraction was repeated for these specific species using the obsolete names listed in the three data sources; and. In total, we obtained 341,670 occurrence records.


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After removing repeated occurrences, 160,169 unique occurrences remained, representing 1,109 species.

Species whose distribution is restricted to the Atlantic Forest biome were considered potentially endemic (GASTON, 1994). To support this classification, we assessed whether all recorded occurrences of a given species were located entirely within the Atlantic Forest. A geospatial data format file (shapefile) containing the Forest's geographic boundaries [defined by Law No. 11,428/2006 - "Atlantic Forest Law" (MMA, 2024a)] and another file containing information on native forest formations and associated ecosystems [as established by Decree No. 6,660/2008 (MMA, 2024b)] were used in the analysis. The latter recognizes the following vegetation cover classes: Dense Ombrophilous Forest; Mixed Ombrophilous Forest (Araucaria Forest); Open Ombrophilous Forest; Semideciduous Seasonal Forest; Deciduous Seasonal Forest; Pioneer Formation (mangroves, restingas, saline fields, and alluvial areas); Vegetation refuges (Relict Communities); Areas of ecological tension (contacts between vegetation types - ecotones and enclaves); and areas of vegetation disjunction such as: Steppe (Campos do Sul do Brasil); Savannah (Cerrado); and Savannah-Steppe (Caatinga do Sertão Árido) (IBGE, 2012a). However, due to the scarcity of occurrence data for some of these classes, we grouped them as follows: Ombrophilous Forest (combining Dense, Mixed, and Open Ombrophilous Forest) and Seasonal Forest (combining Semideciduous and Deciduous Seasonal Forest). The analysis was conducted in the R environment, version 4.4.2 (R CORE TEAM, 2024), using a script adapted from Aciole Barbosa (2024). Moreover, the following R packages were used for plotting: sf (PEBESMA and BIVAND, 2023), dplyr (WICKHAM *et al.*, 2023), ggplot2 (WICKHAM, 2016), circlize (GU *et al.*, 2014) and ggExtra (ATTALI and BAKER, 2023).

**Vulnerability status**

The vulnerability status of potentially endemic species was assessed at two scales: National, based on the "Brazil Red Book of Threatened Species of Fauna" (ICMBIO, 2018a; BRASIL, 2022); International, using the official IUCN (2025) list. The IUCN recognizes nine risk of extinction categories: "Extinct", "Extinct in the Wild", "Critically Endangered", "Endangered", "Vulnerable", "Near Threatened",

"Least Concern", "Data Deficient", and "Not Evaluated". These categories are determined using five criteria: A - Population size reduction; B - Geographic range; C - Small population size and decline; D - Very small or restricted population; and E - Quantitative analysis (IUCN, 2012). These criteria are adopted by ICMBio in compiling Brazil's national list of threatened fauna (ICMBIO, 2018a).

## RESULTS

### Bibliographic review

A total of 533 publications were reviewed, of which 383 focused on the Brazilian Atlantic Forest. These publications span 105 years (from 1918 to 2023), with the highest concentration in 2019 (32 publications; 8.36%), followed by 2020 (30; 7.83%), and both 2004 and 2012 (24; 6.27%) (Figure 1A). The most frequently addressed area of knowledge was Diversity (219 publications; 56.17%), followed by Ecology (139; 35.52%), Taxonomy (14; 4.03%), Ethology (7; 1.76%), Genetics (8; 1.76%), and Phylogeny (3; 0.76%). The Southeast region had the highest number of publications (207; 49.51%), followed by the Northeast (106; 25.98%), South (83; 20.34%), and Central-West (9; 2.21%); for eight publications (1.96%) did not mention the state or municipality, and the region could not be determined.

Four classes were identified among the categories of phytophysiognomies: Ombrophilous Forest (84 publications; 20.74%), Seasonal Forest (82; 20.25%), Pioneer Formation (47; 11.60%), and High-Altitude Fields (4; 0.99%). The phytophysiognomies studied in 188 publications (46.42%) were not mentioned. Pioneer Formation was the first phytophysiognomy mentioned in a publication from 1918. Ombrophilous Forests have been the most studied In recent decades (Figure 1B). Only 113 publications (29.50%) clearly stated which classification system was used for phytophysiognomies, with the most frequently cited (22 publications) being the book by Veloso *et al.* (1991) entitled "Classification of Brazilian vegetation, adapted to a universal system". Soil was the most frequently sampled stratum overall (187 publications; 48.83%) and among phytophysiognomies, followed by leaf litter (137; 35.77%) and vegetation (72; 18.80%) (Figure 2A). Nineteen collection techniques were employed, varying according to the phytophysiognomies (Figure 2B).


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**Figure 1 -** Number of publications per year concerning ants in the Brazilian Atlantic Forest, by total (A) and phytophysiognomy (B).

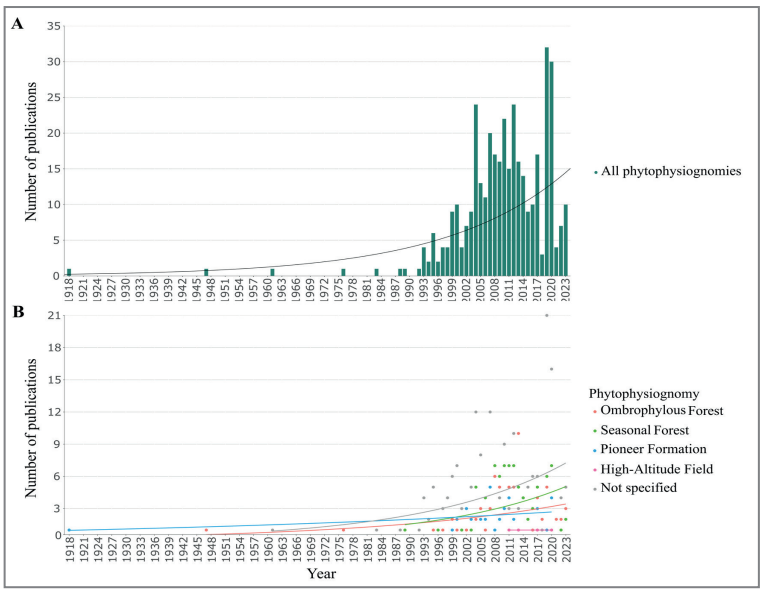
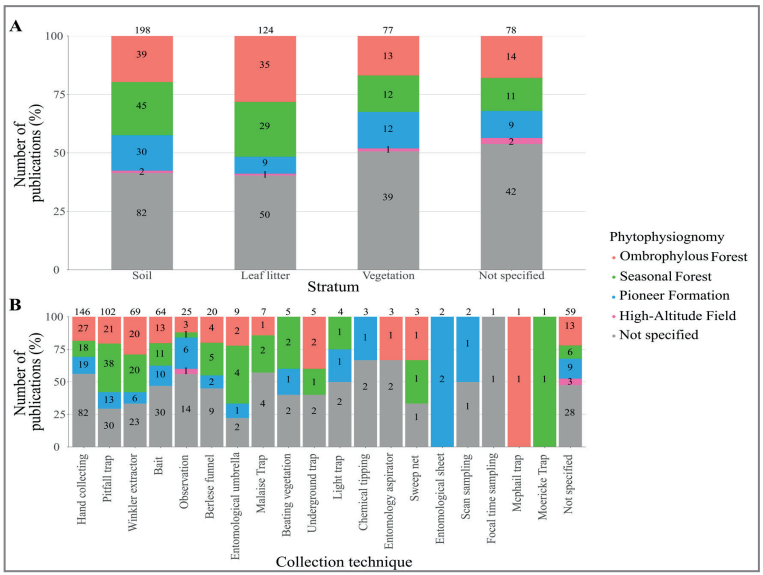



**Figure 2 -** Number of publications concerning ants in the Brazilian Atlantic Forest, by strata (A) and collection technique (B) according to phytophysiognomy (The labels within the columns represent the absolute values of the publications. And the labels above the columns represent the total number of publications per subcategory).



## Endemic species

Only 49 (4.42%) out of the 1,109 analyzed species (99 genera and 10 subfamilies) occur exclusively within the limits of the Brazilian Atlantic Forest. These endemic ants belong to 30 genera, with the most representative being *Pheidole* (11 species; 22.45%) and *Camponotus* (3 species; 6.12%) (Figure 3). Nine subfamilies are represented, the richest being Myrmicinae (28 species; 57.14%), Formicinae (06; 12.24%), and Ponerinae (05; 10.20%).

The endemic ants are distributed across seven vegetation cover classes. Peaks in the distribution of endemic species (Figure 4A), are observed near to latitudes 14 °S (Y1) and 24 °S (Y2) and near to longitudes 47° (X1) and 39°W (X2). Most species (30; 61.22%) occur in more than one phytophysiognomy and/or associated ecosystem, with five species present in four phytophysiognomies, five in three, and 20 in two. Conversely, 19 species (38.78%) were found exclusively in a single phytophysiognomy (Figure 4). The Ombrophilous Forest (42 species; 85.71%) presented the highest concentration of endemic species, followed by: Seasonal Forest (27; 55.10%), Savannah (09; 18.37%), Area of ecological tension (08; 16.33%), Vegetation refuge (05; 10.20%), Steppe (02; 4.08%) and Pioneer Formation (01; 2.04%) (Figure 4).

## Vulnerability status

Few species identified as endemic are included in official lists of threatened fauna (Figure 4C). At the international level, none of the species analyzed is listed by the IUCN. At the national level, nine species were listed (five of which are considered threatened): "Data Deficient" - *Acanthostichus flexuosus* MacKay, 1996 and *Leptanilloides atlanticus* Silva *et al*., 2013 [=*Leptanilloides atlantica*]; "Least Concern" - *Neoponera concava* (MacKay & MacKay, 2010) and *Neoponera latinoda* (MacKay & MacKay, 2010); "Vulnerable" - *Monomorium delabiei* Fernández, 2007; "Endangered" - *Poneracantha wilsoni* (Lattke *et al*., 2007) [=*Gnamptogenys wilsoni*] and *Rhopalothrix plaumanni* Brown & Kempf, 1960; "Critically Endangered" - *Fulakora cleae* (Lacau & Delabie, 2002); and "Critically Endangered/Possibly Extinct" - *Mycetagroicus urbanus* Brandão & Mayhé-Nunes, 2001 (ICMBIO, 2018a).

**Figure 3 -** Brazilian Atlantic Forest endemic ants and total of species in each genera with endemic species (The labels within the columns represent the absolute values of the publications. And the labels above the columns represent the total number of publications per subcategory).

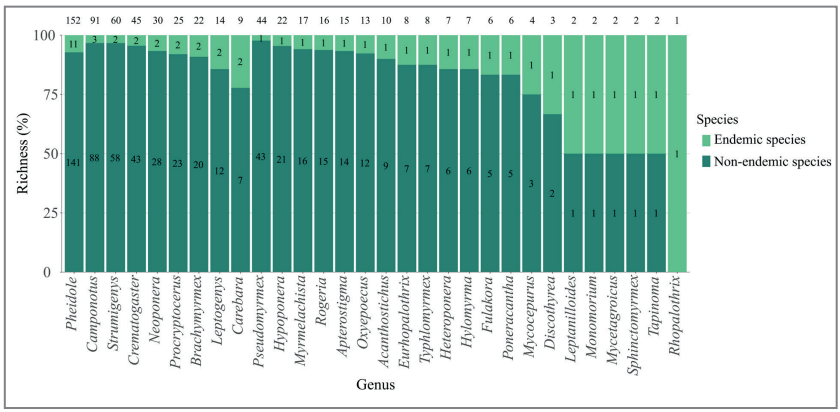
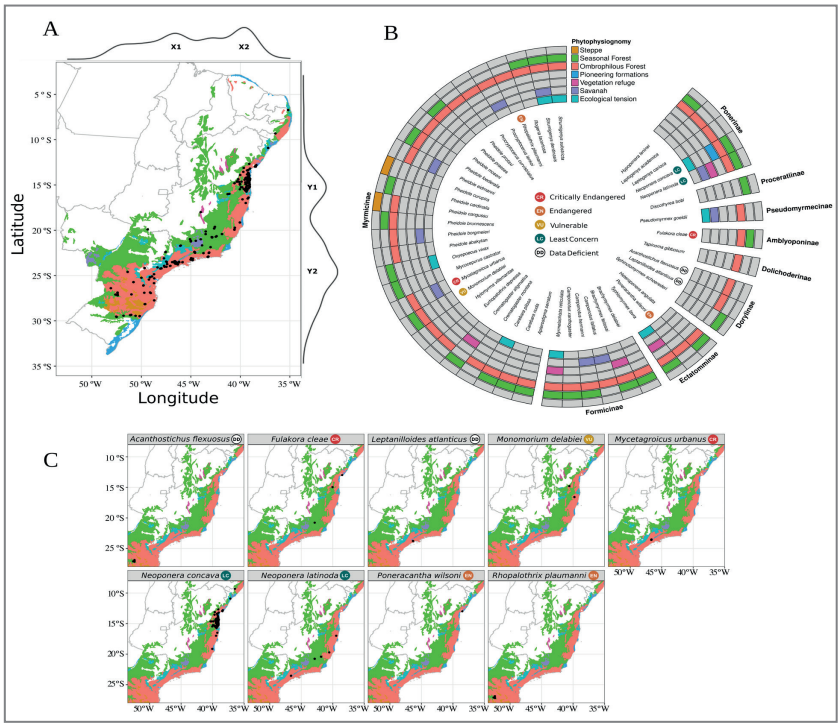



**Figure 4 -** Distribution of ant species endemic to the Brazilian Atlantic Forest, by phytophysiognomy. A: Occurrence distribution of endemic species in the Atlantic Forest and phytophysiognomies (marginal plot represents the density of occurrences along the latitudinal and longitudinal gradients). B: Presence of endemic species in each phytophysiognomy, with their respective IUCN threat of extinction level. C: Distribution of ant species with threat of extinction level.



## DISCUSSION

### Bibliographic review

The number of publications on ants in the Brazilian Atlantic Forest identified in this study is lower than that found by Silva *et al.* (2022), who reported 1,050 publications. This discrepancy arises from differences in methodology, including the scope of the study and the databases consulted. Schmidt *et al.* (2022) and Feitosa *et al.* (2022) emphasize that the Atlantic Forest accounts for a larger share of scientific publications compared to other Brazilian biomes. This trend is closely linked to the country's historical socioeconomic development (SCHMIDT *et al.*, 2022), as well as logistical advantages such as easier access and infrastructure in the Atlantic Forest region. As a result, the Atlantic Forest has become one of the most studied biomes in Brazil (DIVIESO *et al.*, 2020; FEITOSA *et al.*, 2022; SCHMIDT *et al.*, 2022).

The first publication found in our review is from 1918, by Hermann von Lüderwaldt, and concerns ant diversity. Specimens of the tribe Attini, collected by naturalists Hermann von Lüderwaldt and Hermann von Ihering at the beginning of the 20th century, are known to be the first ant records in the Atlantic Forest (FEITOSA *et al.*, 2021). Subsequently, we identified an increase in publications from the year 2000 onwards, likely due to the "The Research Program on Biodiversity Characterization, Conservation, Restoration and Sustainable Use" (Biota-FAPESP) (NOLL *et al.*, 2022). Launched in 1999, this is one of the main public research programs that aimed at documenting and investigating biodiversity in the state of São Paulo, encompassing various scientific fields (BIOTA-FAPESP, 2024). Numerous studies have been conducted, not only in São Paulo, since the creation of this program, generating knowledge about different taxa. Among insects, Hymenoptera is the order with the most publications, with 78 articles on Formicidae (NOLL *et al.*, 2022).

Furthermore, given Biota-FAPESP's objectives, the initiative may have also contributed to the increase in publications in the "Diversity" knowledge area. The Atlantic Forest is currently recognized as having high ant diversity, both taxonomically and functionally (SILVA and BRANDÃO, 2010, 2014; SILVA *et al.*, 2022). This knowledge includes contributions from projects funded by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the program, such as inventory of leaf litter ants throughout the Atlantic Forest published by Silva and Brandão (2014) which reported 530 species and 18,142 records (SILVA and BRANDÃO, 2014; SILVA *et al.*, 2022).

The distribution of publications is uneven across regions of the country, with the highest concentration in the Southeast, and across phytophysiognomies, especially Ombrophilous Forest). Ant record distribution in Brazil is recognized as heterogeneous (DIVIESO *et al.*, 2020), a pattern observed at large [e.g., biomes (DIVIESO *et al.*, 2020)] and small [e.g., state and municipality scales (SILVA *et al.*, 2023)]. This is related to the presence of research centers in these areas and/or proximity to large cities (DIVIESO *et al.*, 2020; SILVA *et al.*, 2023). Although the Central-West had the fewest of publications, this may reflect the scope of the present survey, especially considering that this region is predominantly covered by the Cerrado biome (56.07% of the territory) (Brazilian Institute of Geography and Statistics - IBGE, 2019), which is one of the most studied biomes in Brazil (DIVIESO *et al.*, 2020; SCHMIDT *et al.*, 2022). The present study focuses exclusively on the Brazilian Atlantic Forest, and the number of records found for this region may be lower compared to areas where the Atlantic Forest is predominant.

Research on the classification and standardization of Brazilian vegetation and standardizing its terminology dates to 1824 (IBGE, 2012b). This long history is reflected in the variety of sources used to classify terrain in the analyzed articles. In this regard, IBGE provides the "Technical Manual of Brazilian Vegetation" (2nd edition, 2012), which offers a comprehensive classification of Brazilian phytogeography, incorporating information from the first edition (1992) and the book "Classification of Brazilian Vegetation, Adapted to a Universal System", by Veloso *et al.* (1991), both published by IBGE (IBGE, 2012c). The study by Veloso *et al.* (1991) aimed to support the classification and standardization of Brazilian vegetation (VELOSO *et al.*, 1991), and was the most frequently cited reference in the analyzed publications.

Most of the collections described are based on soil sampling, which may be related to the use of the Winkler extractor. In the early 1990s, this collection technique revolutionized the study of ant diversity worldwide, as it allowed better sampling of ants associated with leaf litter and soil (BRANDÃO *et al.*, 2008; DELABIE *et al.*, 2015). However, the present survey demonstrated that the most widely used technique is manual collection. The predominance of this technique

in publications may be related to: (1) its ability to explore various microhabitats (e.g., bare soil, leaf litter, twigs, branches, and vegetation); (2) the use of simple materials (e.g., tweezers, alcohol, vials, and trays); and (3) the possibility of preparing complete inventories in a few days (BESTELMEYER *et al.*, 2000).

**Endemic species**

Considering the scarcity of information on endemic ants in the Brazilian Atlantic Forest (FEITOSA *et al.*, 2021), this study offers a significant contribution to knowledge on the subject. Forty-nine species with potential endemism in the biome were identified, some of which are also endemic to their specific phytophysiognomies. The proportion of endemic ants relative to the total number of species analyzed (4.59%) is lower than the proportion found in Brazil overall (486 species; 32%) (ANTWEB, 2025a) and lower than that of other taxa in the biome (21% birds, 24% reptiles, 28% mammals, and 70% amphibians) (FIGUEIREDO *et al.*, 2021). Taxa may present distinct patterns of endemism and richness (KERR, 1997), although the Atlantic Forest is a diversity hotspot (MITTERMEIER *et al.*, 2004). Taylor-Smith *et al.* (2020) observed that the level of regional endemism of invertebrates in New Zealand was related to geographic connectivity, that is, the capacity to retain species and environmental variables. In this sense, the richness and distribution of ants are known to be influenced by environmental variables (QUEIROZ *et al.*, 2013; SILVA and BRANDÃO, 2014). In addition, many ants in the Brazilian Atlantic Forest are determined into morphospecies, making comparisons difficult due to varying standards among laboratories and researchers (SILVA *et al.*, 2024). Moreover, some phytophysiognomies and strata are also undersampled (FEITOSA *et al.*, 2021). Consequently, the lack of this information compromises assessments of species endemism (FEITOSA *et al.*, 2021; COWIE *et al.*, 2022).

Endemic species belonging to genera considered generalists and with a wide geographic distribution, for instance, *Pheidole* (BACCARO *et al.*, 2015), were found. This hyperdiverse genus (BACCARO *et al.*, 2015) has 11 species endemic to the Brazilian Atlantic Forest, such as *Pheidole moseni* Wheeler, 1925, and *Pheidole protaxi* Oliveira & Lacau, 2015, collected only in Espírito Santo and Bahia, respectively (KASS *et al.*, 2022b; SILVA *et al.*, 2022), both in Ombrophilous


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Forest. We also found endemic ants from genera with more specific and geographically restricted habits, such as *Leptanilloides* (WONG and GUÉNARD, 2017; ANTWEB, 2025b). This taxon is composed of 19 species, collected in the Americas, and is rarely encountered (BOROWIEC and LONGINO, 2011; WONG and GUÉNARD, 2017; ANTWEB, 2025b). Only *Leptanilloides atlanticus* Silva *et al.*, 2013 was considered endemic in our analysis. The species was originally collected in a Biological Reserve in the state of São Paulo (SILVA *et al.*, 2013), which remains the only known location for its occurrence (DELSINNE *et al.*, 2015; KASS *et al.*, 2022b; SILVA *et al.*, 2022).

At the species level, we found species recognized as endemic to the biome: *Fulakora cleae* and *Monomorium delabiei*. Although both are endemic to the Seasonal Forest (ICMBIO, 2018b), they were also present in the Ombrophilous Forest. Other species considered endemic to the Atlantic Forest, such as *Dinoponera lucida* and *Mycetophylax simplex*, occur outside the forest. This difference may be due to the use of different geographic limits for the Atlantic Forest, which considers different characteristics for its delimitation (e.g., climate, vegetation, and relief) (MUYLAERT *et al.*, 2018; MARQUES *et al.*, 2021). Although there may be overlapping areas ("Consensual limit") between these definitions limits, there are also divergent areas ("Integrative limit") (MUYLAERT *et al.*, 2018).

Furthermore, we highlight the possibility that some species considered endemic are incorrectly classified as such. This phenomenon is also observed in rare species (SILVA *et al.*, 2024) and may be due to: (*i*) lack of biological knowledge about the species [e.g., population fluctuation and foraging habits (ALFIMOV *et al.*, 2011; DONOSO, 2012)]; (*ii*) inadequate sampling techniques [e.g., inappropriate application of collection techniques (GASTON, 1994; BRANDÃO *et al.*, 2008)]; (*iii*) taxonomic complications [e.g., identification errors (GASTON, 1994; FEITOSA *et al.*, 2023); and (*iv*) inaccurate information [e.g., underestimated data (GASTON, 1994; LONGINO *et al.*, 2002; KASS *et al.*, 2022a)]. The lack of knowledge about the real distribution of these species compromises the assessment of endemism (DELABIE *et al.*, 2006). For instance, Teixeira *et al.* (2004) reported the occurrence of *Atta robusta* in Espírito Santo, although the species had previously been considered endemic only to Rio de Janeiro. The species is currently recognized as endemic to restingas (ICMBIO, 2018b).

Occurrence peaks in the distribution of endemic species may be due related: (*i*) sampling in areas close to research centers and/or cities (DIVIESO *et al.*, 2020); (*ii*) known variation in the richness of Atlantic Forest ants along the latitudinal gradient, with an increase in the number of species at higher latitudes (SILVA and BRANDÃO, 2014); and (*iii*) overlap with areas of endemism in the states of Bahia (Figure 4A - Y1 and X2) and São Paulo (Figure 4A - X1 and Y2) ["Central Atlantic Forest Corridor" and "South Atlantic Forest Corridor" (AYRES *et al.*, 2005); "Coastal Bahia" and "Southern Atlantic Forest" (SIGRIST and CARVALHO, 2008); ["Coastal Bahia" and "Serra do Mar" (PERES *et al.*, 2020)].

Ombrophilous Forest and Seasonal Forest were the phytophysiognomies with the highest concentration of endemic species, both in general and exclusive species (Figure 4). This richness may be related to: (*i*) both being the phytophysiognomies with the largest area within the Atlantic Forest, representing 16.94% and 37.68%, respectively (IBGE, 2022); and (*ii*) as previously observed in the bibliographic survey (see Section "4.1 Bibliographic review"), these are the most studied phytophysiognomies of the Atlantic Forest. It can be explained by the presence of research centers and/or proximity to large cities (DIVIESO *et al.*, 2020; SILVA *et al.*, 2023). These same factors are also observed in phytophysiognomies with lower richness, such as Pioneer Formation, which cover a smaller area [1.59% (IBGE, 2022)] and are among the least studied, with about half as many of publications as the Ombrophilous Forest and Seasonal Forest (see Section "4.1 Bibliographic review"). These data demonstrate that although the Atlantic Forest is one of the most studied and sampled Brazilian forests (DIVIESO *et al.*, 2020; SCHMIDT *et al.*, 2022), some phytophysiognomies may still be undersampled (e.g., Pioneer Formation) (Figures 2 and 3), which impacts species discovery. Further studies will aid in detecting of new species, including endemic ones (SILVA *et al.*, 2023).

**Vulnerability status**

The lack of information compromises the assessment of species' vulnerability and, consequently, the conceptualization of conservation plans (BRITO, 2008). This gap becomes even more concerning given that the Atlantic Forest is a threatened forest due to massive habitat loss and fragmentation (RIBEIRO


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*et al.*, 2009; SOLÓRZANO *et al.*, 2021). In addition, endemic species are particularly susceptible to local extinction in response to environmental degradation (ALONSO, 2010), which is among the main causes predicted for future extinctions of Hymenoptera (SÁNCHEZ-BAYO and WYCKHUYS, 2019). Alarmingly, however, few species appear on official lists of threatened fauna, a pattern also observed for rare ants in the Brazilian Atlantic Forest (SILVA *et al.*, 2024). Compared with other taxa, invertebrates tend to have far fewer species evaluated, and a large proportion of described species still lack vulnerability assessments (CAZALIS *et al.*, 2022; COWIE *et al.*, 2022). This is largely due to taxonomic impediments, such as a shortage of experts and/or insufficient available information about the species (DINIZ-FILHO *et al.*, 2010; COWIE *et al.*, 2022), as well as the excessive number of morphospecies (e.g., SILVA *et al.*, 2022), awaiting standardization and/or formal description. Recent initiatives to make comprehensive databases available (e.g., SILVA *et al.*, 2022) and to apply tools for assessing species rarity (Silva *et al.*, 2024) are improving methods for evaluating conservation status. These advances are expected to have a significant impact shortly and contribute to the development of conservation-related public policies.

## CONCLUSION

Significant knowledge gaps remain for most phytophysiognomies, although the Brazilian Atlantic Forest's ant community has been widely studied (DIVIESO *et al.*, 2020; FEITOSA *et al.*, 2021). Furthermore, many previously published studies lack important methodological details, such as the type of collection method used or the strata sampled. These shortcomings hinder the understanding of species diversity and biology, including that of endemic species, thereby compromising vulnerability assessments and, consequently, conservation planning.

We recognize that our classification approach may not completely unveil all the intricate factors that influence decisions on whether species should be affirmatively considered endemic. Nonetheless, we hope that the data consolidated herein will help guide future research toward new perspectives, particularly in this era of rapidly expanding biological databases and groundbreaking data science supported by unprecedented technologies such as machine learning.

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# 17

# GLOBAL CHANGES AND THE FUTURE OF THE CAATINGA DRY FOREST: LESSONS FROM ANTS

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# ABSTRACT

Despite the remarkable diversity and ecological importance of ants in most terrestrial ecosystems, our understanding of ant communities in the Caatinga dry forest remains limited. This chapter provides a comprehensive synthesis of Caatinga ant communities, emphasizing their biogeographic connections to the Cerrado and their relatively low diversity. It also examines how anthropogenic disturbances—including chronic pressures (e.g., extensive grazing and resource extraction) and acute events (e.g., slash-and-burn agriculture)—as well as climate change, particularly increasing aridity, reshape ant communities and affect ecosystem functions mediated by ants. These disturbances drive changes in ant morphology and behavior, reduce functional and phylogenetic diversity, and often favor generalist and disturbance-adapted species, leading to biotic homogenization. This, in turn, disrupts critical functions such as seed dispersal (mediated by key species like *Dinoponera quadriceps*) and plant protection against herbivores. Furthermore, aridity can amplify the negative effects of anthropogenic disturbances. However, ground-foraging ant communities exhibit relatively rapid regeneration, driven by increases in plant biomass, and the ecosystem functions they support also recovering quickly. However, the proliferation of leaf-cutting ants (*Atta* and *Acromyrmex* spp.) in disturbed areas presents a significant challenge to vegetation regeneration by depleting seed banks, reducing seedling survival, and altering nutrient dynamics. As human activities and climate change continue to intensify, the future of the Caatinga remains uncertain. However, as key ecological players, ants offer important insights into these changes, highlighting both the vulnerabilities and resilience of this dry forest. Their responses to ongoing disturbances provide valuable lessons for biodiversity conservation and ecosystem restoration.

**Keywords:** Ant-plant interactions; anthropogenic disturbance; climate change; ecosystem functions; regeneration.

## INTRODUCTION

Due to their ubiquity, high biomass (SCHULTHEISS *et al.*, 2022), and ecological importance (DEL TORO *et al.*, 2012), ants are widely used to study the effects of human disturbances (ANDERSEN, 2019). Research demonstrates that disturbances such as agriculture (PACHECO *et al.*, 2013), agroforestry (PHILPOTT *et al.*, 2008), logging (VASCONCELOS; VILHENA; CALIRI, 2000), pastoralism (ARCOVERDE *et al.*, 2018), mining (MAJER *et al.*, 1984), fire (ANDERSEN *et al.*, 2006; ANDERSEN, 2019), and habitat loss and fragmentation typically shift ant communities from disturbance-sensitive to disturbance-adapted species, favoring open-habitat specialists over forest-dependent ones (LEAL *et al.*, 2012) — but see Neves *et al.* (2023) for potential different responses of Cerrado ant communities. These shifts are often driven by increased habitat openness, which alters microclimates, resource availability, and competition dynamics (ANDERSEN, 2019). Given that ant responses to disturbance are broadly applicable to other taxa (ANDERSEN, 2019), they serve as valuable bioindicators for ecological change. This makes them promising tools for monitoring and guiding sustainable ecosystem restoration. Understanding these responses is therefore essential, as ants also play a central role as modulators of biodiversity (PARKER; KRONAUER, 2021).

As climate change intensifies, its impacts on ants and their ecological roles have been widely studied (PARR; BISHOP, 2022). For instance, ant species are shifting their ranges, with lowland tropical and high-elevation species being particularly vulnerable due to their proximity to thermal limits and limited migration options, respectively (BISHOP *et al.*, 2019; NASCIMENTO *et al.*, 2022). Regions with high species turnover, especially along rainfall gradients, are also expected to be highly sensitive (ANDERSEN *et al.*, 2015). Additionally, invasive ant species may expand their ranges, posing threats to native biodiversity (BERTELSMEIER *et al.*, 2015). At the community level, studies reveal contrasting responses: tropical ants are generally negatively affected, while temperate communities may experience neutral or even positive impacts (DIAMOND *et al.*, 2012). Furthermore, climate change can exacerbate the effects of human disturbance, particularly in hot, arid regions like the Brazilian Caatinga dry forest (ARNAN *et al.*, 2018a).

The Caatinga is the largest continuous block of Seasonally Dry Tropical Forest (hereafter dry forest) on Earth, covering approximately one million km² of northeastern Brazil (SILVA; LEAL; TABARELLI, 2017a). Its most defining feature is an extended dry season with scarce rainfall, high interannual variability, and droughts that can persist for years (SILVA; LEAL; TABARELLI, 2017a). These harsh conditions have driven unique adaptations in the biota of the region, which is the most diverse among dry forests globally (SILVA; LEAL; TABARELLI, 2017a). Home to 28 million people who rely heavily on natural resources, the Caatinga faces significant threats from slash-and-burn agriculture, extensive livestock grazing, firewood collection, timber and non-timber production exploitation, and hunting (SILVA; LEAL; TABARELLI, 2017a; ARNAN *et al.*, 2018b). These activities negatively impact the Caatinga biota at multiple levels: (1) reducing disturbance-sensitive species while favoring disturbance-adapted ones (OLIVEIRA *et al.*, 2017; RITO *et al.*, 2017); (2) causing losses in taxonomic, phylogenetic, and functional diversity, leading to biotic homogenization (RIBEIRO *et al.*, 2015, 2016, 2019; RIBEIRO-NETO *et al.*, 2016, 2023; RITO *et al.*, 2017; ARNAN *et al.*, 2018a; (3) disrupting plant-animal interactions and associated ecosystem functions, such as pollination, seed dispersal, and pest control (LEAL; ANDERSEN; LEAL, 2014, LEAL; WIRTH; TABARELLI, 2014; LEAL; ANDERSEN; LEAL, 2015); and (4) depleting biomass and nutrients across all forest compartments, including soil, aboveground and belowground biomass, and coarse woody debris (KULKA *et al.*, 2024; SANTOS *et al.*, 2024). Furthermore, climate change poses additional threats to the Caatinga, with predictions of higher temperatures, reduced rainfall, increased aridity, and more frequent extreme weather events (SILVA; LEAL; TABARELLI, 2017a). Consequently, climate change is likely to exacerbate the ecological disruptions caused by human disturbances (ARNAN *et al.*, 2018a; RIBEIRO-NETO *et al.*, 2023).


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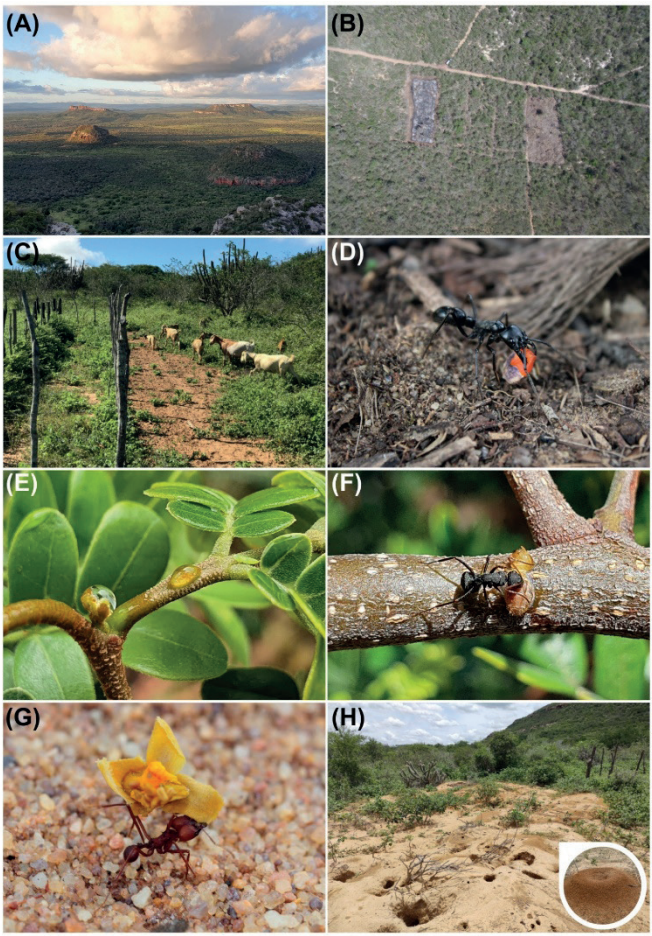
**Figure 1 -** Overview of the research on the ant fauna and ecological interactions in the Caatinga dry forest of Catimbau National Park (8°30′S; 37°20′W), Pernambuco, northeastern Brazil: (A) aerial view of the park; (B) aerial comparison of control and slash-and-burn agriculture experimental plots; (C) experimental setup comparing goat exclosure and free-access paired plots; (D) *Dinoponera quadriceps* (Ponerinae) dispersing a *Commiphora leptophloeos* (Burseraceae) seed; (E) extrafloral nectar secretion on *Pityrocarpa moniliformis* (Fabaceae); (F) *Camponotus crassus* (Formicinae) preying on a termite; (G) *Cenostigma pyramidale* flower being carried by *Atta sexdens* (Myrmicinae); (H) nest of *Atta opaciceps* (Myrmicinae), with the circle indicating the external refuse dump.

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This chapter provides an overview of our research on the ant fauna of the Caatinga dry forest (Fig. 1) encompassing: (1) the biogeography, diversity, and functional composition of the Caatinga ant fauna; (2) a synthesis of ant responses and associated ecosystem functions in relation to human disturbance,

including free-ranging goats and slash-and-burn agriculture and climate change; (3) ant community and ecosystem functioning recovery across a secondary successional gradient; and (4) the proliferation of leaf-cutting ants and their impacts on regeneration, particularly in disturbed areas. This chapter presents insights primarily from long-term ecological research in Catimbau National Park (2012–2025), as well as from other private areas in the Caatinga region where previous studies were conducted, such as Parnamirim municipality in Pernambuco (2008–2012) and the Xingó region, which spans municipalities in Alagoas, Bahia, Pernambuco, and Sergipe (1999–2002). Particularly, Catimbau National Park is a protected area established in 2002 that remains inhabited by rural populations relying on resource-dependent livelihoods, including free-ranging livestock and slash-and-burn agriculture. Despite its protected status, the landscapes of Catimbau are a dynamic mosaic of old-growth and regenerating secondary forests shaped by human activity.

## BIOGEOGRAPHY, DIVERSITY, AND FUNCTIONAL COMPOSITION OF ANTS IN THE CAATINGA

The ant fauna of the Caatinga is characterized by a relatively impoverished community compared to other Brazilian biomes, such as the Cerrado and the Atlantic Forest (LEAL *et al.*, 2017). Most ant species found in the Caatinga are also present in other biomes, particularly the Cerrado, suggesting that the Caatinga ant fauna represents a depauperate subset of the Cerrado fauna, with a low level of endemism (LEAL *et al.*, 2017). Among the few endemic species in the Caatinga, *Dinoponera quadriceps* stands out as one of the largest ants in the world and an important seed disperser in the region, highlighting its significant role in maintaining local biodiversity (LEAL; ANDERSEN; LEAL, 2014; LEAL *et al.*, 2014). Another notable species is the leaf-cutter *Atta opaciceps*, which is the most abundant in the Caatinga and has a substantial impact on local leaf biomass and regenerating individuals due to its foraging behavior and nest-building activities (SIQUEIRA *et al.*, 2017, 2018), thereby negatively affecting Caatinga regeneration (KNOECHELMANN *et al.*, 2020; OLIVEIRA *et al.*, 2022). This impoverished fauna contrasts with the diversity of other taxonomic groups, such as the Caatinga


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flora and other faunal groups (e.g., bees, mammals, and herpetofauna), which exhibit higher levels of endemism (SILVA; LEAL; TABARELLI, 2017a).

The Caatinga has historically been understudied in terms of ant diversity, with the first systematic efforts to catalog its fauna occurring only in the 1990s (ULYSSÉA; BRANDÃO, 2013). Since then, additional efforts, such as those by Ulysséa and Brandão (2013) and Leal *et al.* (2018), have significantly increased the number of known species to 276 species/morphospecies, belonging to 62 genera and ten subfamilies, sampled from 37 localities across the Caatinga region (see Table 3.1 of LEAL *et al.*, (2017) for a complete list of ants from the Caatinga). However, the region remains insufficiently sampled. Studies reveal high species turnover among localities, indicating a heterogeneous fauna despite the apparent environmental homogeneity of the Caatinga (LEAL *et al.*, 2017). The total ant fauna of the Caatinga is estimated to reach or even exceed 400 species (LEAL *et al.*, 2017).

The ants of the Caatinga play diverse ecological roles and can be classified into different functional groups based on their responses to environmental conditions and levels of disturbance (ANDERSEN, 1995; LEAL *et al.*, 2017; OLIVEIRA *et al.*, 2017). The main functional groups include Generalized Myrmicinae, Opportunists, Dominant Dolichoderinae, Subordinate Camponotini, and Specialized Predators. Generalized Myrmicinae is the most common and species-rich group in the Caatinga, predominating in warm environments where Dominant Dolichoderinae are absent (LEAL *et al.*, 2017; OLIVEIRA *et al.*, 2017). This group includes genera such as *Pheidole* and *Crematogaster*, known for their adaptability to a wide range of environments and their abundance in high-temperature sites. Opportunists, which include species from the genera *Ectatomma* and *Dinoponera*, are prevalent in areas with high environmental stress or disturbance, where ant productivity and diversity are limited (LEAL *et al.*, 2017; OLIVEIRA *et al.*, 2017). In contrast, Dominant Dolichoderinae species, such as *Dorymyrmex* and *Forelius*, tend to dominate in open and productive habitats but are rare in the Caatinga due to the low availability of liquid carbohydrates, such as honeydew, which are essential for sustaining their dominance (LEAL *et al.*, 2017). Subordinate Camponotini are represented primarily by the genus *Camponotus*, which has a broad distribution and is competitively subordinate in the presence of Dominant Dolichoderinae but can dominate in their absence.

Specialized Predators, such as *Leptogenys* and *Thaumatomyrmex*, are rare in the Caatinga and tend to decline in disturbed areas due to their specialized diet and typically low population densities (LEAL *et al.*, 2017; OLIVEIRA *et al.*, 2017).

## ANT RESPONSES TO HUMAN DISTURBANCE AND CLIMATE CHANGE IN THE CAATINGA

The Caatinga has been profoundly altered by human activities since the onset of European colonization (SILVA; LEAL; TABARELLI, 2017a). The main sources of disturbance in the region include: (1) firewood extraction for domestic and commercial purposes; (2) timber extraction, primarily for use in rural properties; (3) exploitation of forest products such as plant harvesting for food, medicinal purposes, and raw materials; (4) extensive grazing by domestic animals, especially goats; and (5) shifting agriculture through slash-and-burn cycles (ARNAN *et al.*, 2018b). While slash-and-burn agriculture is often associated with intense and localized events (i.e., acute disturbances), the other four activities are considered chronic disturbances (SINGH, 1998). These pressures are widespread in the dry forests, where local human communities depend heavily on natural resources for subsistence (RITO *et al.*, 2017; TABARELLI *et al.*, 2024). Beyond direct anthropogenic pressures, increasing aridity is one of the major predictions of climate change for the Caatinga region, adding another layer of environmental stress and potentially exacerbating the effects of human disturbances (RITO *et al.*, 2017). Understanding these interactions is crucial for predicting biodiversity responses and informing conservation strategies in the increasingly human-modified landscapes of the Caatinga.

Here, we evaluated the effects of anthropogenic disturbances and their interaction with increasing aridity on ant populations, communities, ant-plant interactions, and associated ecosystem functions (Fig. 2). First, we explored the effects of independent gradients of chronic disturbances (i.e., the combined effects of prolonged livestock grazing, firewood extraction, and miscellaneous resource use) and increasing aridity. We quantified these disturbance effects in 20 0.1-ha plots by identifying primary sources of chronic disturbance, classifying them into broad categories, and developing individual and multi-metric indices to assess overall disturbance intensity (ARNAN *et al.*, 2018b). Aridity was


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measured in these same plots from the updated *WorldClim* global climate data repository, with a resolution of 30 seconds of arc (approximately 1 km spatial resolution at the equator; www.worldclim.org), processed using the *maptools* package for R (RITO *et al.*, 2017; CÂMARA *et al.*, 2018). We also experimentally evaluated the impact of free-ranging goats using exclosure experiments, comparing 22 paired 0.4-ha plots with and without goats (LINS *et al.*, 2022). Finally, we assessed the immediate and short-term effects of slash-and-burn agriculture experimentally, using 18 paired 0.1-ha plots, one where vegetation was cut and burned and another maintained intact as a control (BEZERRA *et al.*, 2022).

**Chronic anthropogenic disturbances and increasing aridity**

Chronic anthropogenic disturbances negatively affected ant species populations and functional groups with specialized feeding and nesting habits (i.e., disturbance-sensitive), while benefiting generalist (i.e., disturbance-adapted) species and functional groups (OLIVEIRA *et al.*, 2017) (Fig.2). Leaf-cutting ants from both *Atta* (SIQUEIRA *et al.*, 2017) and *Acromyrmex* (SANTOS-NETO *et al.*, 2025) genera were prime examples of species that benefited from human disturbance (see section 5 for more detail) (Fig. 2).

Overall, we found that species with distinct morphological and behavioral traits replace each other along the disturbance gradient, while more plastic species persist throughout by adjusting their traits or microhabitat use (SILVA *et al.*, 2019; OLIVEIRA *et al.*, 2022) (Fig. 2). Particularly, colonies of *Ectatomma muticum* and *Dorymyrmex goeldii* transitioned from foraging in open habitats in undisturbed areas to shaded spots as disturbance increased, while colonies of *Tapinoma* sp. A showed the opposite pattern, with its use of shaded microhabitats declining as disturbance intensity increased (SILVA *et al.*, 2019). Four widely distributed and phylogenetically distant ant species presented very high plasticity for several morphological traits (OLIVEIRA *et al.*, 2022). *Pheidole radoskowskii* was the species with the highest morphological variability between plots in response to the environmental gradients, followed by *Dinoponera quadriceps*, *Dorymyrmex goeldii*, and *Ectatomma muticum* (OLIVEIRA *et al.*, 2022). These behavioral and morphological variations are likely to represent key assets,

enabling individuals and populations to inhabit the variety of habitats provided by the Caatinga and to cope with upcoming changes in land use and climate.

At the community level, ant species richness consistently declined in response to most anthropogenic pressures, with human population size emerging as a key driver (OLIVEIRA *et al.*, 2017). These disturbances also reshaped taxonomic and functional composition, leading to a predictable replacement of disturbance-sensitive species with disturbance-adapted ones (OLIVEIRA *et al.*, 2017) (Fig. 2). However, the strength of these effects varied depending on soil type, with clay soils experiencing more pronounced impacts due to higher land use intensity (OLIVEIRA *et al.*, 2017). This underscores the importance of considering environmental context, particularly soil characteristics, when assessing biodiversity responses to disturbance. Furthermore, the multi-metric chronic disturbance index has revealed broader negative consequences, as chronic disturbances alter ant community structure by modifying species abundance and distribution, ultimately driving biotic homogenization in heavily impacted areas (RIBEIRO-NETO *et al.*, 2016). While taxonomic diversity remained relatively stable, functional diversity—and to a lesser extent, phylogenetic diversity—declined with increasing chronic disturbances (ARNAN *et al.*, 2018a), particularly those linked to livestock grazing and resource extraction (RIBEIRO-NETO *et al.*, 2023) (Fig. 2).

Climate change adds another layer of complexity to these chronic disturbance effects (ARNAN *et al.*, 2018a; RIBEIRO-NETO *et al.*, 2023). Increasing aridity led to a decline in species and functional groups with more specialized traits while promoting the proliferation of generalists, similar to what had been observed for chronic disturbance (LEAL *et al.*, 2017) (Fig. 2). Similarly, ant morphology was strongly affected by increasing aridity (OLIVEIRA *et al.*, 2022) (Fig. 2). At the community level, increasing aridity drove not only the loss of functional and phylogenetic diversity (ARNAN *et al.*, 2018a), but also taxonomic, functional, and phylogenetic homogenization of ant communities, with aridity-induced reductions in beta diversity (73%) outweighing those caused by chronic disturbances (27%) (RIBEIRO-NETO *et al.*, 2023) (Fig. 2). Interestingly, in drier areas, chronic disturbances slightly increased beta diversity, likely due to greater spatial heterogeneity in disturbance sources (RIBEIRO-NETO *et al.*, 2023). These findings highlight the intricate and complex ways in which


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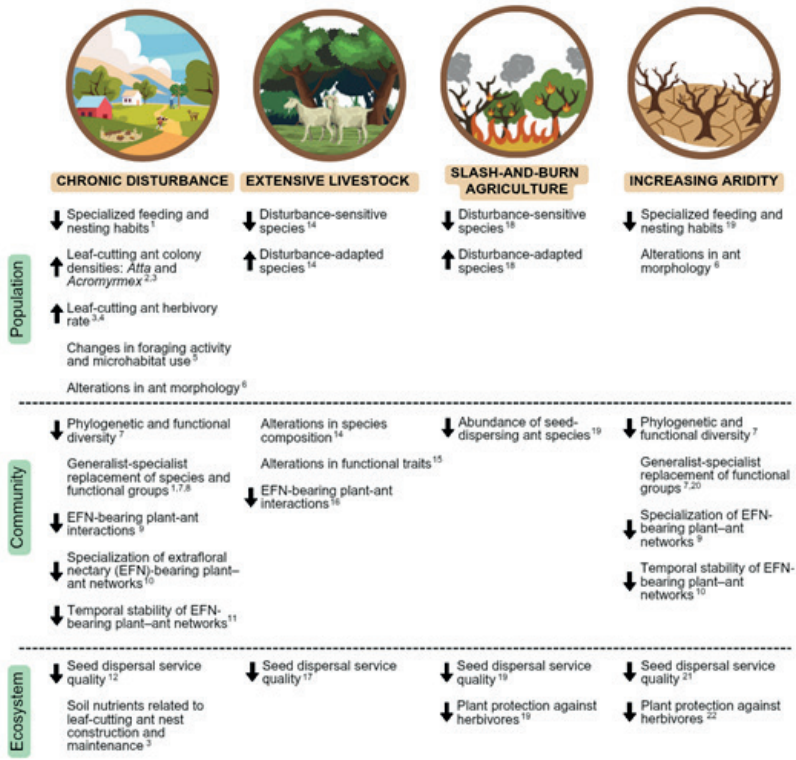
anthropogenic disturbances and aridity interact to threaten ant biodiversity in dry forests (ARNAN *et al.*, 2018a; RIBEIRO-NETO *et al.*, 2023).

**Figure 2 -** Synthesis of ant responses at different levels of ecological organization (population, community, and ecosystem levels) to human disturbances (general chronic disturbance, as free-ranging goats, and acute disturbance, as slash-and-burn agriculture) and climate change. Trends are indicated by arrows, where an upward arrow denotes an increase, and a downward arrow signifies a decrease in the respective variables.




**Sources:** (1) Oliveira et al. (2017); (2) Siqueira et al. (2017); (3) Santos-Neto et al. (2025); (4) Siqueira et al. (2018); (5) Silva et al. (2019); (6) Oliveira et al. (2022); (7) Arnan et al. (2018a); (8) Ribeiro-Neto et al. (2016); (9) Câmara et al. (2018); (10) Câmara et al. (2018); (11) Leal, Andersen and Leal, (2015) ; (12) Leal, Andersen and Leal (2014); (13) Vasconcelos (2018); (14) Neves el al. (2023); (15) Pacheco (2024); (16) Castro-Alves (2024); (17) Costa (2022); (18) Leal (2023); (19) Leal et al. (2018); (20) Oliveira et al. (2019); (21) Oliveira et al. (2021a).

Ants in the Caatinga interact with a wide variety of diaspores, including both myrmecochores and non-myrmecochores seeds (LEAL *et al.*, 2007; OLIVEIRA *et al.*, 2019). Importantly, the Caatinga biome is recognized as a global hotspot for myrmecochory, attributable to the high diversity of plant taxa—particularly within the Euphorbiaceae—that exhibit obligate or facultative ant-mediated

seed dispersal (LEAL *et al.*, 2007). *Dinoponera quadriceps* is a key disperser, but its effectiveness declined under chronic anthropogenic disturbance (LEAL; ANDERSEN; LEAL, 2014) (Fig. 2). Despite the dominance of opportunistic ants such as *D. quadriceps* and *Ectatomma muticum*, the ecosystem function they provide—seed dispersal—is often negatively affected by disturbance resulting in reduced seed removal rates and shorter dispersal distances, particularly for large-seeded species like as *Jatropha mollissima* (LEAL; ANDERSEN; LEAL, 2014). Post-dispersal functions of *D. quadriceps*, including seed protection and seedling establishment, were also evaluated by comparing ant nest refuse piles with control areas along a disturbance gradient (LEAL *et al.*, 2017). While ant nests exhibited lower seed predation and higher seedling recruitment, these benefits were not significantly related to disturbance intensity, indicating that this function was maintained even in more disturbed sites (ARCOVERDE, 2012; LEAL *et al.*, 2017).

Increasing aridity also negatively affects ant-mediated ecosystem functions, including seed dispersal and ant protection against herbivory. Six plant species—three myrmecochores (*Croton nepetaefolius*, *Jatropha mutabilis*, and *Jatropha ribifolia*) and three fleshy-fruited species (*Melocactus bahiensis*, *Sideroxylon obtusifolium*, and *Simaba ferruginea*)—interacted with 33 ant species, with approximately 65% of interactions involving myrmecochorous seeds (OLIVEIRA *et al.*, 2019). Seed interactions, removal rate, and dispersal distance declined with increasing aridity (Fig. 2). Notably, the high-quality disperser, *D. quadriceps*, played a dominant role in this pattern, with its dispersal functions decreasing markedly in dryer areas. This species particularly favored large-seeded plants, as demonstrated by *J. mutabilis* and *S. obtusifolium*, which exhibited enhanced dispersal in more humid environments (OLIVEIRA *et al.*, 2019) (Fig. 2). Regarding plant protection against herbivory, key ant species such as *Camponotus crassus and Cephalotes pusillus* exhibited reduced extrafloral nectary (EFN) visitation in drier areas, while others, like *Crematogaster crinosa* and *Camponotus cingulatus*, provided critical anti-herbivore protection, particularly in wetter conditions (OLIVEIRA *et al.*, 2021a) (Fig. 2). These findings highlight the sensitivity of plant-ant interactions to environmental stressors, emphasizing the need to conserve key species and interactions to maintain ecosystem function under changing conditions in the Caatinga.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In addition to the individual effects of disturbance and aridity, there is evidence of interactive effects threatening mutualistic interactions between EFN-bearing plants and ants, as observed through complex network metrics (CÂMARA *et al.*, 2018, 2019) (Fig. 2). On the one hand, the specialization of EFN--bearing plant-ant interactions decreased with increasing forest resource use (CÂMARA *et al.*, 2018) (Fig. 2). On the other hand, livestock grazing increased interaction specialization, suggesting that extrafloral nectar production may have been induced in response to goat herbivory (CÂMARA *et al.*, 2018) (Fig. 2). Although EFN-bearing plant-ant communities exhibited structural resilience along environmental gradients, the temporal stability of their interactions declined with increasing chronic disturbance, with a more pronounced effect in more disturbed and wetter areas (CÂMARA *et al.*, 2018) (Fig. 2). Together, these results indicate that Caatinga dry forests experience highly heterogeneous anthropogenic disturbances and rainfall patterns, creating a geographic mosaic of selective forces that may shape the co-evolution of interactions between ants and EFN-bearing plants (CÂMARA *et al.*, 2018, 2019).

**Extensive goat livestock**

Goat grazing and trampling did not affect ant species richness or abundance but altered species composition, with distinct species present in exclosure and free-access plots (VASCONCELOS, 2018) (Fig. 2). In general, the same pattern was observed for all chronic disturbances, with disturbance-sensitive species predominating in exclosure plots and disturbance-adapted species occurring more frequently in free-access plots (VASCONCELOS, 2018) (Fig. 2). Changes in functional attributes were also reported, as *Dorymyrmex thoracicus* exhibited larger clypeus and eyes in goat-exclosure plots, indicating trait plasticity (THIERRY, 2024) (Fig. 2). Interestingly, goat presence reduced seed dispersal for non-myrmecochorous *Commiphora leptophloeos* (Burseraceae), with seeds being deposited in *D. quadriceps* nests in exclusion plots, enhancing germination (CASTRO-ALVES, 2024). Ant-mediated herbivore protection remained effective despite fewer interactions in free-access plots (PACHECO, 2024).

**Slash-and-burn agriculture**

Overall, immediate effects of slash-and-burn agriculture (i.e., one month after burning) on ant populations and communities were minimal, indicating a high resilience of Caatinga ant fauna to this practice (COSTA, 2022). However, six months after burning, during the regeneration process, the proportion of generalist species progressively decreased (COSTA, 2022). Ant communities also exhibited low sensitivity to slash-and-burn agriculture, showing similar richness, relative abundance, and species composition when comparing plots subjected to this practice with undisturbed control plots (COSTA, 2022) (Fig. 2). In the Cerrado, which shares several compositional features with the Caatinga in terms of its ant fauna (LEAL *et al.*, 2017), fire effects on ground-nesting species also tend to be minimal or short-lived (OLIVEIRA *et al.*, 2021b). However, fire has a markedly different impact on arboreal ants, with sharp declines in species richness and major shifts in composition following high-severity fires (ROSA *et al.*, 2021). Whether similar patterns occur in the Caatinga remains unknown, but lower fuel availability may result in less intense fires and distinct ecological responses. Regarding ant-mediated ecosystem functions, seed removal rates and the abundance of both low- and high-quality dispersers declined immediately after burning (LEAL, 2023) (Fig. 2). High-quality dispersers, which transport seeds over longer distances, recovered rapidly, whereas low-quality dispersers remained suppressed even a year post-burn (LEAL, 2023). This differential recovery explained the observed pattern of reduced seed removal rates without changes in dispersal distances: fewer ant-seed interactions led to fewer seeds being removed, but the persistence of high-quality dispersers maintained the average dispersal distance (LEAL, 2023). In terms of plant protection functions, on the one hand, slash-and-burn agriculture enhanced ant visitation to extrafloral nectaries (EFNs) and increased nectar volume secretion but did not affect nectar sugar concentration or termite attack rates (LEAL, 2023). On the other hand, despite increased ant activity, ants spent more time attacking simulated herbivores, and plants experienced greater leaf damage in burned areas (LEAL, 2023). These findings indicate that although slash-and-burn poses both negative and positive effects on the ant-mediated plant protection functions, the net output appears to be negative for plants.


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## REGENERATION RECOVERY AFTER SLASH-AND-BURN AGRICULTURE

Forest regeneration following slash-and-burn agriculture has complex effects on ant communities, with potential differences between terrestrial and arboreal strata. Research indicated that species composition, whether in the soil or vegetation, did not differ significantly between regenerating and mature forests (BOMBI-HAEDO *et al.*, 2025). However, plant biomass played a central role in structuring terrestrial ant diversity, with both ant taxonomic and functional diversity increasing as biomass accumulates (BOMBI-HAEDO *et al.*, 2025). In contrast, arboreal ant communities appeared less influenced by biomass variation, suggesting distinct ecological responses between the ants of these strata. The same pattern was observed for species composition, as the recovery trajectories of terrestrial ants were closely tied to plant biomass accumulation, whereas arboreal ants might be shaped by other ecological processes (BOMBI-HAEDO *et al.*, 2025). These findings suggest that ground-nesting ant communities from Caatinga recover rapidly during secondary succession (BOMBI-HAEDO *et al.*, 2025). In this context, vegetation regrowth emerges as a key driver of terrestrial ant assemblage dynamics, while the responses of arboreal ants require further investigation.

In addition to changes in community structure, seed dispersal functions recovered rapidly during secondary succession, emphasizing the strong link between the recovery of ant communities and the restoration of their ecosystem functions (OLIVEIRA *et al.*, 2024). Key seed-dispersing ants, such as *Dinoponera quadriceps* and *Ectatomma muticum*, transported seeds up to 15 meters, aiding the establishment of new plant populations. Alongside seed dispersal, plant protection functions mediated by ants in EFN-bearing plants also recovered during secondary succession (SILVA, 2020). Although plant and ant species richness, as well as the overall number of ant-plant interactions, remained relatively stable across the biomass gradient, the efficiency of the protection function tended to increase as biomass accumulated. This response varied according to the nesting habits and foraging strategies of different ant groups. Ground-nesting and arboreal generalist ants maintained consistent interaction rates and attack behaviors across different successional stages

(SILVA, 2020). In contrast, arboreal specialist ants exhibited higher interaction frequencies and attack rates as forest biomass increased, although their activity remained lower in regenerating forests compared to mature ones (SILVA, 2020). These findings underscore the importance of ant functional diversity in shaping ecosystem processes and suggest that forest regeneration not only restores ant communities but also enhances the recovery of their ecosystem functions.

## LEAF-CUTTING ANT PROLIFERATION AND IMPACTS ON REGENERATION

Leaf-cutting ants are widespread in tropical and subtropical landscapes across the Americas, particularly in disturbed areas (WIRTH *et al.*, 2003; SIQUEIRA *et al.*, 2017). In these environments, they act as voracious herbivores and ecosystem engineers, altering soil attributes and light regimes (LEAL; WIRTH; TABARELLI, 2014), thereby influencing plant community composition and regeneration dynamics (LEAL; WIRTH; TABARELLI, 2014; SIQUEIRA *et al.*, 2017; 2018). While their ecology has been extensively studied in tropical forests and savannas, their role in the Caatinga dry forest has recently gained attention (SIQUEIRA *et al.*, 2017; 2018; KNOECHELMANN *et al.*, 2020; OLIVEIRA *et al.*, 2023; OLIVEIRA *et al.*, 2024; SILVA *et al.*, 2024; SANTOS-NETO *et al.*, 2025). Within the context of intense human activity, leaf-cutting ants of the genus *Atta*, including *A. opaciceps*, *A. laevigata*, and *A. sexdens* (SIQUEIRA *et al.*, 2017), as well as *Acromyrmex*, such as *A. balzani* and *A. rugosus* (SANTOS-NETO *et al.*, 2025), have proliferated in disturbed areas of the Caatinga. This may be driven by several non-exclusive factors, such as increased palatability of pioneer plant species in disturbed areas, or reduced top-down control by natural enemies (LEAL; WIRTH; TABARELLI, 2014). This proliferation is particularly evident in areas influenced by human activity, where vegetation cover is lower (SIQUEIRA *et al.*, 2017). For instance, the density of active *Atta* colonies increased significantly from 2.55 ± 1.65 colonies $ha^{-1}$ in less disturbed sites to 15 ± 2.92 colonies $ha^{-1}$ in areas closer to roads, where anthropogenic disturbance and habitat modification are more pronounced (SIQUEIRA *et al.*, 2017) (Fig. 3). Similarly, *Acromyrmex* colonies, absent in less disturbed areas, reached densities of up to 81 colonies $ha^{-1}$ in these highly modified environments (SANTOS-NETO *et al.*, 2025) (Fig. 3).


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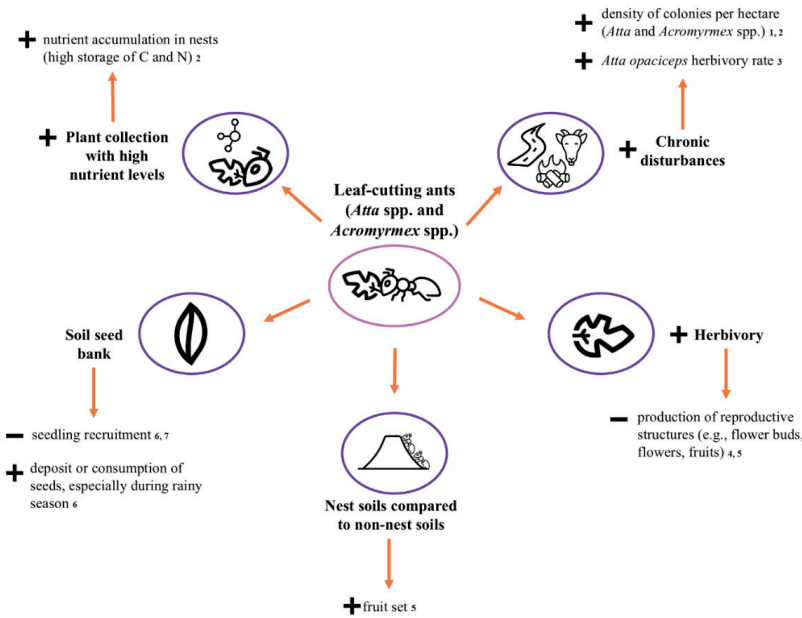
Disturbance not only promotes the proliferation of leaf-cutting ants but also amplifies their herbivory impact in the Caatinga. As disturbance intensity increased, the herbivory rate of *A. opaciceps* colonies rose significantly from 1.6 to 98.8% (SIQUEIRA *et al.*, 2018) (Fig. 3). This occurred because *A. opaciceps* adopted an opportunistic foraging strategy, expanding its diet to include herbs (such as *Portulaca elatior* Portulaceae *and Sida galheirensis* Malvaceae), cacti, dry leaves from the forest floor, biological soil crusts, and even animal feces especially during the dry season when tree vegetation is scarce (SIQUEIRA *et al.*, 2018). Such dietary flexibility is uncommon among leaf-cutting ants from rainforests (SIQUEIRA *et al.*, 2018). Regarding the two studied *Acromyrmex* species, *A. balzani* and *A. rugosus*, there was no effect of disturbance on the biomass harvested by individual colonies (SANTOS-NETO *et al.*, 2025). However, when considering the entire population (i.e., accounting for colony densities), the total biomass harvested by both species increased considerably as disturbance intensified (SANTOS-NETO *et al.*, 2025).

erbivory by *A. opaciceps* can significantly impact plant reproduction of adult plants, which have effects that vary according to the plant species and the type of damage inflicted (OLIVEIRA *et al.*, 2024; SILVA *et al.*, 2024) (Fig. 3). While these ants can negatively affect the production of reproductive structures (e.g., flower buds, flowers, fruits) in *Croton argyrophylloides* (Euphorbiaceae), *Cenostigma pyramidale* (Leguminosae), and *Indigofera suffruticosa* (Leguminosae), the proportion of buds and flowers that develop into fruits (i.e., fruit set) was negatively affected only in the case of *C. argyrophylloides* (SILVA *et al.*, 2024) (Fig. 3). Moreover, effects of herbivory and soil changes via nest construction and maintenance linked to *A. opaciceps* on the reproduction of *Indigofera suffruticosa* and *Cenostigma pyramidale* (Leguminosae) also indicated species-specific results. While *C. pyramidale* reproduction was not affected, in *I. suffruticosa*, ant herbivory and nest-related soil changes boosted fruit set (OLIVEIRA *et al.*, 2024) (Fig. 3).

**Figure 3 -** Leaf-cutting ants and their impacts on regeneration dynamics. Trends are indicated by red arrows: upward and downward arrows denote increases and decreases in the respective variables.




**Sources:** (1) Siqueira et al. (2017); (2) Santos-Neto et al. (2025); (3) Siqueira et al. (2018); (4) Silva et al. (2024); (5) Oliveira et al. (2024); (6) Oliveira et al. (2023); (7) Knoechelmann et al. (2020).

HLeaf-cutting ants have a profound impact on the regeneration dynamics of the Caatinga dry forest (KNOECHELMANN *et al.*, 2020; OLIVEIRA *et al.*, 2023). *Atta opaciceps* colonies altered soil seed bank, with areas under their influence exhibiting lower seed density and richness, as well as a different taxonomic composition compared to control, non-nest soil areas (OLIVEIRA *et al.*, 2023) (Fig. 3). It is thought that ants deposit or consume seeds in their underground nests, reducing the availability of viable seeds for regeneration (LEAL *et al.*, 2017; OLIVEIRA *et al.*, 2023). These effects were more pronounced during the rainy season, which is critical for plant recruitment in dry forests (OLIVEIRA *et al.*, 2023). Additionally, *A. opaciceps* colonies negatively affected seedling recruitment and assemblages, which are already naturally sparse and species-poor, especially in terms of woody species (KNOECHELMANN *et al.*, 2020). Their nests and foraging areas supported lower seedling abundance and species richness compared to areas outside their influence (KNOECHELMANN *et al.*, 2020) (Fig. 3). In an environment already harsh for seedling recruitment and growth due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to water scarcity (KNOECHELMANN *et al.*, 2020), the proliferation of leaf-cutting ants and their ability to harvest large amounts of foliage year-round raise serious concerns about their ecosystem-level impacts (SIQUEIRA *et al.*, 2018; KNOECHELMANN *et al.*, 2020; OLIVEIRA *et al.*, 2023).

Beyond the direct impact of herbivory, leaf-cutting ants can also significantly influence soil properties and ecosystem processes in the Caatinga dry forest (WIRTH *et al.*, 2003; SANTOS-NETO *et al.*, 2025). For instance, *Acromyrmex rugosus* collected plant material with higher nutrient (N, Ca, S, Sr, Fe, and Mn) concentrations than *Acromyrmex balzani,* leading to greater nutrient accumulation in its nests (SANTOS-NETO *et al.*, 2025) (Fig. 3). On the other hand, *A. balzani* shifted from less nutritious to more nutritious plant sources (particularly herbs) in more disturbed and even in more arid habitats (SANTOS-NETO *et al.*, 2025) (Fig. 3). Together, these two *Acromyrmex* species collectively can store more than 126 kg of carbon per hectare and around 6 kg of nitrogen per hectare per year in their nests (SANTOS-NETO *et al.*, 2025). These findings demonstrate that *Acromyrmex* species are also key herbivores capable of reallocating substantial amount of forest biomass, creating temporary nutrient sinks with potential impacts on the Caatinga resilience (SANTOS-NETO *et al.*, 2025). Given the proliferation of leaf-cutting ants in human-modified landscapes of the Caatinga dry forest, the net output of their interactions with plants might be vital to plant recruitment and forest regeneration dynamics.

## CONCLUSIONS

The Caatinga is one of the largest and most diverse dry forests in the world, yet its future is increasingly uncertain due to escalating anthropogenic pressures and climate change (SILVA; LEAL; TABARELLI, 2017a). As key ecological players, ants provide a valuable perspective for understanding the complex interplay between biodiversity, ecosystem functions, and environmental change in this ecosystem. Our findings indicate that, despite its relatively low species richness, the Caatinga ant fauna exhibits high functional diversity, with species playing critical roles in seed dispersal, herbivory, and nutrient cycling, highlighting the need for further research to understand their contributions to ecosystem processes and resilience.

Our results also reveal that anthropogenic disturbances and increasing aridity affect ants at multiple ecological levels, from individual populations to entire ecosystems. In general, as disturbance-sensitive species decline, generalist and disturbance-adapted species tend to proliferate, driving biotic homogenization. This shift reshapes ant communities in ways that reverberate throughout the ecosystem, particularly by altering essential functions such as seed dispersal and plant protection. For example, species responsible for long-distance seed dispersal, like *Dinoponera quadriceps*, are highly sensitive to disturbance, which may compromise the distribution of plant populations that rely on ants for dispersal. Increasing aridity can negatively impact ant communities in ways similar to anthropogenic disturbance, often even more severely. Moreover, when combined, aridity can amplify the effects of disturbance on functional and phylogenetic diversity, disrupting ant–plant interactions and threatening ecosystem resilience. However, in some cases, aridity may mitigate the impact of disturbances. For example, while disturbance generally homogenizes communities taxonomically, functionally, and phylogenetically, we found that in more arid areas, it can actually increase community heterogeneity.

Amid these challenges, ants demonstrate remarkable resilience. Their communities and the essential functions they provide—such as seed dispersal, nutrient cycling, and herbivory—are capable of recovering rapidly during forest regeneration following disturbances like slash-and-burn agriculture. This quick recovery highlights the adaptability of ant communities in the face of environmental change (SILVA *et al.* 2019, OLIVEIRA *et al.* 2022). However, the long-term resilience of ant-mediated ecosystem processes remains uncertain. One of the key challenges is determining the thresholds at which biodiversity loss begins to undermine ecosystem functioning. Understanding the capacity of different ant species to adapt to ongoing environmental changes is also crucial, as their responses may vary depending on the specific stressors they face. This knowledge is essential for predicting how these communities may evolve and whether their resilience can sustain critical ecosystem functions in the long term. Additionally, the proliferation of leaf-cutting ants in disturbed areas poses a significant threat to this regeneration process. By depleting seed banks, reducing seedling recruitment, and altering nutrient cycling, these ants


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can create feedback loops that hinder forest recovery and disrupt the natural balance of the ecosystem.

Despite significant advances in understanding Caatinga ants and their responses to disturbance and climate change, critical knowledge gaps remain. A deeper understanding of how ant responses align with those of other organisms and broader ecosystem functions is essential to determine whether our findings reflect general ecological patterns in the Caatinga. Additionally, exploring how ant-mediated processes contribute to forest regeneration—and whether these processes can be harnessed to promote ecosystem recovery—remains a key area for future research. Furthermore, most studies have been conducted in a limited number of sites, despite evidence that soil type and aridity strongly influence ant responses to disturbances. Since the Caatinga is a mosaic of diverse soil types, vegetation topologies, and climatic conditions, expanding research to include a wider range of sites is crucial for developing a more comprehensive, region-wide perspective on biodiversity responses and ecosystem resilience. Addressing these gaps will not only enhance our understanding of the Caatinga's ecological dynamics but also provide valuable insights for the conservation of dry forests worldwide. This is particularly important given that many dry forests around the world face similar anthropogenic pressures as the Caatinga (TABARELLI *et al.*, 2024), making the findings relevant for broader conservation efforts.

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# 18

# PANTANAL ANTS: ESTABLISHING A DATA SET OF ANT COMMUNITIES FROM THE BRAZILIAN WETLAND

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# ABSTRACT

In this chapter, we propose to provide a comprehensive repository of available information on the myrmecofauna of the Pantanal, identifying sampling biases and knowledge gaps. The Pantanal is the world's largest tropical wetland and is currently under intense anthropogenic pressure. It covers approximately 160,000 km² distributed across three countries: Brazil (~140,000 km²), Bolivia and Paraguay. Following the examples of existing Formicidae databases, such as those from the Amazon (Sciants) and the Atlantic Forest (Atlantic Ants), we started the search for articles in Scopus, Periódicos Capes, Web of Science and Google Scholar using the following keywords: ants+Pantanal, formicidae+Pantanal, ants+wetland+Brazil, formicidae+wetland+Brazil. We found 30 papers that include a sampling methodology, location, and a list of recorded species. Most of the studies are ecological (11), followed by studies on record of new occurrence (five), insect-plant interaction (three), species list (three), ant-insect interaction (one), collection method (two), nest architecture (one), biodiversity conservation and species distribution (four). Among the evaluated studies, only the three articles, that consist of checklists, recorded more than 100 morphospecies. Through this survey, we identified significant knowledge gaps regarding ants in the Pantanal. For instance, there are few studies on ant species in Mato Grosso do Sul, the Brazilian state that contains the largest portion of the Pantanal biome. To address this, we have initiated a database to provide structured information for researchers interested in the myrmecofauna of this biome.

**Keywords:** Biodiversity; myrmecology; conservation; ant list.

## INTRODUCTION

The Pantanal is the largest continuous floodplain in the world, covering 151,939 km² (91.6%) in Brazil in addition to smaller extensions in Bolivia 10,924 km² (6.6%) and Paraguay 2,980 km² (1.8%) (IBGE, 2019; JUNK *et al.*, 2006; FERNANDES *et al.*, 2010).

It is located in the Upper Paraguay Basin and comprises a lowland area (Pantanal biome) in addition to a plateau that includes the Pantanal and the surrounding Cerrado and Amazon biomes (SOS PANTANAL *et al.*, 2015, 2017).

The Pantanal harbors one of the greatest biodiversities in the world, with over 4,700 recorded species, including mammals, birds, reptiles, amphibians, and fish, many of which are endemic or threatened with extinction (ALHO & SABINO, 2012; JUNK *et al.*, 2006). However, this exceptional biodiversity is currently under strong anthropogenic pressure: until 2018, around 83% of the area was preserved, but it has lost around 30% of its total area since then due to the expansion of agricultural frontiers and fires in 2020 (PIVELLO *et al.*, 2021; SILGUEIRO *et al.*, 2021; MAPBIOMAS, 2025).

The Pantanal is characterized by an annual flood pulse, which varies in duration and extent depending on environmental heterogeneity (NOGUEIRA *et al.*, 2002; JUNK *et al.*, 2013). This phenomenon is known as the flood period. This flood pulse is what shapes the terrestrial and aquatic environments in the lower lands (ASSINE & SOARES, 2004; ABREU *et al.*, 2010). Meanwhile, in the dry season, most of these plains dry out completely, and it is in this scenario that most fire events occur (NUNES DA CUNHA *et al.*, 2006). Although fires can have natural causes, those of anthropogenic origin have become increasingly frequent in recent decades, representing one of the greatest threats to the biodiversity of the Pantanal (LIBONATI *et al.*, 2020).

This biome, considered one of the richest biodiversity in the world and a true hotspot of biological diversity, is home to approximately 1,800 species of plants and around 1,200 species of vertebrates (ICMBIO, 2025). In addition, the Pantanal is home to an immense diversity of insects, which play fundamental ecological roles, such as pollination, decomposition of organic matter, and biological control of pests (RODRIGUES *et al.*, 2010; LOPES *et al.*, 2017; ALGARVE *et al.*, 2020).

Among insects, ants are one of the most diverse and abundant groups on the planet, with more than 16,800 valid species described (FISHER & FONG, 2025). In the Neotropical region, where the Pantanal is located, 14 subfamilies are known, represented by more than 3,800 species (FISHER & FONG, 2025). These insects play crucial ecological roles, as predators, primary and secondary consumers, and as a food base for other consumers (RETANA *et al.* 2004; HANISCH *et al.* 2020). However, in the Pantanal, a complex and dynamic ecosystem, ants face challenges such as periodic flooding and fire, which influence the structure of their communities (ARRUDA *et al.*, 2022). Ants have several adaptations to survive these conditions, including vertical migrations and escape strategies from their nests (ADIS *et al.*, 2001; BATTIROLA *et al.*, 2005). Some of the strategies adopted by ants in response to fire and flooding, for example, are shown in Arruda *et al.* (2022) and Parr *et al.* (2007). After a fire, a difference of 10 species between plots can be observed, with 10 species being found exclusively in burned areas (ARRUDA *et al* 2022). This can be explained by the increased foraging activity of species due to habitat simplification and the reduction of soil-dwelling arthropod prey (PARR *et al.*, 2007). Ants are well adapted to flooding in the Pantanal (ARRUDA, 2022), which may be related to the biome's millions-of-years history of flooding (ASSINE & SOARES, 2004), and it is known that this environmental filter has shaped its habitat structure and the distribution of plant species (SCREMIN-DIAS *et al.*, 2011), a fundamental resource for ant species.Even with these aspects of the biome that can trigger evolutionary processes and an unparalleled diversity (VICENTE, personal communication), there is a predominance of ant studies in the Atlantic Forest, Amazon Rainforest, and Cerrado (FEITOSA *et al.*, 2022). Therefore, knowing the Pantanal myrmecofauna is essential to understanding the dynamics of this ecosystem and how these insects respond to environmental changes (BATTIROLA *et al.*, 2005).

In this chapter, we provide a comprehensive repository of available information on the myrmecofauna of the Pantanal biome, identifying sampling biases and knowledge gaps. By gathering and analyzing the data available in the literature, we aim to provide an updated overview of the knowledge about the myrmecofauna of the Pantanal, since understanding the myrmecofauna of the Pantanal is crucial for the development of conservation strategies and the sustainable management of this important biome.


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This database was created to answer the following questions: "How many articles have been published? What is the subject and what do these articles cover?", "Which scientific journals, authors, and research institutions have published the most articles?", "Which articles have had the most significant impact on the community based on the number of citations?", "What topics have guided research on ants in the Pantanal, considering the keywords?", "Which groups (subfamilies, genera, and species) of ants occur in the Pantanal?", "How are the studies distributed temporally and spatially?".

## METHODS

The search for articles was carried out in two databases: Periódicos Capes and Google Scholar; using the keywords: ants+Pantanal; formicidae+Pantanal; ants+wetland+Brazil; formicidae+wetland+Brazil and their respective Portuguese versions. The search for articles was limited to the year 2024. We restricted the location to studies located in the Brazilian Pantanal.

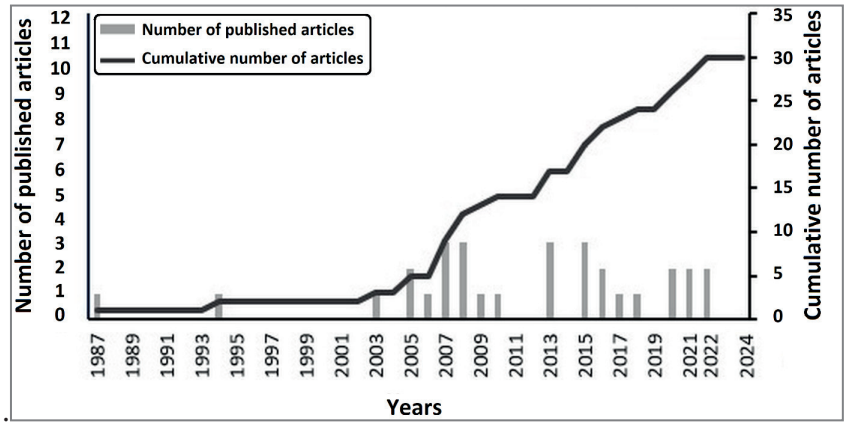
For the species list; we collected the data present in the articles and verified the nomenclature according to AntCat - An Online Catalog of the Ants of the World by Barry Bolton. At the genus level; the update was carried out when possible; and those with uncertain identities were not counted. At the subfamily level; all records were updated.

To create the maps; we gathered the coordinates of collection points reported in each article. The heat map was generated using the kernel method in QGIS 3.14. The visualization of the network of collaborators was performed using the Kamada-Kawai algorithm (KAMADA & KAWAI; 1989); in the Pajek software. The algorithm positions the vertices in the two-dimensional space minimizing an energy function; allowing connected vertices to be closer and disconnected vertices to be positioned further apart; facilitating the graphical interpretation of the relationships. To define the authors' roles within the network; we based ourselves on their interactions within the modules (z) and their interactions between the modules (c) (using standard values for the metric proposed by OLESEN *et al.*; 2007). The word cloud was generated by the free software Word Cloud Generator; in which we considered only words cited in two or more articles.

## RESULTS

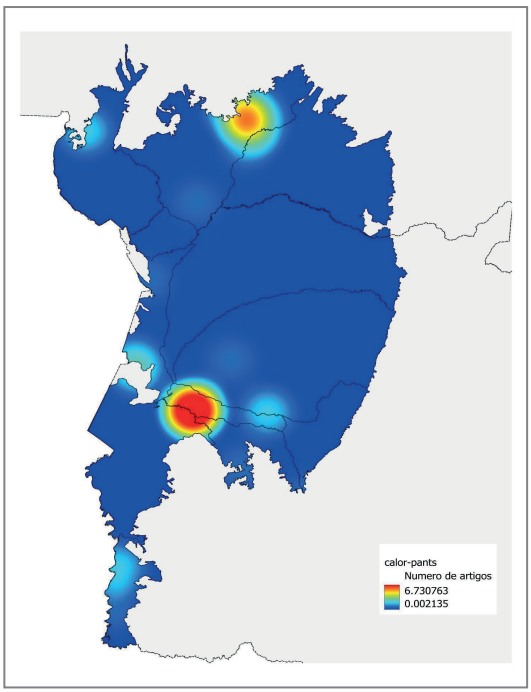
Our search returned 30 scientific articles, temporally distributed between 1987 and 2022, without a highlighted period of production (Figure 1). Most of the studies are ecological (11), followed by studies on record of new occurrence (five), insect-plant interaction (three), species list (three), ant-insect interaction (one), collection method (two), nest architecture (one), behavior, biodiversity conservation and species distribution (four).

**Figure 1 -** Annual number of publications and their cumulative number during the period 1987 to 2024.




These studies carried out between 1987 and 2022, were concentrated especially in the northern part of the biome, in the region of Poconé and Cáceres (Figure 2), and in the southern part of the biome, covering the regions of Miranda, Aquidauana, and Corumbá. Other isolated points were also recorded but with limited studies.

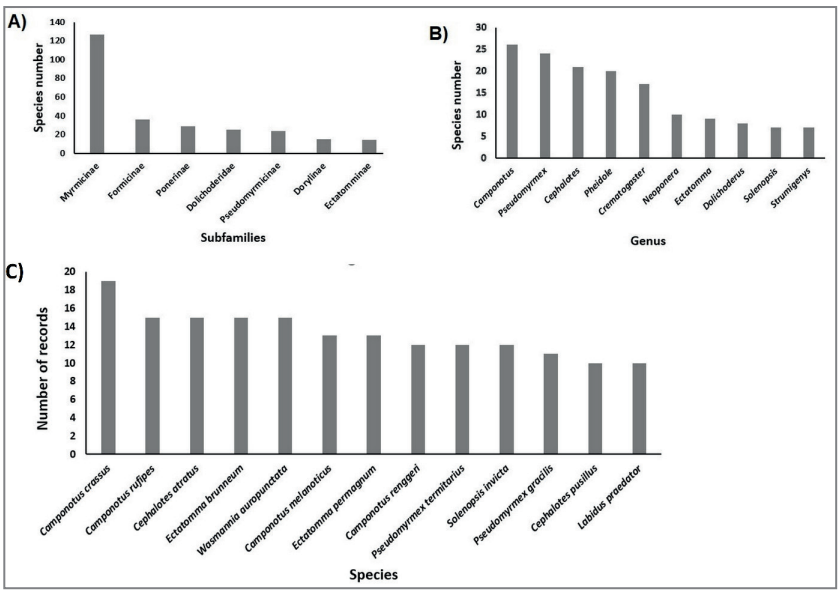
**Figure 2 -** Heat map showing the regions of the Pantanal where the greatest number of studies on ants occurred.




We recorded a total of 272 ant species, distributed across 75 genera and 10 subfamilies (Table 1. Supplementary material). Among the subfamilies, Myrmicinae was, by far, the richest, with (126 species), followed by Formicinae (33 species), Ponerinae (29), Dolichoderinae (25) and Pseudomyrmicinae (24) (Figure 3A). Regarding the genera, *Camponotus* (26), *Pseudomyrmex* (24), *Cephalotes* (21), and *Pheidole* (20) were the richest in the Pantanal (Figure 3B).

As for the species, *Camponotus crassus* (19 occurrences), *Camponotus rufipes* (15), *Cephalotes atratus* (15), *Ectatomma brunneum* (15) and *Wasmannia auropunctata* (15) constitute the most frequently recorded species (Figure 3C). Of the species studied, five are considered exotic and were recorded in the biome: *Cardiocondyla emeryi, Cardiocondyla obscurior, Monomorium floricola, Paratrechina longicornis,* and *Tapinoma melanocephalum* (according to classification of FEITOSA *et al.*, 2022).

**Figure 3 -** Subfamilies (A) and genera (B) of ants richest in the Pantanal and most frequently sampled species (C).




Regarding the collection methodologies, nine types were used in the studies, namely: canopy traps, trays, canopy fogging, manual active collection, entomological umbrella, baits (varied), pitfall, underground film pots, winkler/mini winkler. The use of pitfall was the most used in the studies, approximately 29%, and only three studies used more than one sampling method (Silva *et al.*, 2013; Demétrio *et al.*, 2017; Martins *et al.*, 2021). The species *Wasmannia auropunctata, Camponotus crassus, Camponotus novogranadensis, Linepithema humile,* and *Solenopsis invicta* were collected using the largest number of different methodologies.

A total of 88 (co)authors were involved in these publications (Figure 4). Most authors had few partners in the collaboration network ($z<2.5$ and $c<0.62$), being designated as peripheral. Wedson D. Fernandes, a researcher at the Federal University of Grande Dourados (UFGD), acts as a module hub (high values of z and low c); he is highly connected, but only within his module. Jacques H. C. Delabie, a researcher affiliated with the State University of Santa Cruz and the Federal University of Bahia, is an author with many connections who acted as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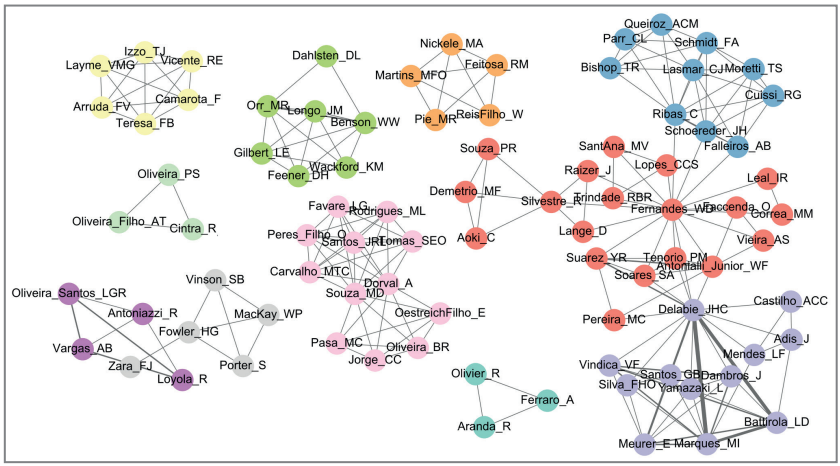
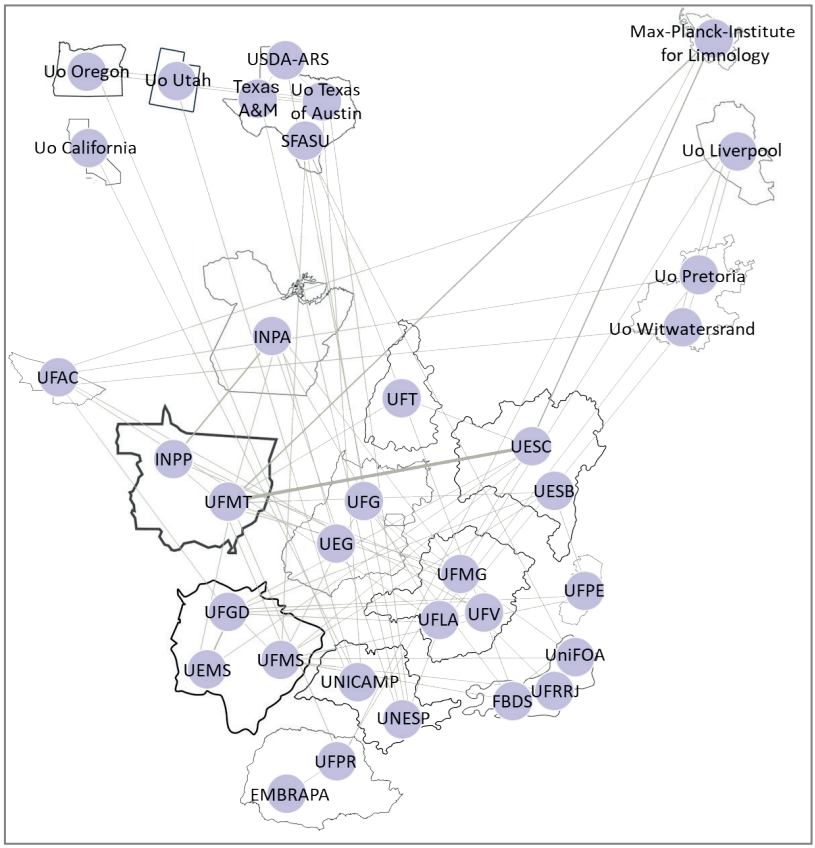
a network hub, connecting several authors within and between modules (high values of c and z). He is considered a network hub.

**Figure 4 -** Network of interaction between authors who publish articles on ants in the Pantanal.




Thirty-four institutions were involved in the publications, five of which were located in states that comprise the Pantanal (MS and MT). The Federal University of Mato Grosso (UFMT) was the institution involved in the largest number of articles (12), followed by the State University of Santa Cruz (UESC, 8), the Federal University of Grande Dourados (UFGD, 7), the State University of Mato Grosso do Sul (UEMS, 5), and the Federal University of Mato Grosso do Sul (UFMS, 5) (Figure 5). The institutions that interacted the most were the Federal University of Mato Grosso and the State University of Santa Cruz (6 collaborative articles). These interactions primarily involved researchers Jacques Hubert Charles Delabie, Marinêz Isaac Marques, Eliandra Meurer, and Leandro Dênis Battirola.

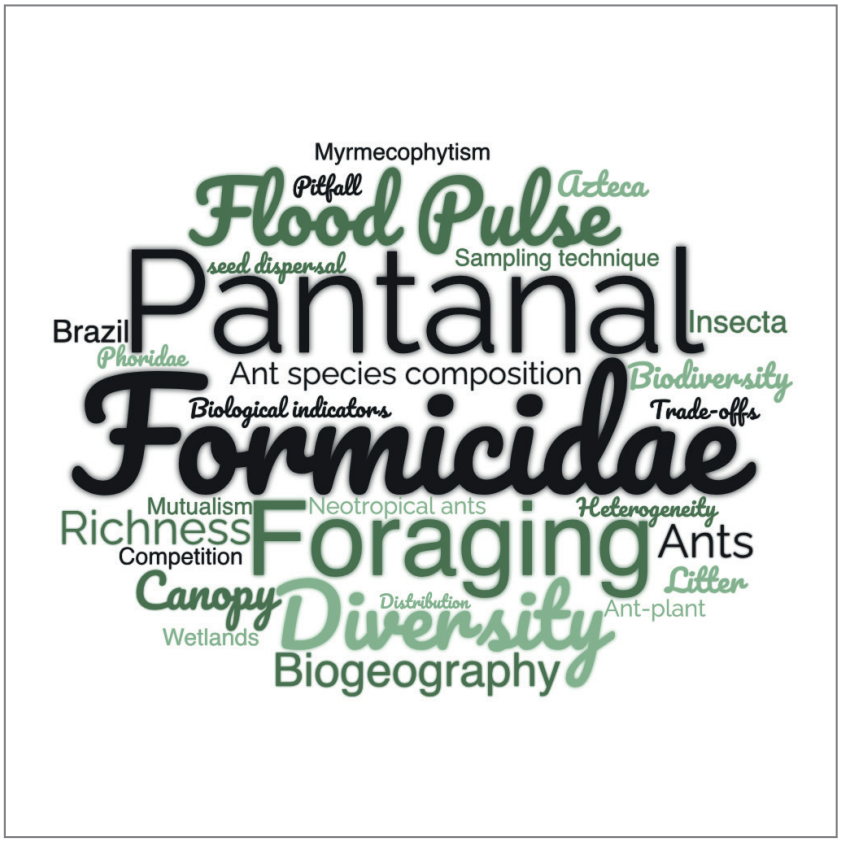
**Figure 5 -** Collaboration network of institutions involved in the publications.




The articles were published in 17 journals, with an emphasis on Sociobiology (8 articles) and Neotropical Entomology (4 articles). The article with the highest number of citations is that of Ribas and Schoereder (2007), published in Biodiversity and Conservation (100 citations).

The word cloud highlighted the most cited keywords in the articles, and the following terms were most prominent throughout the works: “Pantanal” and “Formicidae” (7 citations), followed by “Foraging” (5 citations), “Ants”, “Canopy”, “Diversity”, “Flood Pulse”, “Richness” (4 citations each) (Figure 6).

**Figure 6 -** Word cloud of most cited keywords in articles on Pantanal ants.




## DISCUSSION

The number of articles providing information on Pantanal ant fauna is very small compared to the scientific production of myrmecology in Brazil. For context, the first ant inventories in Brazil date back to 1878 and 1888 (EMERY, 1888; MAYR, 1878) and between 1970 and 2021, 491 articles on ant diversity in Brazil were produced (FEITOSA *et al.*, 2022). Meanwhile, as we saw in our inventory, in the Pantanal the first study dates back to 1987, and until 2022 only 30 studies were carried out. This implies a time gap of 17 years until (1970 - 1987) the first studies on ants in Brazil were developed in the Pantanal. This scenario of studies gaps in Pantanal hinders the advancement of our understanding of the

determining factors in the establishment of spatial patterns of ant biodiversity and prevents the improvement of taxonomic resolution (FEITOSA *et al.*, 2022).

According to Feitosa *et al.* (2022), the low number of studies in the Pantanal, as well as in the Pampas, is due to several factors. For example, Brazil's socioeconomic development has historically been concentrated on the coast, resulting in a greater presence of research institutions in the Atlantic Forest and less attention to other regions. In addition, research funding, mostly from Brazilian agencies, has recently been cut, further affecting less-studied biomes. In the case of the Pantanal, environmental challenges such as seasonal flooding and logistical difficulties also limit the conduct of surveys. These factors reinforce the need for more research to better understand the biodiversity of these regions, and also explain the gap in studies found here.

The present study significantly expands the known ant diversity of the Pantanal, adding 132 species to the previous list of 143 reported by Feitosa *et al.* (2022), resulting in a total of 275 recorded species for the Pantanal. The four richest subfamilies in the present survey are in accordance with their representation at the national level. Among these, the subfamily Myrmicinae comprises almost 50% of all known ant species in the world, with approximately 6,500 known species distributed in 140 genera (BACCARO *et al.*, 2015; BOLTON, 2025), of which 60 genera and approximately 650 species occur in Brazil (BACCARO *et al.*, 2015). Myrmicinae's remarkable diversity is reflected not only for its species richness, but also for its wide variation in morphological aspects, reproductive strategies, feeding modes, and nesting patterns (BACCARO *et al.*, 2015). These ants occupy different habitats, from underground layers to the forest canopy, explaining their high prevalence in the studies analyzed in this work. In the Pantanal, this pattern is likely reinforced by the mosaic of habitats ranging from periodically flooded grasslands to gallery forests, that provides suitable conditions for both ground-dwelling and arboreal Myrmicinae. Moreover, the seasonal flood pulse generates temporal variation in resource availability, which can favor generalist and opportunistic taxa within the subfamily.

In the Pantanal, we have records of 71% of the 106 genera documented nationally (FEITOSA *et al.*, 2022). Notably, 8 of the 10 most speciose genera at the national level were also prominent in our Pantanal dataset, with only *Acromyrmex* and *Neivamyrmex* being exceptions. At the species level, *Camponotus*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*crassus*, *Camponotus rufipes* and *Wasmannia auropunctata* were among the ten most frequently recorded species in the Pantanal (Figure 6). This pattern is unsurprising given that *Camponotus* is a genus of ants with more than a thousand described species, of which about 200 occur in Brazil (BACCARO *et al.*, 2015) and ecologically versatile. Similarly, *W. auropunctata* adapts well to disturbed areas and agricultural crops, owing to its omnivorous diet and highly competitive dominance, which often leads to the displacement of native ants in regions where it is introduced (BRETON *et al.*, 2003; BACCARO *et al.*, 2015). Beyond their ecological versatility, the high frequency of these species in our dataset may also reflect methodological bias. The predominant use of pitfall traps favors the capture of ground-foraging ants, while the limited adoption of complementary methods, such as canopy fogging, baiting, or Winkler extraction, may underrepresent strictly arboreal or cryptic taxa, potentially biasing richness and composition estimates. Studies have demonstrated that combining multiple sampling techniques significantly improves the inventory completeness of ant communities (SOUZA *et al.*, 2012, 2024; VICENTE *et al.*, 2016; DELABIE *et al.*, 2020), especially in complex tropical environments where ant guilds differ in microhabitat use and activity patterns. This dominance of a few versatile genera in the Pantanal may reflect ecological filtering by seasonal inundation, a pattern also observed in other seasonally flooded tropical ecosystems such as the Amazonian floodplain (várzea) forests, where ground-nesting ant diversity and abundance are reduced due to flooding (MERTL *et al.*, 2009; BACCARO *et al.*, 2012; SOUZA-HOLANDA *et al.*, 2021).

**Figure 7 -** Ants from the Pantanal, being (a) *Wasmannia auropunctata* ants preying on a termite, (b) a *Cephalotes atratus* worker carrying food, (c) two *Camponotus crassus* workers, (d) a *Camponotus rufipes* worker and (e) an *Ectatomma brunneum* worker. Photos by: Paulo Robson Souza. Available at: https://uk.inaturalist.org/people/souza_pr.

Regarding researchers, the collaboration network points to the need for more groups studying ants diversity and the need for better-structured research groups in the states that comprise the Brazilian Pantanal (Mato Grosso and Mato Grosso do Sul). Given this concentration of expertise in a few individuals and institutions, strengthening collaboration between research groups across different states and institutions could help expand sampling coverage, share logistical costs, and standardize methodologies. Establishing long-term monitoring plots in underrepresented regions would be a key step to reduce current knowledge gaps (BERGALLO *et al.*, 2023; CARVALHO *et al.*, 2023; GUIMARÃES *et al.*, 2024). Among the authors, Jacques H. C. Delabie is a prominent researcher


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in studies of ants in the Pantanal, as well as in other Brazilian biomes, contributing significantly to the knowledge of ant biodiversity in the Neotropical region. It is also worth mentioning that Delabie's research has been fundamental in the training of new researchers in the area. His mentorship has helped consolidate ant research capacity in the region. His scientific investigation focuses mainly on the ecology of ant communities, taxonomy, and biogeography.

Among the journals selected by the authors to publish research on ants in the Pantanal, the journal Sociobiology stood out. The publication of a considerable number of papers on ants in Sociobiology can be justified by three main factors: (1) its recognition as a specialized and prestigious vehicle in the area of myrmecology (2) its specific target audience interested in social insects (especially ants, termites, bees, and wasps), and (3) its open access policy, which ensures broad visibility and accessibility to researchers worldwide. These characteristics make Sociobiology a preferred choice for myrmecologists working in the Pantanal region.

The most cited study on Pantanal ants in our survey was Ribas & Schoereder (2007), published in Biodiversity and Conservation (100 citations), which can be verified through Google Scholar. In this article, the authors investigate the influence of environmental factors on the richness and species composition of arboreal ants in the Pantanal, concluding that the structural heterogeneity of the environment is a determining factor for species richness, while tree density affects species composition. Also noteworthy in terms of citations is the article by Feener *et al.* (2008) published in the journal Ecology (93 citations). In this article, the authors explore interactions between species and indirect effects mediated by Phoridae parasitoid traits and how they affect the ecological success of the red fire ant (*Solenopsis invicta*).

Taken together, the words highlighted in the word cloud reflect the areas of greatest interest to researchers studying Pantanal ants, such as Foraging, Canopy, and Flood pulse. The selected articles explore various aspects of ant ecology in the Pantanal, focusing on their diversity, distribution, interactions, and study methods. The studies demonstrated the importance of structural heterogeneity and tree density in the richness and composition of ant communities (CORRÊA *et al.*, 2006; RIBAS & SCHOEREDER, 2007), as well as the influence of flooding on communities, with some species presenting vertical migration

strategies (BATTIROLA *et al.*, 2005). Ant foraging activity apparently varies between different environments, such as forest and grassland, with greater species richness in more open environments (SANT'ANA *et al.*, 2008). The studies also encompass interactions between ant species and plants (e.g. BATTIROLA *et al.*, 2005; VIEIRA *et al.*, 2010).

The studies were mainly concentrated in regions where the study bases are located, both in the north and in the south. In the northernmost region of the map, we have the Sesc Pantanal study base and easier access to farms and UFMT laboratories. In the southernmost region, we have the BEP - Pantanal Study Base and several UFMS *campus*es in the region. As we can see in figure 5, a large part of the Pantanal has not yet been sampled, which is considered a major gap in the knowledge of the biome's myrmecology. We believe that the reason for this large unsampled area is the difficulty of accessing the regions, in addition to the lack of local infrastructure to set up a support base. This logistical challenge limits the establishment of long-term monitoring sites and comprehensive sampling efforts, which in turn constrains our understanding of spatial patterns in ant diversity across the Pantanal.

## CONCLUSION

The data compiled in this study provide the most comprehensive repository of information on the myrmecofauna of the Pantanal to date. By consolidating and analyzing 30 scientific studies spanning more than three decades, we have significantly expanded knowledge of the diversity, distribution, and ecological roles of ants in this biome. Our dataset includes 275 ant species distributed across 75 genera and 10 subfamilies, revealing patterns of richness and species composition that were previously undocumented. Despite the ecological significance of ants as key players in ecosystem functioning—acting as predators, decomposers, and mutualists—research on the Pantanal's ant communities remains limited when compared to other Brazilian biomes. This gap underscores the urgent need for further studies, especially in underexplored regions where knowledge is scarce due to logistical and environmental challenges. By identifying knowledge gaps and spatial biases in existing research, our work provides a solid foundation for future investigations and conservation strategies. The data compiled here can


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support public policies, guide environmental monitoring efforts, and contribute to the sustainable management of the Pantanal, a biome increasingly threatened by anthropogenic pressures and climate change. We hope this study stimulates further research initiatives and encourages collaboration among scientists, policymakers, and conservationists to enhance our understanding and protection of this unique wetland ecosystem.


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19

# ANTS OF THE BRAZILIAN PAMPA: INSIGHTS INTO DIVERSITY, DISTRIBUTION AND CONSERVATION

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# ABSTRACT

The Brazilian Pampa biome is characterized by extensive subtropical grasslands shaped by climatic patterns and natural disturbances. It is one of the Brazilian biomes with the lowest levels of formal protection and faces increasing threats from land-use conversion, while remaining among the least studied in terms of biodiversity. Ants represent an important component of its fauna, playing fundamental ecological roles, yet they remain particularly understudied in this biome. In this chapter, we provide a comprehensive review of the current state of knowledge on the ant fauna of the Brazilian Pampa. We first compiled a database of ant species records and their distribution across different ecological systems. We then reviewed published and gray literature on ant diversity to assess what is known about their responses to anthropogenic threats, ecological interactions, and occurrences in urban environments. Our synthesis documented 205 nominal species, along with many unidentified morphospecies, distributed across different grassland physiognomies and associated ecosystems. This review highlights major spatial, taxonomic, and thematic knowledge gaps and underscores the urgent need for more comprehensive and integrative studies. We hope our synthesis provides a baseline for future research, supporting biodiversity monitoring and the development of conservation strategies for the increasingly threatened Brazilian Pampa.

**Keywords:** Pampa biome; formicidae; campos; Grasslands; ecological systems.

## INTRODUCTION

Ants (Formicidae) are among the most ecologically dominant and functionally diverse groups of terrestrial invertebrates (HÖLLDOBLER; WILSON, 1990). They play key roles in a wide range of ecosystem processes, including soil bioturbation, seed dispersal, herbivore deterrence, and the regulation of other arthropod populations (DEL TORO *et al.*, 2012). Their social organization, high abundance, and sensitivity to environmental variation make them excellent indicators for monitoring habitat quality and assessing the impacts of anthropogenic disturbances (TIEDE *et al.*, 2017). In Neotropical ecosystems, ants contribute significantly to biodiversity and are critical components of both above- and below-ground ecological networks (COSTA *et al.*, 2010).

Brazil is a megadiverse country with six officially recognized biomes (IBGE, 2019). One of them is the subtropical grassland known as the Pampa, which occupies about 2.3% of Brazil's territory. Located in the southernmost state of Rio Grande do Sul, it covers about 63% of the state's area (ANDRADE *et al.*, 2018) and extends into Uruguay and Argentina, where it forms part of the Río de la Plata grasslands (RPG), covering nearly 700,000 km² across South America (BAEZA *et al.*, 2022). While grasslands are the dominant physiognomy, the region also includes forests, palm groves, rock outcrops, dunes, wetlands, and water bodies. Based on plant community composition and its correlation with biophysical variables such as soil type, elevation, and slope, 10 distinct ecological systems have been classified within the Brazilian Pampa (HASENACK *et al.*, 2022; Figure 1). Altogether, this biome harbors more than 12,500 species of plants, animals, fungi, and bacteria—approximately 9% of Brazil's biodiversity (ANDRADE *et al.*, 2023).

In addition to its ecological importance, the Brazilian Pampa plays a key socioeconomic role, especially in meat production. Traditional cattle ranching in native grasslands is a culturally and economically significant activity and is often cited as a model for sustainable development, as it can maintain both biodiversity and economic productivity (BAGGIO *et al.*, 2021). However, in recent decades, the region has experienced rapid landscape transformation due to the expansion of agriculture, forestry, and urban development. These changes have severely impacted native ecosystems (MAPBIOMAS PROJECT,


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2023). Currently, only 3.2% of the Brazilian Pampa is protected by conservation units, with most of the territory under private ownership, representing one of the lowest levels of formal protection among Brazilian biomes. At the same time, the Pampa remains one of the least studied biomes, especially regarding invertebrate biodiversity, including ants.

This chapter aims to provide a comprehensive synthesis of current knowledge on the ant fauna of the Brazilian Pampa. We compile available records of ant species and their distribution, and assemble a database of studies on ant diversity, identifying the main research themes and the ecological systems covered. We review the existing literature on how anthropogenic disturbances, such as agriculture, silviculture, grazing, fire, mining, and urbanization, affect ant communities, and summarize studies on ecological interactions between ants and plants, as well as those focused on ants in urban environments. Through this synthesis, we aim to identify key knowledge gaps and offer research perspectives to support ant biodiversity studies and inform conservation strategies in this increasingly threatened biome.

## THE PAMPA ANT FAUNA

Ant communities in the Brazilian Pampa have long been studied from both naturalistic and taxonomic perspectives. Emery (1888) produced the first comprehensive catalog of ants from Rio Grande do Sul, based on specimens collected by Hermann von Ihering. Years later, Elena Diehl, a remarkable myrmecologist and pioneer scientist in Rio Grande do Sul, led the compilation of a checklist of ants in the state based on 30 years of sampling, additional inventories, and a literature review (DIEHL *et al.*, 2014). Her work documented 127 ant species across the Pampa and Atlantic Forest biomes. Feitosa *et al.* (2022), in a review of Brazilian ant diversity based on published data, documented 89 species for the Pampa. More recently, Andrade *et al.* (2023) increased to 192 the number of ant species for the biome through literature review. Based on this list, we incorporated species records from recent publications, additional articles from our collection, and ant collections from the Laboratório de Interações at Universidade Federal do Rio Grande do Sul and the scientific collection of the

Museu Entomológico Ceslau Biezanko at Universidade Federal de Pelotas, Rio Grande do Sul.

We present in Supplementary Table S1 (https://doi.org/10.6084/m9.figshare.29824808.v1) the most comprehensive ant species list for the Brazilian Pampa to date, documenting a total of 205 nominal species (morphospecies not included). The subfamily Myrmicinae presents most of the species (119 spp.), followed by Formicinae (32 spp.), Ponerinae (29 spp.), Dolichoderinae (12 spp.), Dorylinae (6 spp.), Pseudomyrmecinae (4 spp.), and Ectatomminae (3 spp.). The genera with the highest species richness are *Pheidole* (36 species), *Camponotus* (22), and *Acromyrmex* (15). Following bioregional classifications, and using occurrence records from AntMaps (JANICKI *et al.*, 2016), we found that 189 species occur within the Neotropical region. Of these, 122 species are present only in South America. Additionally, ten species extend their range into both the Neotropical and Nearctic regions. Six species are considered exotic: three Afrotropical (*Cardiocondyla emeryi, Monomorium pharaonis,* and *Pheidole megacephala*), two Oriental (*Paratrechina longicornis* and *Tapinoma melanocephalum*) and one Australasian (*Tetramorium bicarinatum*). Seventeen species have distributions restricted to Brazil, of which 4 (*Crematogaster peristerica, Mycetophylax daguerrei, Pheidole pullula, Pogonomyrmex lobatus*) are endemic to the Pampa biome. Notably, fifteen species recorded in our survey have no prior records for Rio Grande do Sul according to AntMaps (JANICKI *et al.*, 2016).

Two studies on the ants of Rio Grande do Sul provide valuable insights into the structure of Pampa ant communities. The ant survey by Dröse *et al.* (2017) in natural grasslands is the longest-running study (four years) using standardized sampling methods. The most frequently sampled species using pitfall traps were *Solenopsis invicta*, followed by *Cyphomyrmex* gr. *rimosus* sp. 1, *Brachymyrmex* sp. 1, *Pheidole radoszkowskii*, *Pheidole* gr*. tristis* sp. 1, and *Pheidole obtusopilosa*. The most frequent species in vegetation, collected using sweep nets, were *Camponotus punctulatus*, *Brachymyrmex* sp. 1, and *Camponotus* sp. 2. The study by Dröse *et al.* (2019) took a broader geographic approach, describing the ant fauna in grasslands and associated forests across nine sites (six of them in Pampa) using a rapid biodiversity assessment method (bait traps). The most frequently sampled species were *Pheidole radoszkowskii*, *Pheidole* nr. *pubiventris*, and *Solenopsis invicta*. Together, these two studies highlight the


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dominance of *P. radoszkowskii*, a species that is widely distributed across the Neotropics, and *S. invicta*, which, while invasive in other parts of the world, is native to the Río de la Plata grasslands (CALCATERRA *et al.*, 2014). Interestingly, in these studies, *Acromyrmex* species were recorded at low frequencies within the diverse ant communities, despite their wide distribution throughout the Pampa (Supplementary Table S1: https://doi.org/10.6084/m9.figshare.29824808.v1).

The ant diversity in grasslands and forests of the Pampa did not seem to differ significantly (DRÖSE *et al.*, 2019). Nevertheless, ant community composition is remarkably distinct, likely due to environmental filtering processes, which favors species best suited to each habitat. Dröse *et al.* (2019) recorded 85 morphospecies, 22 species exclusively in forests, while 25 species only in grasslands. Additionally, both Dröse *et al.* (2017) and Dröse *et al.* (2019) showed that ant composition varies considerably across regions, indicating that each region harbors distinct ant assemblages. From a conservation perspective, these findings highlight the importance of preserving both different habitat types and multiple regions within the biome to maximize ant biodiversity conservation.

It is also worth noting that more than 40% of the ant species from these studies were identified as morphospecies, remaining undescribed or undetermined, including some of the most frequently sampled species. This indicates that a significant portion of the ant fauna in the Pampa ecosystems is still poorly documented, requiring further taxonomic investigation.

## ANT DIVERSITY STUDIES ON PAMPA

Studies on ant diversity in the Pampa biome remain underrepresented compared to other Brazilian biomes (SCHMIDT *et al.*, 2022). To provide an updated overview of ant diversity research in this biome, we compiled a database through a comprehensive literature survey. To achieve this, we conducted a systematic search using ISI Web of Science and Google Scholar (for Portuguese-language terms), applying the following keyword combinations: "Pampa biome," "South Brazil," "grassland," and "ants." We selected only studies that included ant species lists. Additionally, we incorporated articles from our personal collection, and searched for gray literature (e.g., Theses, Dissertations and Monographies) to identify unpublished research. For each published article, we recorded whether

the journal was indexed in major scientific databases, the language of publication, the geographic coordinates, the study duration, and the study type (e.g., species survey, biomonitoring, ecological interactions). We also categorized the sampled habitat and, in the case of biomonitoring studies, the type of land-use or disturbance evaluated. Articles covering multiple topics were assigned to all relevant categories. Based on the geographic coordinates we assigned the studies to the ecological systems of the Brazilian Pampa (HASENACK *et al.*, 2022).

We identified 43 articles published between 1998 and 2024, with an average of only 1.6 articles per year. A notable finding is that 42% of these studies were published in journals not indexed in major academic databases, while 20% were indexed in SciELO (Scientific Electronic Library Online), a platform that primarily supports Brazilian journals. Additionally, Portuguese was the most common language of publication (58%). These findings indicate that much of the research on Pampa ant diversity has limited accessibility to the broader scientific community.

Most studies on ant diversity have focused on faunal inventories and monitoring (60%). Among these, a considerable portion specifically addresses the distribution of leaf-cutting ants (*Acromyrmex* and *Atta*; 23%) in many municipalities of the state for agronomic purposes, potentially serving as a basis for integrated management programs. Approximately 18% of the studies examined ant-plant interactions. Around 40% used ants as environmental bioindicators, assessing the impacts of land-use changes such as agriculture and tree plantations, as well as disturbances like grazing, fire, and mining. Urban environments were the focus of 20% of the studies, primarily evaluating ant communities in hospitals, residences, and urban green spaces. These studies will be discussed later in this chapter.

Despite advances in understanding ant diversity and its ecological drivers in the Pampa biome, significant knowledge gaps remain. Most research has concentrated on anthropogenic environments, while native grassland habitats remain under-sampled. Moreover, the lack of long-term studies (only 13% of the studies sampled ants for periods longer than two years) underscores the need for extended temporal research to better understand seasonal and interannual variations in ant diversity. Additionally, we identified 25 unpublished Doctoral Theses, Master's Dissertations, and Undergraduate Monographs (gray literature)


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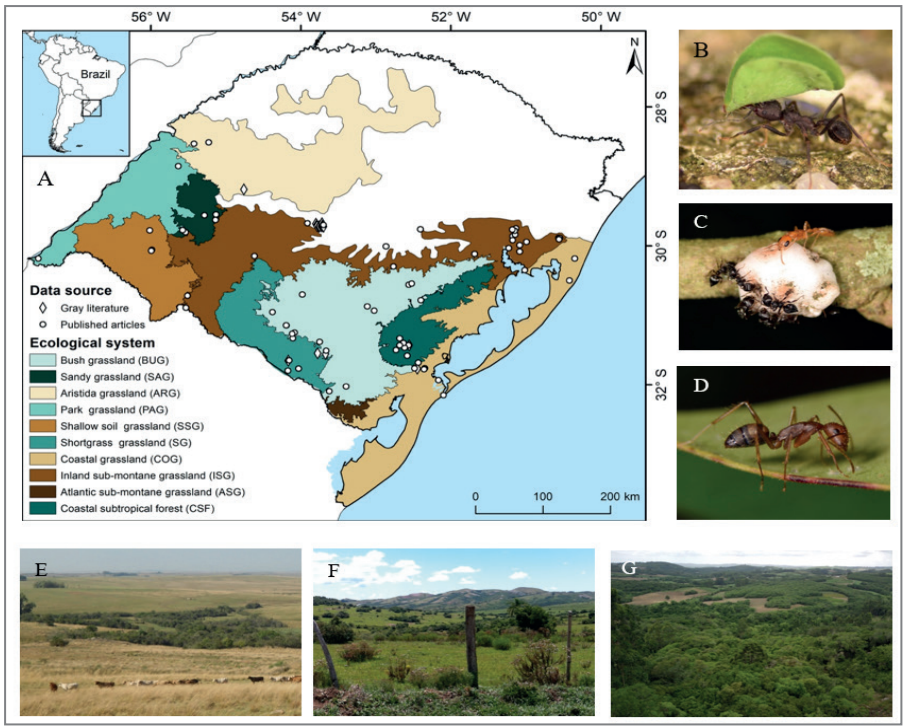
from various universities (e.g., UFRGS, UFPel, UFSM, UNISINOS and PUCRS), suggesting that ant fauna has been more extensively studied than what is reflected in published research. These findings remain largely inaccessible to the scientific community, limiting their contribution to broader biodiversity assessments.

The geographical analysis of ant diversity studies revealed an uneven distribution of sampling efforts across different ecological systems of the Pampa biome (Figure 1). In this analysis, we did not include the extensive surveys focused exclusively on leaf-cutting ants, as these data do not represent a comprehensive assessment of overall ant diversity. The "Inland Sub-Montane Grasslands" (ISG) are the most studied system and also harbor the highest number of nominal ant species (120 spp.; Supplementary Table S1: https://doi.org/10.6084/m9.figshare.29824808.v1). It extends through the Vacacaí and Jacuí Rivers, reaching the metropolitan region of Porto Alegre, where most of the studies were conducted. The "Bush Grasslands" (BUG) are the second richest system in terms of ant nominal species (62 spp.), characterized by upper and lower vegetation strata, high plant diversity, undulated relief, and high soil heterogeneity, which likely contribute to its high ant diversity. The "Coastal Grasslands" (COG) are also among the most studied regions, harboring 28 nominal species. In contrast, "Park Grasslands" (PAG) and "Atlantic Sub-Montane Grasslands" (ASG) were the least represented in terms of research coverage, which is reflected in their low recorded ant diversity (i.e., only six and five species records, respectively). In the case of ASG, which is the smallest grassland type, no dedicated ant diversity studies are found, and the available records come exclusively from occasional samplings reported in taxonomic reviews. The lack of studies in these underrepresented ecological systems (Figure 1) underscores the need for further investigations to gain a comprehensive understanding of ant diversity across the entire biome.

**Figure 1 -** A - Distribution of studies on ant community diversity across ecological systems (Hasenack et al., 2022) in the Brazilian Pampa biome. B - Leaf-cutter ant *Acromyrmex lundii;* Author: Sebastian Sendoya. C- Ants *Crematogaster curvispinosa* and *Pseudomyrmex flavidulus* interacting with a wax scale trophobiont (Hemiptera:Coccidae); Author: Sebastian Sendoya. D - Ant *Camponotus cingulatus;* Author: Sebastian Sendoya. E- Cerro do Jarau, Quaraí (SSG); Author: Luciana R. Podgaiski. F- Santana da boa vista (BUG); Author: Luciana R. Podgaiski. G- Agroecosystem in Morro Redondo municipality (COG); Author: Sebastian Sendoya.




## THREATS TO ANT DIVERSITY

Among the main threats to biodiversity in the Brazilian Pampa, the conversion of natural areas into agricultural land and tree plantations stands out. This process, which intensified in the late 20th century, has led to the rapid loss of native grasslands, positioning Rio Grande do Sul among Brazil's top agricultural producers (i.e., corn, soybeans, rice, wheat). Large-scale silviculture only began in 2004, driving an 11% annual increase in *Eucalyptus* plantations. By 2011, these plantations covered 5.7% of Brazil's total eucalyptus-planted area (ABRAF, 2012). By 2022, the net loss of native grasslands reached 19,000 km², while agricultural land expanded by 21,000 km² and cultivated pastures grew by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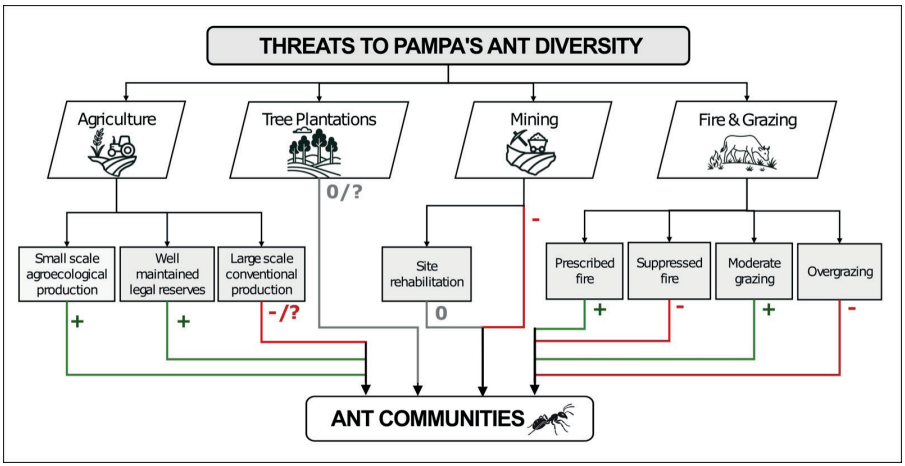
6,000 km² (BAEZA *et al.*, 2022). As a result, the Pampa became the second most degraded biome in Brazil in terms of native vegetation loss (MAPBIOMAS PROJECT, 2023), with remaining native grasslands estimated to occupy only one-third of their original area (BAEZA *et al.*, 2022). This transformation not only threatens local biodiversity but also disrupts ecosystem functionality and services. Studies on ant diversity in the Pampa primarily focus on the effects of different land uses, such as agriculture, tree plantations, and mining, as well as the impacts of management practices in native grasslands, particularly grazing and fire regimes (Figure 2).

**Figure 2 -** Main threat and management drivers affecting ant diversity in the Pampa biome, based on published studies. Arrows indicate potential effects: green (+) for positive effects, red (–) for negative effects, grey (0) for neutral effects, and uncertain labels (–/?, 0/?) for effects that are poorly understood or highly context-dependent. Overall, all these topics remain understudied and require further research.




## Agriculture

Given the ongoing transformation of the Pampa biome to agriculture (44.3 %; MAPBIOMAS PROJECT, 2023) a significant portion of its fauna may depend on agroecosystems. Some studies have evaluated ant diversity in agricultural systems, either by compiling species lists or using ants as bioindicators. These studies recorded 83 nominal ant species, and were conducted on small-scale farms (15–40 ha).

Inventory studies were conducted in olive (*Olea europaea*; RICALDE *et al.*, 2015) and canola (*Brassica napus*; JUNIOR *et al.*, 2023) crops. Moraes and Diehl (2009) assessed the impact of rice cultivation cycles (planting, harvesting, and fallow periods) on ant community structure, finding no significant changes in species richness or composition throughout the cycles. Rosado *et al.* (2013) found that vineyards undergo lower ant diversity than grasslands, attributing this to landscape homogenization and pesticide use. Carvalho *et al.* (2021) compared peach orchards, finding higher ant diversity in agroecological orchards than in conventional ones, emphasizing the role of pesticide-free management and ground cover maintenance. More recently, Carvalho *et al.* (2024) examined Legal Reserves (RLs) on family farms and the influence of the surrounding landscape on ant fauna, highlighting the role of both legal reserves and native forests as ecological refuges for ants. However, they did not observe significant differences in ant communities between conventional and organic agroecosystems.

Overall, studies highlight the negative effects of monocultures on ant fauna and the potential of agroecological practices and protected areas to mitigate these impacts (Figure 2). Nevertheless, research on this topic has only focused on small-scale farms, not reflecting the dominance of large-scale agriculture in many regions of Rio Grande do Sul. Effects of large areas with intensive soybean and rice farming remain understudied, despite their major role in landscape homogenization and biodiversity loss. Meanwhile, new agricultural frontiers are emerging, particularly in the Central Depression, Coastal Plain, and Planalto das Missões, where grasslands have declined by 50% (ANDRADE *et al.*, 2015; VÉLEZ-MARTIN *et al.*, 2015). Future research should prioritize these at-risk regions, assessing for example how large-scale vs. small-scale farming affects ant communities and providing insights into sustainable agricultural alternatives.

**Tree plantation**

Regarding the studies that evaluated the effects of tree plantations on ant fauna, most focused on the influence of *Eucalyptus* species. Two studies specifically compared a single plantation to a nearby native forest. Lemes *et al.* (2017) reported negative effects of *E. saligna* on ant diversity, while Frohlich *et al.* (2011) found no significant differences between the habitats, likely due to the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presence of a well-developed understory in the evaluated plantation. Beyond habitat comparisons, Boscardin *et al.* (2016) analyzed the effects of different agrochemicals in *E. grandis* plantations on ants but did not find consistent results. Similarly, two studies that examined the relationship between plantation age and ant species richness or composition (FONSECA *et al.*, 2004; BOSCARDIN *et al.*, 2012) did not detect clear patterns, suggesting that other environmental factors may influence ant diversity more than plantation age alone. In another study, Boscardin *et al.* (2011) tested different bait types in an *E. grandis* plantation but found no effects on ant communities (Figure 2). A crucial limitation of most of these studies is their sampling design, which often lacks treatment replication, making it difficult to draw robust conclusions about the true impact of tree plantations on ant communities. Notably, no studies have assessed the impact of converting native grasslands into tree plantations on ants, despite this being one of the primary drivers of grassland biodiversity loss.

**Grazing and Fire**

Similar to other grassland ecosystems worldwide, the characteristic biodiversity of the Brazilian Pampa has evolved under, and continues to be maintained by, natural disturbances such as grazing and fire, which have shaped the region for millennia (BERNARDI *et al.*, 2016; OYARZABAL *et al.*, 2019). Livestock production in native grasslands is one of the main economic activities in the region, and when managed sustainably, it can reconcile meat production with biodiversity conservation (BAGGIO *et al.*, 2021). In the absence of grazing, grasslands become more fire-prone, making prescribed burns a valuable tool for removing dead biomass, reducing wildfire risk, enhancing forage quality, and increasing landscape heterogeneity (BOND & PARR, 2010). However, both the suppression and the intensification of these disturbances can lead to biodiversity loss and grassland degradation (FERREIRA *et al.*, 2020), highlighting the need for balanced management strategies that integrate economic and conservation goals.

Grazing and fire impact grassland ant communities primarily through indirect mechanisms, such as alterations in habitat structure (e.g., vegetation, soil properties; VAN KLINK *et al.*, 2015). Ants predominantly nest underground

in the Pampa grasslands, where the direct mortality of colonies caused by trampling, or fire-induced heating is expected to be minimal. Some studies have evaluated the effects of grazing on ants, focusing on grazed vs. ungrazed areas, rotational grazing, and different grazing intensities in both ground-dwelling and subterranean ant communities. However, all of them remain confined to gray literature, limiting their accessibility and scientific reliability. A notable study by Dröse *et al.* (2019) used herbaceous vegetation height as a proxy for grazing intensity and found a negative relationship between ant diversity and vegetation height. Low disturbance levels lead to biomass accumulation from dominant plant species and dead organic matter, reducing plant diversity. Consequently, this habitat simplification negatively impacts ant communities, likely by reducing the diversity of foraging habitats.

Similar patterns are observed when considering fire disturbance, not only in the Pampa biome but also in other open ecosystems, such as the Cerrado, where fire suppression leads to vegetation homogenization and a decline in ant diversity (MARAVALHAS & VASCONCELOS, 2014). Barbosa *et al.* (2022) evaluated the effects of fire on grassland ant communities within a long-term undisturbed area using a BACI (before-after and control-impact) experimental design. Their findings revealed that one month after fire, burned plots exhibited higher ant species richness and increased foraging activity (seed removal). Furthermore, one year after the fire, both ant and plant richness increased in burned plots, showing a positive correlation between fire, plant diversity, and ant communities. Similarly, Silva *et al.* (2020) investigated extrafloral nectary (EFN)-visiting ants along a post-fire successional gradient. They found increased ant densities in freshly burned sites, likely driven by greater resource availability and habitat openness. However, as time since fire increased, ant density declined, and interactions with nectar-producing plants became less frequent. In summary, these studies highlight the critical role of grazing and fire disturbances in maintaining grassland ant community diversity, activity, ecosystem functions and interactions (Figure 2).

### Mining

The Pampa biome is also a region for mineral extraction, making it subject to mining-related disturbances. Some ant studies assessing the impacts of coal mining in the Campanha region are found in gray literature. One published study (DIEHL *et al.*, 2004) evaluated the effects of soil copper levels on ant communities in Caçapava do Sul (Minas do Camaquã). The study found that mining areas and sites with high copper waste exhibited significantly lower ant diversity compared to a control site. Nevertheless, a waste disposal site that had been rehabilitated with a *Pinus elliottii* plantation showed intermediate ant diversity levels, suggesting some potential for ecological recovery (Figure 2).

## ANT-PLANT INTERACTIONS

Ants frequently visit plants for foraging or nesting, engaging in interactions that range from antagonistic to mutualistic. They can act as leaf-cutters, nectar consumers, seed predators or dispersers, pollinators, or indirectly as bodyguards (RICO-GRAY &OLIVEIRA, 2007). In many ecosystems, these interactions form a complex web of relationships that are essential for various ecological functions. Nevertheless, grassland habitats, particularly those in subtropical regions of South America, remain understudied regarding ant-plant interactions (JUÁREZ--JUÁREZ *et al.*, 2023), although several recent studies are found in gray literature.

Myrmecochory, or ant-mediated primary seed dispersal, is a mutualistic interaction driven by elaiosomes—lipid-rich appendages that attract ants. Ants often consume the elaiosomes and discard the intact seeds, promoting their germination in nutrient-rich spots (BEATTIE; HUGHES, 2002). In the Brazilian Pampa, no studies have specifically addressed myrmecochory. However, Barbosa *et al.* (2022) examined non-myrmecochorous seed removal patterns by ants following habitat simplification caused by fire. Using a standardized seed mixture simulating the natural composition of grassland seed banks, they found removal rates ranging from 20% to over 80% within six days, with higher rates in simplified vegetation. However, the fate of these seeds remains uncertain, as they may be predated, lost along the way to the ant nests, or potentially germinate within the nests. In the neotropical savannas (Cerrado), ants are

estimated to remove up to 20% of non-fleshy diaspores (FARNESE *et al.*, 2011). Nevertheless, the role of ants in seed dynamics within the Pampa remains an open and promising field of research.

A few studies have described ants on plants in different ecological contexts. Junqueira *et al.* (2001) investigated ant interactions with *Ilex paraguariensis* (erva-mate; Aquifoliaceae), an economically important tree with extrafloral nectaries (EFNs). They found that some ant species, such as *Crematogaster* sp. and *Cephalotes depressus*, nest within galleries left by the erva-mate beetle (*Hedypathes betulinus*). Additionally, the study detected interactions between ants and trophobiotic insects, as well as a moderate protective effect against herbivory, which was more pronounced on the trunk than on the leaves. Silva *et al.* (2020) examined ant-plant networks involving *Chamaecrista repens* (Fabaceae), an EFN-bearing subshrub in grasslands recovering from fire. Their findings revealed that three ant species (*Camponotus punctulatus*, *Camponotus personatus*, and *Crematogaster evallans*) formed the generalist core of the network, with a progressive decline in interaction frequency as post-fire succession advanced. Over time, *Crematogaster evallans* remained the only core species, while the others became peripheral or absent. Carvalho *et al.* (2024) highlighted the association between *Camponotus termitarius* and *Eryngium chamissonis* (gravatá do banhado, Apiaceae) in flooded habitats. Ants use this plant to build nests in seasonally inundated areas, feed on floral resources, and defend flowers from herbivores. Their presence alone is sufficient to repel floral visitors, suggesting a potential trade-off between plant protection and pollination.

Beyond these targeted studies, general surveys of ant fauna associated with tree species have been conducted. Flores *et al.* (2002) and Diehl *et al.* (2006) reported ant assemblages on species such as *Inga marginata* (Fabaceae), *Jacaranda micrantha* (Bignoniaceae), *Caesalpinia ferrea* (Fabaceae), *Tabebuia chrysotricha*, and *Tabebuia rosea* (Bignoniaceae). These studies emphasize that most recorded ants were occasional foraging visitors, rather than being strictly arboreal, while some genera, such as *Brachymyrmex*, *Cephalotes*, and *Pseudomyrmex*, exhibit stronger associations with arboreal environments. Taken together, these studies illustrate the complexity of ant-plant interactions, which are influenced by plant traits, habitat disturbances, and ecological succession.


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Understanding these dynamics is crucial for assessing how environmental changes may reshape mutualistic and antagonistic interactions in different ecosystems.

## ANT URBAN DIVERSITY

Several animal populations coexist with humans in urban areas, and ants are one of the dominant invertebrate groups in these environments. Brazil is the country with the second-largest number of publications on urban ants worldwide (BUENO *et al.*, 2017). However, knowledge about urban ant fauna in the Pampa biome remains limited. Only nine articles have been published, covering topics such as ants sampled in trees used in urban arborization, residential environments, and hospitals. Across these studies, 44 nominal ant species have been documented. The most diverse genus is *Camponotus* (eight species), followed by *Pheidole* (seven species) and *Acromyrmex* (six species) (Supplementary Table S1:https://doi.org/10.6084/m9.figshare.29824808.v1). The most frequently recorded species is *Nylanderia fulva*, appearing in six studies, followed by *Camponotus rufipes* (five studies), *Camponotus mus*, *Monomorium pharaonis*, and *Solenopsis saevissima*, each recorded in four studies. Additionally, six non-native species are identified: *Cardiocondyla emeryi*, *Monomorium pharaonis*, *Paratrechina longicornis*, *Pheidole megacephala*, *Tapinoma melanocephalum*, and *Tetramorium bicarinatum*. Among them, *P. longicornis* and *T. melanocephalum* are the predominant urban ant species in Brazil, both in terms of number of occurrences and distribution (BUENO; CAMPOS, 2017).

In residences, Silva and Loeck (1999) sampled 24 ant species/morphospecies in four neighborhoods of Pelotas municipality. Gonçalves *et al.* (2014) reported *Camponotus cingulatus* for the first time in the state of Rio Grande do Sul in a flower shop in Capão do Leão municipality, where its aggressive behavior caused economic problems for the establishment. A recent study documented *C. cingulatus* in the diet of the lesser anteater (*Tamandua tetradactyla*) in natural grasslands of the Pampa biome (DELOSS *et al.*, 2023), indicating that the species is not restricted to urban areas, as expected. Ant fauna in hospitals has been studied in the municipalities of Bagé (BICHO *et al.*, 2007), Pelotas (GONÇALVES *et al.*, 2011; KOPERECK *et al.*, 2019), Porto Alegre (GARCIA *et al.*, 2011) and its metropolitan region (LUTINSKI *et al.*, 2015). These studies highlight

the role of ants as potential vectors of pathogens in hospitals. However, only Gonçalves *et al.* (2011) identified pathogenic bacteria associated with ant species.

Understanding which ant species inhabit urban areas is essential for their management, control, and ultimately, conservation. The importance of green areas within cities (e.g., urban parks, natural or planted fragments) for maintaining ant community diversity has been widely emphasized (BONFIM *et al.*, 2017; SANTOS *et al.*, 2019). However, no studies have specifically addressed this issue in the Pampa biome. Given the increasing urban expansion and habitat fragmentation in this region, understanding how urban green spaces contribute to the persistence of native ant species is crucial. Future research should focus on assessing the role of these environments in sustaining ant diversity, mitigating the impacts of urbanization, and promoting conservation strategies that integrate biodiversity within city landscapes.

## FINAL CONSIDERATIONS

Despite recent advances, our synthesis reveals that the myrmecofauna of the Brazilian Pampa remains significantly understudied. Inventories and diversity studies are heavily concentrated in a few subregions, while several ecological systems remain poorly represented in the published literature. This spatial bias limits our ability to grasp the full extent of ant diversity in the biome and hampers the development of broad-scale conservation strategies. Additionally, a substantial portion of existing studies is published in non-indexed journals, in Portuguese, or remains in the gray literature, significantly reducing accessibility and visibility within the broader scientific community.

In the face of escalating land-use changes such as agricultural expansion, afforestation, urbanization, and climate change there is an urgent need to expand research on ant communities in the Pampa biome. We may be losing species, interactions, and ecological functions before they are even documented. It is therefore critical to prioritize integrative research efforts that encompass neglected regions and underexplored ecological systems, using updated taxonomic, functional, and phylogenetic approaches. We hope this review can serve as a baseline and an incentive for future studies, helping to strengthen biodiversity monitoring programs, support conservation planning, and promote


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the integration of invertebrate fauna, particularly ants, into broader ecological and land-use discussions in southern Brazil.

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# 20

# THE WESTERN FRONTIER OF BRAZILIAN ANT DIVERSITY: CONTRIBUTIONS OF *REDE BIA* TO KNOWLEDGE ON ANT DIVERSITY IN THE SOUTHWESTERN AMAZON

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# ABSTRACT

Brazil is the country with the greatest diversity of ants. However, due to its vast size and uneven scientific development, there are still considerable areas with extensive gaps in diversity records. One of these gaps is the state of Acre, located in the southwestern Brazilian Amazon, which represents the western most frontier of Brazilian ant diversity. A total of 394 ant species has been recorded in Acre so far, which is relatively low compared to neighboring regions. In an effort to reduce knowledge deficits in insect biodiversity in the Amazon, the project "*Biodiversidade de Insetos da Amazônia (Rede BIA)*" conducted samplings at 16 sites across the region from 2014 to 2019. As a result, *Rede BIA* added 40 new ant species records for the state and 66 to the collection of the *Laboratório de Ecologia de Insetos*. With these and more recent contributions, the current number of recorded ant species in Acre has reached 479. Given the recent findings of ant occurrence and the lack of stabilization in the sampling efficiency in the Rede BIA project, a conservative estimate places the ant species richness in Acre between 750 and 800 species. Considering the high biodiversity value of unsampled areas in Acre, we proposed the implementation of 16 additional sampling sites to increase representativeness and approach the expected ant species richness. However, significant barriers remain, including insufficient funding for field expeditions and a shortage of myrmecologists in the region, both critical obstacles to reaching the expected number.

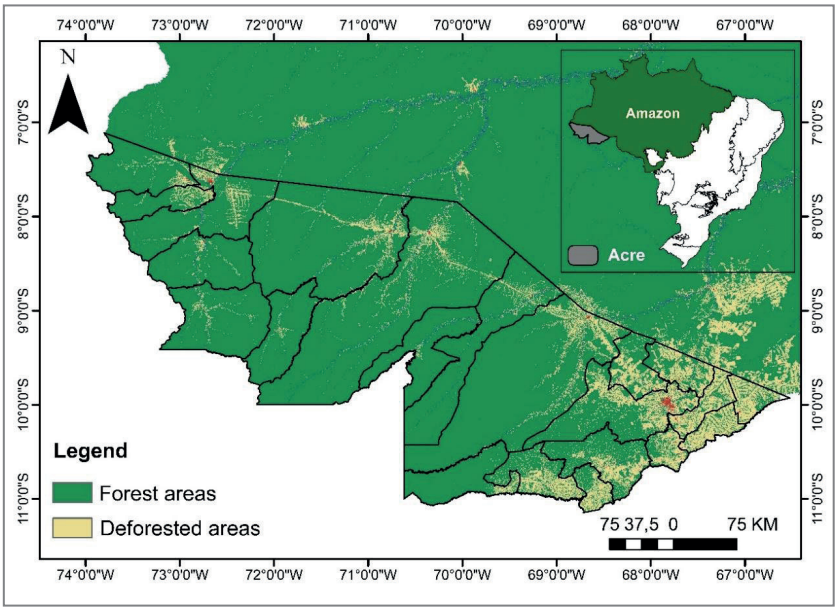
**Keywords:** Amazon; biodiversity; sampling efficiency; wallacean shortfall.

## INTRODUCTION

In Brazil, due to its vast territorial extension and inequalities in scientific development (STEGMANN *et al.*, 2024), knowledge about the geographic distribution of most species remains incomplete. This lack of information is referred to as the Wallacean Shortfall (LOMOLINO, 2004; HORTAL *et al.*, 2015), which hinders efforts to preserve biological diversity. The absence of accurate data can lead to inadequate conservation efforts. The state of Acre, the most portion of southwestern Brazilian Amazon, serves as an example of the Wallacean Shortfall for numerous terrestrial and aquatic organisms (CARVALHO *et al.*, 2023).

Acre is geographically located in a transition area between the eastern Andes Mountain range, the Central Amazonian lowlands and the northern Bolivian Savanna (SOUZA *et al.*, 2003), representing 4% of the Brazilian Amazon (ACRE, 2010). The diversity of soil types, topography, climate, and river basins endows the region with a remarkable heterogeneity of ecosystems and landscapes, which harbor an exuberant biodiversity (ACRE, 2010). Acre has a great variety of vegetation types, with open rainforests, palm trees, bamboo, and lianas covering most of the state (80%), although small patches of dense rainforest and white-sand vegetation are found mainly in the northwestern portion (ACRE, 2010; DALY *et al.*, 2016). Despite approximately 80% of Acre's original vegetation being conserved due to a diversified system of protected areas (ACRE, 2010), an intensive process of land occupation, mainly for pasture establishment has led to around 13% of the state being converted to human-modified landscapes (Figure 1) (INPE, 2024; MAPBIOMAS, 2024).

**Figure 1 -** Forest cover in Acre state, southwestern Brazilian Amazon in 2023.



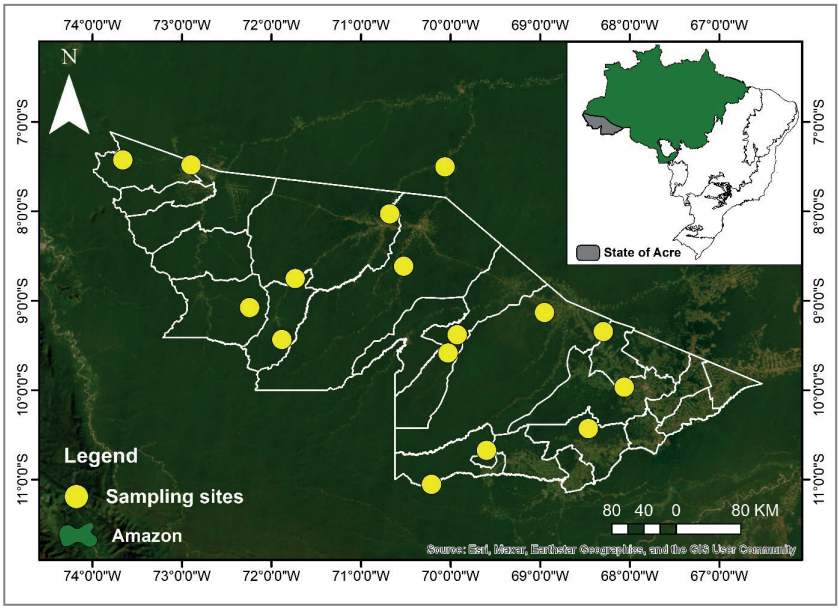

**Source:** MAPBIOMAS (2025).

Regarding the ant fauna, 394 ant species have been recorded in Acre so far (DUTRA *et al.*, 2024). In comparison to neighboring regions, such as Amazonas (717 species) and Peru (756 species) (JANICKI *et al.*, 2016), this represents a relatively low number of species. Although Acre is much smaller in size than these regions, its limited species record is likely not only related to its area but also to a lack of sampling in southwestern Brazilian Amazon (SCHMIDT *et al.*, 2022). Current sampling efforts are limited to areas surrounding Rio Branco (SCHMIDT *et al.*, 2020), the capital of the state and home to the main *campus* of the *Universidade Federal do Acre (UFAC)*, the primary research institution in the region.

Thus, aiming to reduce knowledge deficits in insect biodiversity in the Amazon, the "*Biodiversidade de Insetos da Amazônia* (*Rede BIA*)" project conducted ant samplings at 15 sites across Acre and one in southern Amazon from 2014 to 2019 (Figure 2). Specifically, we compared the ant fauna sampled by *Rede BIA* with previous records for Acre from the literature (*i.e.*, DUTRA *et al.*, 2024) and with records from specimens deposited in the ant collection of the *Laboratório de Ecologia de Insetos* (*UFAC)*. This comparison aimed to assess the increase in knowledge about the ant diversity in Acre and Brazil brought by

*Rede BIA*. Here, based on the contributions of *Rede BIA* and the recent paper by Dias and Feitosa (2024) on the myrmecofauna of Serra do Divisor National Park — western edge of the state of Acre, we present an updated list of ant species to Acre. Additionally, we evaluate the sampling efficiency of *Rede BIA,* and estimate the expected number of ant species for the state. Finally, we discuss the efforts required to uncover the true diversity of ants in Acre in the coming years.

**Figure 2 -** Sampling sites of *Rede BIA* project across Acre State an southern Amazonas, southwestern Brazilian Amazon.




**Source:** Authors collections (2025).

## DEVELOPMENT

### *Rede BIA* project

We delineated the 16 sites of *Rede BIA* across the region to achieve a geographically representative range regarding climate, soil types, hydrological basins and forest types (Figure 2). Ant sampling at these sites was carried out from 2014 to 2019, always in forest habitats. In each site, we distributed 10 plots along a transect of 200 m, with plots spaced 20 m apart. Each plot had an area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of 25 $m^2$, and in each one, we installed a pitfall trap on the ground surface, one on a tree trunk, and one underground (BESTELMEYER *et al.*, 2000; RIBAS *et al.*, 2003; SCHMIDT; SOLAR, 2010). Additionally, we collected a 1 $m^2$ litter sample. The pitfall traps remained in the field for 48 hours, and the ants in the litter sample were extracted using a mini-Winkler extractor for 48 hours. The ants collected from both the pitfall traps and the litter together formed the ant sample for each plot, while the set of ants collected in the ten plots (one transect) formed the ant assemblage for each sampling site, resulting in 16 sample units.

For genus-level identification, we used the key by Baccaro *et al.* (2015), and for the species-level identification, we compared our specimens with those in the ant collection of the *Laboratório de Ecologia de Insetos* (UFAC) and the *Museu de Zoologia da Universidade de São Paulo* (MZSP). We also received assistance from ant taxonomists: Lívia P. Prado, Mônica A. Ulysséa and Gabriela P. Camacho. All specimens have been deposited in the ant collection at the *Laboratório de Ecologia de Insetos.*

To verify the contribution of *Rede BIA* to the knowledge of Acre's ant fauna, we conducted two comparisons: i) with the ant species list for Acre from Dutra *et al.* (2024), and ii) with the ant collection of the *Laboratório de Ecologia de Insetos*. In both cases, we determined the number of species added and calculated overall dissimilarity ($\beta_{sor}$) and its components of turnover ($\beta_{sim}$) and nestedness ($\beta_{nes}$) (BASELGA, 2010).

To assess the sampling efficiency of *Rede BIA*, we used species accumulation curves. From a species presence-absence matrix, we determined the observed number of species at each sampling site. Additionally, we estimated the species richness for all the sampling sites (n = 16) using Chao2 estimator. Given the high number of rare species (only found in one sampling site, i.e., singletons), we opted for the Chao2 estimator as it accounts for rare species and can be derived from a species presence-absence matrix (MAGURRAN, 2011). The analysis was conducted using the vegan package (OKSANEN *et al.*, 2020) in R program (R Core Team, 2023).

### *Rede BIA* contributions

The *Rede Bia* project reported a total of 405 species, of which 152 were nominally identified and 253 were classified as morphospecies. Among the ants identified at species-level, *Rede BIA* is responsible for three new species records for Brazil: *Pseudomyrmex crudelis* Ward, 1999, *Stegomyrmex connectens* Emery, 1912, and *Strumigenys gundlachi* (Roger, 1862). Notably, *S. connectens* not only represents the first occurrence of the species in Brazil but also includes an undescribed worker of this species, which is only known from its queen and male.

**Figure 3 -** New ant species records for Brazil provided by *Rede Bia* project. A) *Pseudomyrmex crudelis* Ward, 1999. B) *Stegomyrmex connectens* Emery, 1912. C) *Strumigenys gundlachi* (Roger, 1862).

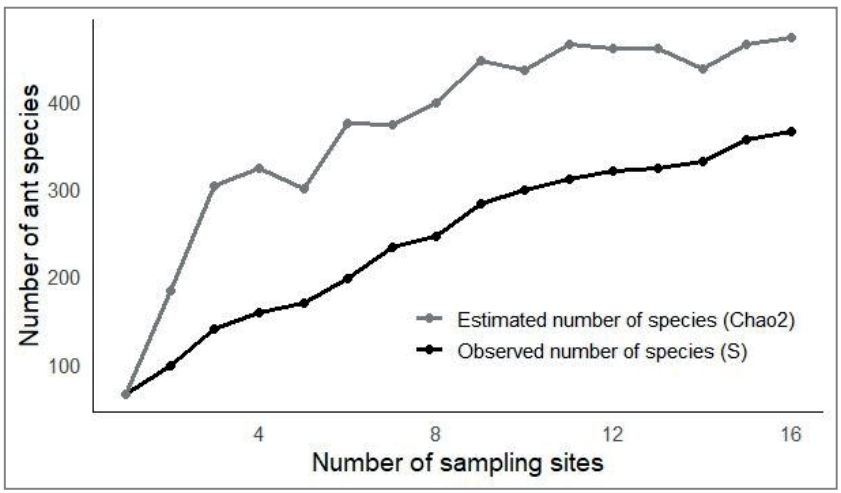
**Source:** Ant Web (2025). www.antweb.org.

The total dissimilarity between the ant fauna of *Rede Bia* and that reported by Dutra *et al.* (2024) was $\beta_{sor}$ = 0.59, with the turnover component ($\beta_{sim}$) accounting for 0.27 and the nestedness component ($\beta_{nes}$) for 0.32, which was the major factor contributing to this dissimilarity. In absolute terms, *Rede BIA* added 40 new ant species to the list previously registered by Dutra *et al.* (2024), increasing the ant species richness in Acre to 434.

The total dissimilarity between the ant fauna of *Rede Bia* and the ant collection records of the *Laboratório de Ecologia de Insetos (UFAC)* was 0.52, with the turnover component ($\beta_{sim}$) accounting for 0.43 and the nestedness component ($\beta_{nes}$) for 0.09. This indicates that the *Rede Bia samples* greatly expanded the material available for ant identification in Acre. In total, *Rede Bia* added 66 new species to the ant collection at UFAC.

Regarding the analysis of sampling efficiency, the total number of species observed across the 16 sampling sites was 365, and the estimated richness was 472,40. Both accumulation curves (Figure 3) showed a non-stabilizing trend, indicating that more ant species are likely to be found with increased sampling effort in the region.

**Figure 3 -** Sampling efficiency of the Rede BIA project in Acre State, southwestern Brazilian Amazon.




**Source:** Authors' collections (2025).

**Updated list of ant species in Acre and its potential richness**

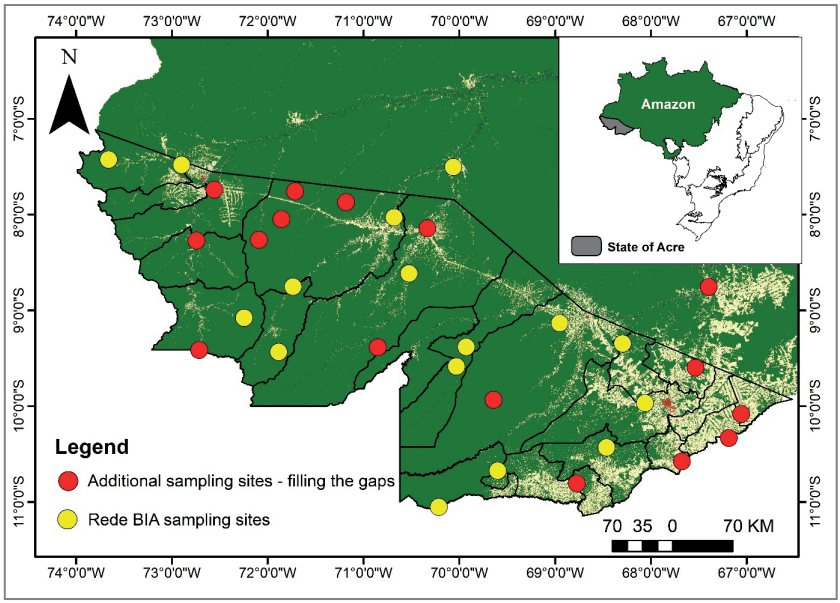
We compiled an updated list of ant species in Acre by incorporating the species occurrence records reported by Dias and Feitosa (2024) and the *Rede BIA* project to the list published by Dutra *et al.* (2024). We considered only once the occurrence of the ant species shared throughout the three species list (e.g. Dias and Feitosa 2024; Dutra *et al.* 2024; *Rede BIA* project). Altogether, these combined records resulted in a total of 479 ant species currently listed for the state of Acre (see Supplemental material: https://doi.org/10.6084/m9.figshare.29815364.v2). As an unorthodox attempt to calculate the potential ant species richness in Acre, we added the number of morphospecies sampled by *Rede BIA* (n = 253) to this compiled total, resulting in 732 potential species richness to the state. Thus, at a conservative approach, we can postulate that Acre would be the home of 750 – 800 ant species.

## FINAL REMARKS

Based on both the estimated species richness from the *Rede BIA* data and the summed potential species richness for Acre, all efforts made thus far have brought us to the midpoint of our journey in documenting the ant diversity in the state. The persistent sampling gaps that still exist in the state continue to reinforce the Wallacean Shortfall (HORTAL *et al.*, 2015). However, our results indicate that southwestern Brazilian Amazon is not only the western frontier of Brazilian ant diversity, but represents one of the highest richness documented for ants with the least sampling effort applied in a single locality worldwide (DIAS; FEITOSA, 2024).

To address the remaining knowledge gaps, we propose the establishment of 16 additional sampling sites (Figure 4, in red), designed to complement the efforts of the *Rede BIA* project (Figure 4, in yellow). According to the sampling relevance analysis provided by Schmidt *et al.* (2020), almost the entire Acre's territory has high sampling relevance due to its environmental heterogeneity and lack of ant surveys.

**Figure 4 -** Map showing the sampling design of the Rede BIA project (yellow dots) and the 16 additional sampling sites (red dots) in Acre State, southwestern Brazilian Amazon.




**Source.** Authors' collections (2025).

However, the effectiveness of this complementary sampling design in yielding new ant species records depend on overcoming two key drawbacks: i) securing financial support for biodiversity inventories, and ii) developing human resources specialized in ant diversity.

In terms of financial support, the Amazon region in Brazil receives the lowest level of funding for biodiversity research (STEGMANN *et al.*, 2024). Additionally, nearly all (90-92 %) of the limited funding available in the Amazon region goes to individuals (i.e., CAPES scholarships) and institutions (i.e., CNPq Universal Grants) in Belém and Manaus (STEGMANN *et al.*, 2024). This lack of financial resources lead to sampling efforts being predominantly restricted to easily accessible areas (CARVALHO *et al.*, 2023), thereby limiting the representativeness of biodiversity surveys in regions considered to be frontiers for Amazon biodiversity.

Thus, Brazilian and international funding agencies should create targeted calls to support research projects in regions that represent frontiers for Amazon biodiversity (CARVALHO *et al.*, 2023). However, this support should

be structured carefully to avoid scientific colonialism in the Amazon, such as the dominance of research groups from outside the region or well-established institutions in Amazon in approved projects. Importantly, these calls should allocate a significant percentage of funding for people and institutions based in remote corners of the Amazon, regions that are both biodiversity frontiers and face the greatest limitations in infrastructure and human-resources. One possible requirement could be proof of formal employment at Amazon-based institutions, such as universities and regional research centers, as a criterion for eligibility. This would help ensure that projects are led by professionals who live and work in the region.

Mirroring the trends in financial support, graduate programs focused on biodiversity-related fields, such as botany, ecology, and zoology, are primarily located in Manaus and Belém. In contrast, the *Universidade Federal do Acre,* which maintained a graduate program in Ecology for over 30 years, was ultimately forced close it due to difficulties in meeting the high standards set by *CAPES – Coordenação de Aperfeiçoamento de Pessoal de Nível Superior*. This situation perpetuates scientific colonialism in the Amazon, where knowledge of biodiversity in remote areas is often advanced by research groups based outside the Amazon or well-established groups from Manaus and Belém without significant involvement or leadership from local scientists.

Our research group - Ant Ecology Group at the *Universidade Federal do Acre* - has supported the graduation of eight master's students and contributed to four doctoral theses over the past 10 years. Most of the ant records in Acre have come from projects developed by the group. However, sampling the expected or the potential ant species richness suggested by our results remains a significant challenge for this group in terms of ant taxonomy and identification to the species-level. In this context, it is essential to strengthen collaborations with major centers of ant diversity research. In this chapter, such collaboration is evidenced by the co-authorship of taxonomists and by providing the names of consulted specialists and referenced collections (see also Acknowledgments section). Additionally, securing financial support is crucial for conducting sampling expeditions across the countryside of Acre, specifically for establishing the 16 additional sampling sites recommended above.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Acre also lacks centers or institutions for biodiversity research. Most of the existing biodiversity research is conducted by professors at the two *campi* of the *Universidade Federal do Acre,* located in Rio Branco and Cruzeiro do Sul. Since 2008, with the establishment of the *Instituto Federal do Acre*, more researchers have begun exploring the Acre's biodiversity. Regarding ant diversity, to effectively document the expected or the potential ant species richness mentioned above, we suggest the establishment of at least two more research groups led by scientists with permanent positions (*i.e.*, professor or researcher) in existing biodiversity research centers in Acre.

Therefore, the challenge is huge and overcoming it depends not solely on our efforts and actions but also on financial support and the creation of job opportunities in the region. Until then, the pace toward cataloging the full extent of Acre's ant biodiversity will be slow, but we will continue to track the trails of the ants in the southwestern frontier of the Brazilian Amazon.

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# 21

# ANTS FROM THE STATE OF PARAÍBA: PAST, PRESENT AND FUTURE

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# ABSTRACT

Myrmecological research in Paraíba, northeastern Brazil, has advanced significantly in recent years, but important knowledge gaps persist, particularly in the Caatinga biome. This study aimed to compile and analyze all available ant species records for the state, identifying spatial patterns of species richness and areas with sampling deficits. We conducted an extensive review of published articles, technical reports, and scientific collections, including both published and unpublished data. In total, 833 records were recovered from 91 unique sampling points, distributed across 43 municipalities. These records comprise 9 subfamilies, 58 genera, and 185 species of ants. Despite these gaps, the existing data provide a valuable foundation for understanding ant diversity in Paraíba. We highlight an urgent need for systematic sampling in underrepresented regions, employing standardized methods such as pitfall traps, leaf litter sifting, subterranean sampling, and vegetation surveys. The integration of genetic sequencing and georeferencing tools can further enhance species identification and distribution mapping. Moreover, expanding collaboration networks and training new researchers are essential to advance the field. We conclude that addressing these knowledge gaps is essential for a better understanding of ant biodiversity in Paraíba and for assessing their ecological roles in the face of climate change and habitat loss.

**Keywords:** Priority collection areas; formicidae; myrmecofauna.

## INTRODUCTION

Myrmecology has significantly advanced in Brazil in recent years, with particular emphasis on studies addressing the diversity and ecological role of ants within the context of environmental changes (Costa *et al.*, 2023; Lutinski *et al.*, 2023; Oliveira *et al.*, 2017; Rocha *et al.*, 2015). Currently, approximately 1,500 ant species are catalogued in the country (Baccaro *et al.*, 2015), and every year dozens of new species are described and numerous new records published (FEITOSA *et al.*, 2022). However, sampling efforts aimed at mapping the ant fauna have been highly uneven between biomes, regions and states in Brazil (Divieso *et al.*, 2020). Several factors may influence this phenomenon, such as the concentration of researchers in major urban centers, the scarcity of financial resources, and spatial limitations related to the difficulty of accessing remote or poorly studied regions. The Northeast region of Brazil, specifically the area north of the São Francisco River and including the state of Paraíba, exhibits both significant gaps in ant sampling and high rates of habitat loss, underscoring the urgency of conducting new local surveys (Divieso *et al.*, 2020).

The state of Paraíba, located in the Northeast region of Brazil, has a territorial area of approximately 56,467 km² (IBGE, 2024). This territory is divided into two main biomes: the Caatinga, which covers approximately 93% of the total area, and the Atlantic Forest, which is present in about 7% of the state (RAD, 2024). The Caatinga biome, which predominates in the interior of Paraíba, is characterized by a tropical semi-arid climate and by vegetation types that range from arboreal to shrubby Caatinga (Cortés-Ballén, Souza & Lima, 2022; Silva, Leal & Tabarelli, 2017). It is also notable for plant species adapted to water scarcity, such as cacti and bromeliads (Giulliete *et al.*, 2004). According to Francisco *et al.* (2016), rainfall in the state shows high spatial variability: in the Cariri and Curimataú regions, levels range from 300 to 500 mm; in the Sertão and Alto Sertão, the annual average is between 700 and 900 mm; while in the Agreste and Brejo regions, annual totals range from 700 to 1.200 mm.

The coastal portion of the state harbors significant remnants of the Atlantic Forest, predominantly composed of Montane Semi-deciduous Seasonal Forest formations and, to a lesser extent, Submontane Ombrophilous Forest (Cunha & Silva-Júnior, 2014). With its warm and humid climate, the coastal strip hosts


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the highest rainfall index in the state, with average annual precipitation ranging from 1,200 to 1,600 mm (Francisco *et al.*, 2016). According to the *Atlas dos Remanescentes Florestais da Mata Atlântica* (Fundação SOS Mata Atlântica & INPE, 2024), the original area of Atlantic Forest in Paraíba was approximately 599,000 hectares; currently, only about 53,755 hectares remain, which corresponds to 9% of the original native forest cover.

In the Atlantic Forest, recurring problems include the degradation of mangrove ecosystems, contamination of water resources by domestic and industrial sewage, and real estate speculation aimed at industrial facilities and housing developments (Alves *et al.*, 2012; Carvalho *et al.*, 2008; Maracajá *et al.*, 2010; Morais, 2014; Sales *et al.*, 2016; Pereira Filho, 2023). In the semi-arid region, between 1985 and 2020, the state lost approximately 280,000 hectares of native vegetation cover, corresponding to about 3% of the biome's native vegetation (MAPBIOMAS, 2021). This reflects a significant advance in the degradation process across 45 municipalities classified as Environmentally Susceptible to Desertification Areas in the region (MAPBIOMAS, 2021). The main drivers of degradation are goat farming, agricultural expansion, and real estate speculation resulting from rural exodus (Costa *et al.*, 2008; Sales *et al.*, 2016; Silva *et al.*, 2015).

Currently, according to the Global Ant Biodiversity Informatics Database (GABI) (Guénard *et al.*, 2017) available at antmaps.org (Janicki *et al.*, 2016), 104 species have been recorded in the state of Paraíba, based on data compiled from museum collections, literature records, and online databases, totaling 268 occurrence records. In this chapter, we present an overview of the state of myrmecological research in Paraíba, outlining its origins, development, and current status. We draw a timeline detailing the essential milestones of ant studies in the state, such as the first official record, seminal publication, and the most intensely surveyed areas (e.g. municipality with the most records, biome with the most records, micro-region of the state with the most sampling effort). In addition, we compiled records from public online databases, published literature, and material deposited at the Entomological Collection of the Department of Systematics and Ecology (DSEC) of the Federal University of Paraíba. From this dataset we estimate the number of subfamilies, genera and species recorded for the state and estimate priority areas for future sampling. We conclude with future directions for myrmecology in the region. In summary, this chapter is structured

around three central axes: (1) the history of myrmecology in Paraíba; (2) current diversity and spatial gaps in sampling; and (3) perspectives for advancing the field in the state.

## History of Myrmecology in Paraíba

The state of Paraíba is heavily affected by anthropogenic disturbances such as deforestation, slash-and-burn agriculture and overgrazing (Antongiovanni *et al.*, 2020). However, there is a significant gap in ant sampling in the state (Divieso *et al.*, 2021). Research on ants in Paraíba began in the early 20th century and has continued sporadically to the present (Silva *et al.*, 2022). The studies cover areas of the Caatinga, Atlantic Rainforest and Restinga, including different forest formations, such as highland swamps and Caatinga *stricto sensu* (Dantas *et al.*, 2022; Silva *et al.*, 2022; Dantas and Fonseca, 2024*)*.

The first official records of ants in Paraíba date back to 1916, following an expedition led by the English researcher William M. Mann (1916), and were followed by several studies led by German-Brazilian researcher Thomas Borgmeier (Borgmeier, 1923; Borgmeier, 1927). The first studies conducted by a Brazilian-born researcher also took place in the first half of the 20th century, with a focus on understanding taxonomy of *Acromyrmex* leaf-cutting ants, carried out by Cincinnato Rory Gonçalves (Gonçalves, 1961). In the second half of the 20th century, studies focused on the description and distribution of species continued, with rare studies examining ecological, behavioral, morphological or genetic aspects of ants (Kempf, 1971; Watkins, 1976). During this period, several notable myrmecologists conducted expeditions in Paraíba, part of an effort to map and describe ant species in Brazil, as German entomologist living in Brazil, Walter Wolfgang Kempf (Kempf, 1971).

In the first decade of the 21st century, species descriptions persisted (Lapolla, 2004; Feitosa & Brandão, 2008), associated with work focused on describing behavioral patterns (e.g. foraging and nesting) of ant species (Vasconcellos *et al.*, 2004). From the 2010's to present day, there has been an increase in the number of studies in Paraíba examining ecological questions, including diversity, biological community structure and population patterns of ants in Caatinga and Atlantic Forest areas (Silva and Brandão, 2014; Silva *et al.*,


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2017; Dantas *et al.*, 2022). Most studies were led by researchers from institutions outside the state or internationally, as the University of São Paulo, the Federal University of Pernambuco and the University of Oxford (Ulysséa & Brandão, 2013; Leal *et al.*, 2017), while little research has been carried out by researchers based in Paraíba institutions, for example, the Federal University of Paraíba (Vasconcellos *et al.*, 2004). This historical process is mainly due to the lack of training of new myrmecologists in the state.

Currently, there is only one researcher dedicated to the study of ants in the state: Professor José Domingos Ribeiro Neto (Federal University of Paraíba, *campus* II Areia), who holds a PhD in Plant Biology and has experience in ant-plant interactions, landscape ecology and ant community structure communities. His research is focused in both the Caatinga and the Atlantic Forest, and since 2017 he has been supervising students in the field of ant ecology. However, lack of resources and other limiting factors, such as insufficient funding for fieldwork, limited laboratories and infrastructure, have restricted the development of research focused on ants in the state.

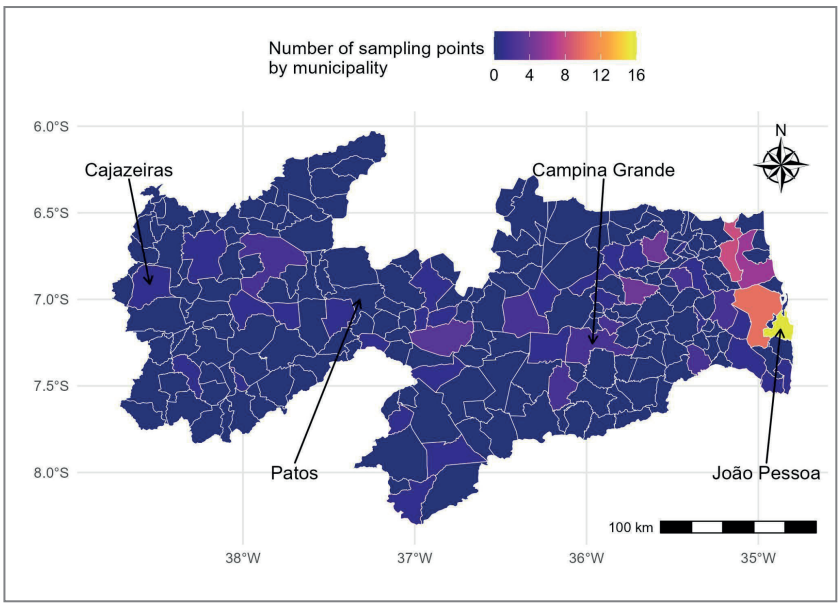
Many myrmecologists relocate to institutions in other states for their research, particularly at the graduate level. This is because Professor José Domingos is primarily responsible for supervising ant-focused studies within the state, and he usually does so only at the master's level. A reflection of these limitations in human resource training is that only one of the authors of this chapter completed a master's degree in the state under the supervision of Professor José Domingos, having built most of his academic career in the Northeast. This situation highlights not only the structural challenges but also the urgent need to strengthen local academic capacities. In essence, the consolidation of myrmecology in the state depends not only on overcoming logistical and financial constraints but also on fostering a new generation of researchers rooted in the region. Therefore, it is crucial to promote and incentivize the arrival of new faculty members, expand the training of master's and doctoral students focusing on ant ecology, and advance the internalization of higher education.

**Current diversity patterns and priority areas for further sampling**

To describe the diversity patterns of ants in the state of Paraíba, we compiled species distribution records from Antmaps (https://antmaps.org/) and accessed articles through a systematic search on Google Scholar and Web of Science, using the following combination of terms: "ants" and "State of Paraíba". The search resulted in six articles, listed below: Dantas & Fonseca (2023), De Sousa *et al.* (2015), Dantas *et al.* (2022), Dantas *et al.* (2024), De Kassia Muniz-Araujo *et al.* (2021), and Silva *et al.* (2022). In addition, we included information on the species deposited in the collection of the Department of Systematics and Ecology (DSEC) of the Federal University of Paraíba, João Pessoa *Campus*. The Hymenoptera collection at the DSEC Entomology Laboratory has approximately 5,000 deposited ant specimens. However, to date, only 972 ant specimens have been formally catalogued, of which 774 were collected in the state of Paraíba, distributed across 62 species, 36 genera, and nine subfamilies: Amblyoponinae, Dolichoderinae, Dorylinae, Ectatomminae, Formicinae, Myrmicinae, Proceratiinae, Ponerinae, and Pseudomyrmecinae.

A total of 833 records were compiled from 91 unique sampling sites distributed across 43 municipalities in the state (19.7%), while 180 municipalities remained unsampled (80.3%) (Figure 1). Our dataset contains only specimens identified at the species level, with names validated according to Antcat (https://antcat.org). These records span 9 subfamilies, 58 genera and 185 identified species (Table 1 - Supplementary Material). The subfamily Myrmicinae was the most common, accounting for 35.6% of the species and records. In contrast, the subfamilies Amblyoponinae and Proceratiinae were the least represented, with only one species each. The most frequently collected genera were *Pheidole*, with 49 records, followed by *Strumigenys* and *Dinoponera*, both with 48 records. At the species level, *Dinoponera quadriceps* (Kempf, 1971) was the most commonly collected, with 48 records, followed by *Strumigenys denticulata* (Mayr, 1887), with 16 records.

**Figure 1 -** Number of sampling points per municipality in Paraíba. Cool tones indicate a low number of sampling points and warm tones a high number of sampling points.




Sampling across the biomes present in the state seems relatively balanced at first, with 53 records in the Caatinga and 42 records in the Atlantic Forest (Figure 2). However, the Caatinga covers approximately 92.7 % of Paraíba's territory, while the Atlantic Forest comprises only 7.3 %. Despite being 11.5 times larger than the Atlantic Forest, the number of ant species recorded from Caatinga is only 1.26 times higher, revealing a disproportionate sampling effort. This discrepancy is presumably attributable to a historical endeavor to map the biodiversity of the Atlantic Forest at the expense of the Caatinga. In addition, the creation of research centers in the interior of the state (Caatinga regions) is recent, driven mainly by initiatives such as REUNI — a program aimed at restoring and expanding federal universities (https://reuni.mec.gov.br/) that began in 2007. For example, through REUNI, undergraduate courses in biological sciences and postgraduate courses in Biodiversity were created at UFPB's *Campus* II in the municipality of Areia (in the interior of Paraíba), where Professor José Domingos Ribeiro Neto, the only researcher dedicated exclusively to myrmecology, is currently based.

**Priority areas for new ant surveys in Paraíba**

Paraíba has experienced a substantial decline in its natural forest cover, as indicated by data from the MapBiomas project over the past three decades (Souza *et al.*, 2020). This is alarming, given that increasing deforestation is the main driver of species loss across different regions and biomes (Arnan *et al.* 2018, Dantas and Fonseca 2024). This necessitates prioritizing future surveys of ant distribution, taking into account historical sampling gaps and areas with high levels of habitat loss (deforestation). Furthermore, defining priority areas for new surveys can contribute to strategic planning for the use of resources, whether temporary or financial, which are specific limiting factors in the accumulation of knowledge about biodiversity (Blackburn and Gaston, 2003).

To identify priority areas for ant sampling in Paraíba, we used the index proposed by Divieso *et al.* (2020), defined as: UI: (P / Pmax) / (D / Dmax), where P is the habitat loss per area during a given time period, Pmax is the maximum recorded habitat loss, D is the estimated average sampling density for each area, and Dmax is the maximum recorded average sampling density. We chose to define our study area as the microregions of Paraíba, based on the IBGE definition (IBGE, 2016), as they are often defined by climatic and topographic conditions, as well as cultural and social factors that influence land use and anthropogenic disturbance regimes. Sampling density (D) was calculated as the average for each microregion of Paraíba obtained from values extracted from a Kernel map constructed with a resolution of 1 $km^2$ per pixel and a radius of 50 km around each sampling point. Habitat loss data were obtained from the MapBiomas project - Collection 9 [Land Cover and Use] (Souza *et al.*, 2020). Essentially, areas with high sampling urgency values exhibit high rates of habitat loss and low sampling densities, highlighting locations at greatest risk of biodiversity loss with limited existing documentation.

The urgency index (UI) ranged from 0.028 to 6.508 (Figure 3), a 232-fold variation in the priority of sampling between the state's micro-regions. The Cajazeiras micro-region, in the state's far west , has the highest urgency of sampling (urgency index (UI) = 6.508, habitat loss rate (P) = 0.144, sampling density (D) = 2.559), followed by the Itaporanga (UI = 5.046, P = 0.119 and D = 2.6954) and Umbuzeiro (UI = 3.417, P = 0.232 and D = 7.786) micro-regions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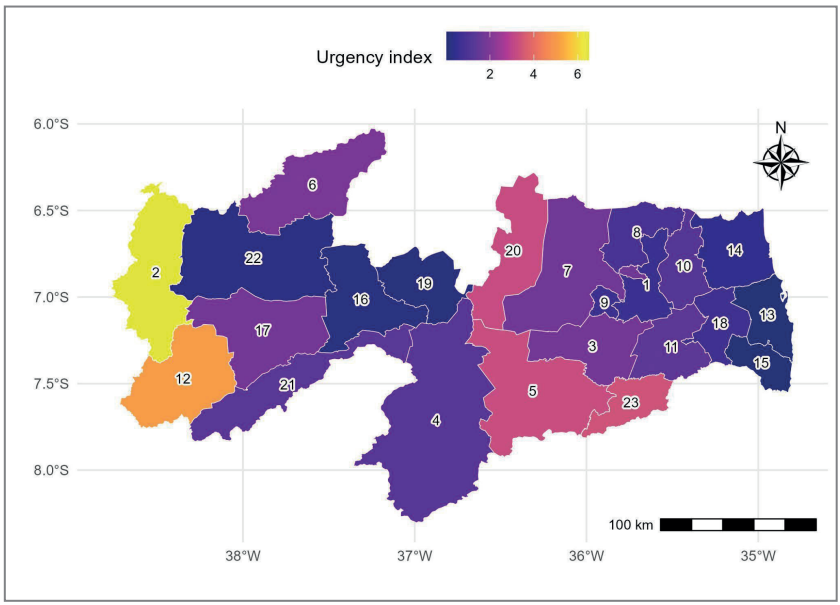
(Table 1). In contrast, the micro-regions of João Pessoa (UI = 0.028, P = 0.010 and D = 41.361), Litoral Sul Paraibano (UI = 0.037, P = 0.010 and D = 31.846) and Seridó Ocidental Paraibano (UI = 0.163, P = 0.010 and D = 7.198) had the lowest urgency indices (Table 1).

**Figure 2 -** Sampling urgency index (UI) by micro-region in Paraíba. Each micro-region is indicated by a number (code), in order: 1 - Brejo Paraibano, 2 - Cajazeiras, 3 - Campina Grande, 4 - Cariri Ocidental, 5 - Cariri Oriental, 6 - Catolé do Rocha, 7- Curimataú Ocidental, 8 - Curimataú Oriental, 9 - Esperança, 10 - Guarabira, 11 - Itabaiana, 12 - Itaporanga, 13 - João Pessoa, 14 - Litoral Norte, 15 - Litoral Sul, 16 - Patos, 17 - Piancó, 18 - Sapé, 19 - Seridó Ocidental Paraibano, 20 - Seridó Oriental Paraibano, 21 - Serra do Teixeira, 22 – Sousa, and 23 - Umbuzeiro. Cool tones indicate less urgent sampling, and warm tones indicate more urgent sampling.




Our results indicate an uneven distribution of ant surveys in Paraíba, with a strong concentration in the João Pessoa microregion, home to the state's capital and most populous city. In contrast, the western region is underrepresented, which is reflected in higher sampling urgency values. Densely populated areas tend to have more complete fauna and flora inventories, due to greater accessibility and the presence of a higher number of active researchers and research institutions (Hortal *et al.*, 2015). This compromises the current understanding of diversity patterns, as the concentration of surveys in easily accessible areas

(regardless of the actual species distribution) tends to favor the recording of abundant and common species (Grand *et al.* 2007; Boakes *et al.* 2010).

However, the uneven sampling distribution can significantly compromise the understanding of regional biodiversity and, consequently, support inefficient public policies for conservation. The Caatinga regions of Paraíba, which are less sampled, harbor a unique biological diversity and have species adapted to extreme environmental conditions. These areas are also likely more strongly affected by global climate change, since predictive models indicate an increase in average temperature and a reduction in precipitation over the coming decades (Pontes *et al.*, 2020). These factors could push many species to their physiological limits, increasing the risk of local extinctions and reducing the resilience of ecosystems (Nascimento *et al.*, 2022).

In addition, the absence of data from less sampled regions can introduce bias into conservation planning, underestimating the vulnerability of these areas and limiting the ability to mitigate environmental impacts. Future studies should, therefore, prioritize data collection in these regions, ensuring a more equitable representation of the state's biodiversity and allowing for a more accurate assessment of environmental impacts and conservation needs. In this way, expanding sampling in the Caatinga would not only contribute to a more comprehensive understanding of local biological diversity, but also strengthen ecosystem management strategies.

**Table 1 -** Sampling density values, habitat loss rate and urgency index for the micro-regions of Paraíba.

| Micro-region code | Paraíba micro-region | Sampling density (D) | Habitat loss rate (P) | Urgency index (UI) |
|---|---|---|---|---|
| 1 | Brejo Paraibano | 27.894 | 0.147 | 0.606 |
| 2 | Cajazeiras | 2.560 | 0.144 | 6.508 |
| 3 | Campina Grande | 15.518 | 0.240 | 1.777 |
| 4 | Cariri Ocidental | 5.506 | 0.060 | 1.250 |
| 5 | Cariri Oriental | 7.631 | 0.217 | 3.268 |
| 6 | Catolé do Rocha | 1.556 | 0.025 | 1.865 |
| 7 | Curimataú Ocidental | 13.970 | 0.211 | 1.734 |
| 8 | Curimataú Oriental | 19.496 | 0.154 | 0.908 |
| 9 | Esperança | 20.618 | 0.116 | 0.648 |
| 10 | Guarabira | 35.081 | 0.363 | 1.190 |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| Micro-region code | Paraíba micro-region | Sampling density (D) | Habitat loss rate (P) | Urgency index (UI) |
|---|---|---|---|---|
| 11 | Itabaiana | 26.882 | 0.319 | 1.365 |
| 12 | Itaporanga | 2.695 | 0.119 | 5.046 |
| 13 | João Pessoa | 41.361 | 0.010 | 0.028 |
| 14 | Litoral Norte | 35.847 | 0.138 | 0.442 |
| 15 | Litoral Sul | 31.846 | 0.010 | 0.037 |
| 16 | Patos | 6.327 | 0.010 | 0.184 |
| 17 | Piancó | 5.248 | 0.081 | 1.770 |
| 18 | Sapé | 41.746 | 0.260 | 0.716 |
| 19 | Seridó Ocidental Paraibano | 7.198 | 0.010 | 0.163 |
| 20 | Seridó Oriental Paraibano | 6.885 | 0.193 | 3.224 |
| 21 | Serra do Teixeira | 3.818 | 0.043 | 1.297 |
| 22 | Sousa | 4.594 | 0.010 | 0.255 |
| 23 | Umbuzeiro | 7.786 | 0.232 | 3.417 |

## The future of Myrmecology in Paraíba

Myrmecology in Paraíba is currently in a flourishing stage of development, but substantial knowledge gaps remain regarding ant species distribution (Wallacean deficit), population dynamics and abundance (Prestonian deficit), taxonomy (Linnean deficit) and evolutionary relationships (Darwinian deficit. These deficits are particularly pronounced in the Caatinga regions of the state's far west, where large areas remain vastly unexplored. This scenario represents a huge challenge in view of climate change and biodiversity loss, while it represents opportunities for new research focused on mapping Paraíba'sant, with the potential to expand the known distributions of many ant species in Brazil, describe new taxa and investigate relevant ecological questions. Advancing myrmecological research in the state could be accelerated with the use of modern data collection methodologies, such as specialized traps for different strata (e.g. subsoil, leaf litter and vegetation), genetic sequencing technologies and geospatial analysis. However, we argue that the main driver for advancing myrmecology in Paraíba is the expansion of human resource training through the establishment of new researchers and the expansion of partnerships for

new collections and research within the state. Future research should focus on the interface between ant fauna mapping and the impacts of climate change, including the impact on ecological interactions and the delivery of ecosystem services (e.g. seed dispersal).


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# People and Ants

# 22

# WOMEN'S JOURNEY THROUGH MYRMECOLOGY: AN INSPIRING STORY

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# ABSTRACT

Historically, science has been dominated by men. Despite some advances throughout history, recent studies highlight the underrepresentation of women in STEM fields, including Myrmecology. While ant colonies are female-dominated, scientific production in this field is the complete opposite, not only male-dominated but also far from achieving gender equity. In Brazil, only 20 out of 70 Myrmecology laboratories are coordinated by women. This is reflected in the low rate of women in senior research positions, often they abandon their scientific careers early, before completing undergraduate studies. As in society, women's persistence and involvement in the academic environment are hindered by barriers including pervasive belittlement harassment and societal stigmas around motherhood and family responsibilities, compounded by insufficient institutional support. Nevertheless, many women have overcome these challenges, making significant contributions to Brazilian Myrmecology. This chapter aims to highlight some of the many inspiring stories. Just as these stories have inspired us, we hope that new ones will emerge and inspire a new generation of myrmecologists.

**Keywords:** Ants; equity; gender disparity; woman in science.

## INTRODUCTION

A queen ant descends to the ground and searches for a place to nest. Once she settles and finds food, she lays the first brood, and thus a new ant colony is born. The subsequent steps will be carried out by the worker ants, all of which are female. In greater numbers, they are responsible for caring for the offspring, maintaining, and growing the colony. Without them, nothing presented in this book would have been documented.

Although the all-female workers make up the majority of ant colonies and their labor force is widely recognized, the story in the field devoted to studying them looks a little different. The term "Myrmecology," referring to the study of ants, was first used in 1910 by a man, William Morton Wheeler (Georgiadis & Trager, 2015) and similarly, the first recognized myrmecologists were also European and American men who studied ants between the late 19th and early 20th centuries (Lucky *et al.*, 2020). The first ant species of the Brazilian fauna were described around the 19th century (Baccaro *et al.*, 2015), and although ant taxonomy is entirely based on female workers, of the 117 genera currently described for Brazil (Feitosa & Dias, 2024), only seven have women as authors or co-authors (*Amoimyrmex* Cristiano *et al.*, 2020; *Bazboltonia* Camacho & Feitosa, 2022; *Corrieopone* Esteves & Fisher; *Cyatta* Sosa-Calvo *et al.*, 2013; *Gracilidris* Wild & Cuezzo, 2006; *Kalathomyrmex* Klingenberg & Brandão, 2009; and *Xerolitor* Sosa-Calvo *et al.*, 2018). This scenario has been changing in recent years, with a series of review works published under the leadership of women (Cuezzo, 2000; De Andrade, 2001; Klingenberg & Brandão, 2009; Fernandes *et al.*, 2014; Jesovnik & Schultz, 2017; Oliveira & Feitosa, 2019; Ladino & Feitosa, 2020; Barrera *et al.*, 2022; Oliveira *et al.*, 2021; Ulysséa & Brandão, 2021; Dias & Lattke, 2021; Camacho *et al.*, 2020 and 2022). Although we can observe advances, whether in taxonomy or other areas of myrmecology, women remain a minority in the community compared to men (Lucky *et al.*, 2020). Moreover, they are fewer in number among the first and last authors of papers, with the latter being an important detail since it is usually associated with the coordination of research groups (Ramalho *et al.*, 2020a). In Brazil, for example, of the 70 laboratories working with ants, only 20 have women in leadership positions.


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But why are the numbers so disproportionate? Myrmecology, as a branch of society, is not immune to the issues that plague it. Male dominance persists across many facets and becomes even more evident in the subfields, where women must constantly prove themselves to secure increasingly scarce positions. Yet, to achieve the same goals as men, women often face obstacles in their trajectories due to sexism and machismo. These result in moral and sexual harassment, stereotyping, embarrassment, discrediting, as well as imposter syndrome and all the associated mental health issues that ultimately drive women away from academia lead to the end of their careers. Despite the obstacles and male predominance, some women began to engage in the study of ants in Brazil as late as the 20th century, opening doors and clearing trails for all of us who came after.

**The pioneer queens**

A pioneer not only in the study of ants but also for women in Brazilian scientific research, Elena Maria de Oliveira Diehl was born in 1949 in Porto Alegre, the capital of Rio Grande do Sul. Encouraged by her parents to study from an early age, Elena Diehl graduated in Natural History from the Universidade do Vale do Rio dos Sinos (UNISINOS) in 1970. The following year, she enrolled in a Master's program in Genetics at the Universidade Federal do Rio Grande do Sul (UFRGS), completing it in 1972. Shortly after her postgraduate studies, she began her career as a full professor at UNISINOS. Her remarkable journey in Myrmecology began in 1982 when she founded the Laboratório de Genética de Insetos Sociais, becoming one of the first women to lead a research laboratory in the country. Elena was a pioneer in multiple aspects: not only did she pave the way for other women in science, but she was also the first researcher to investigate the use of entomopathogenic fungi to control leaf-cutting ants, with an emphasis on the genus *Acromyrmex*. Her work extended across various areas of myrmecology, including genetics, evolution, reproductive biology, ant-plant interactions, and the ant fauna of Rio Grande do Sul; which has yielded the publication of nearly 100 works, among them articles, chapters, and books like "Formigas: Organização social e ecologia comportamental" (Diehl-Fleig, 1995). Her contribution was so significant that she founded what is now known as

the International Symposium on Myrmecology. Throughout her 36-year career, Elena took on essential roles: she was a researcher, professor, department head, course coordinator, and advisor to over 64 students, many of whom now work in institutions across Brazil and remember her affectionately for the dedication she bestowed upon them. Amid all these achievements, Elena also raised three children, introducing them early to the world of ants. One of them, Eduardo, followed in her footsteps and became her co-author on numerous works. Though no longer with us, Elena Diehl's legacy as a myrmecologist, scientist, professor and mother endures as an inexhaustible source of admiration and inspiration for present and future generations (Albuquerque *et al.*, 2020).

Terezinha Maria Castro Della Lúcia is another example. Following in the footsteps of her father, she earned her degree in Biology from Purdue University in the United States, far from her hometown of São João Nepomuceno in Minas Gerais, Brazil. After four years abroad, Terezinha returned to Viçosa in 1977, where she grew up and still lives today, now retired. She began her studies at the Universidade Federal de Viçosa (UFV), focusing on leaf-cutting ants, which became her lifelong passion. After completing her master's and doctoral programs, she became a full professor at UFV in 1987 and founded a research group dedicated to understanding the behavior and biology of leaf--cutting ants, with an emphasis on their control. As one of the first women to research leaf-cutting ants in Brazil and a pioneer in Brazilian myrmecology, her career paved the way for other female researchers in the field. Her research on controlling became essential references on the subject, particularly her book "Formigas cortadeiras: da bioecologia ao manejo" (Della Lucia, 2011) and the article "Managing leaf-cutting ants: peculiarities, trends and challenges" (Della Lucia *et al.*, 2014). While carving her path in myrmecology, Terezinha became a mentor for a generation of students, from undergraduates to doctoral candidates. She understood the unique needs of each student, providing not only academic guidance, as a dedicated and meticulous advisor, but also personal support, whether as friend or even financial assistance when needed.

Also from Minas Gerais is the pioneer in the study of urban ants in Brazil. Ana Eugênia de Carvalho Campos was born in the capital state, Belo Horizonte, and began her academic journey at the Universidade Federal de Uberlândia (UFU). Although Minas is her hometown and where she became a biologist, it


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was in the state of São Paulo that the trail of ants crossed her path. Her career in myrmecology began in 1989 when she enrolled in a master's program at Universidade Estadual Paulista Júlio de Mesquita Filho (UNESP) in Rio Claro. Ana studied ants of the genus *Solenopsis* and, in the process, became interested in invasive ants. After completing her Ph.D. at the same institution, in 1997 Ana Eugênia passed the selection process for the Instituto Biológico de São Paulo. From then on, driven by the curiosity sparked during her postgraduate studies, Ana established a research line focused on the identity, distribution, impacts, ecology, and control of urban ants. Her contributions in studies, such "As formigas urbanas no Brasil: Retrospecto" (Campos *et al.*, 2002) were pivotal to our current understanding of these insects in the country's urban areas, a subject that impacts not only myrmecology but society as a whole. Today, in addition to being a mother, researcher, and advisor, Ana Eugênia is the General Director of the Instituto Biológico under the Secretaria de Agricultura e Abastecimento do Estado de São Paulo, an important milestone in the representation of women in leadership roles within major institutions.

In taxonomy, Ana Yoshi Harada was the first to make her contributions. She began her studies on ants in 1982 at the Instituto Nacional de Pesquisas da Amazônia (INPA), where her master's thesis updated knowledge on the distribution and ecology of the genus *Azteca*, often associated with *Cecropia* plants. In 1984, Ana moved to Curitiba to complete her doctorate at the Universidade Federal do Paraná, focusing on the taxonomy and systematics of the tribe Tapinomini. Her work included redescribing genera, describing new ones, creating identification keys, and proposing a phylogeny for the group. In 1996, she became a senior researcher at the Museu Paraense Emílio Goeldi (MPEG), where she still works today. During her years at MPEG, Ana curated one of the most important neotropical ant collections in Brazil and remains a key figure in the study of the Dolichoderinae family.

Ecology is the primary field for ant studies in Brazil and has the highest number of women researchers. In this context, we highlight the story and contributions of Inara Roberta Leal. Inara Leal, a native of Florianópolis in southern Brazil, began her ant research at the Universidade Federal de Santa Catarina (UFSC) during her undergraduate studies. In 1992, she moved to state of São Paulo, earning her master's and doctorate at the Universidade de Campinas

(Unicamp), where she studied the behavioral ecology of *Pachycondyla marginata* and the natural history of Attini ants in the Cerrado. In 2002, Inara became a professor in the Botany Department at the Universidade Federal de Pernambuco (UFPE), where she still works today as a professor and coordinator of the Laboratório de Interação Planta-Animal (LIPA). With over 30 years of experience in myrmecology, Inara's career features pivotal contributions to ecology, using ants as a model to study habitat loss and conservation, for example the work "Effects of habitat fragmentation on ant richness and functional composition in Brazilian Atlantic forest" (Leal *et al.*, 2012). Her studies are critical for their focus on highly threatened biomes, such as the Caatinga and Atlantic Forest.

Cléa dos Santos Ferreira Mariano, born in Bahia, and became the first woman to use cytogenetics as a tool in ant taxonomy. She earned her degree in Biology from the Universidade Estadual de Santa Cruz (UESC) and her interest in ants began in this period, while helping a friend collect nests of Ectatomma tuberculatum. Focused on the morphology of these creatures, Cléa began observing individuals with malformations, most likely caused by genetic mutations. Her desire to understand the origin of these anomalies and the genetics behind such patterns led her to turn her curiosity into a research focus. During her master's and Ph.D., both completed at the Universidade Federal de Viçosa, she used cytogenetics to study the diversity and evolutionary relationships within Formicidae. In 2008, Cléa became a Professor at the very university that trained her as a biologist, the UESC. There, she founded the Laboratório de Artrópodes Sociais (LABAS) and continued her research while mentoring undergraduate and graduate students. Today, Cléa has grown interested in the diversity of commensal organisms near ant nests. Her research, such as "Contribution of cytogenetics to the debate on the paraphyly of *Pachycondyla* spp. (Hymenoptera, Formicidae, Ponerinae)" (Mariano *et al.*, 2012), serves as a reference for ant cytogenetics studies and her career serves as an inspiration for women, especially mothers and those from Brazil's Northeast.

All the woman cited here, and many other examples such as Maria de Lurdes de Andrade and Maria Jose Aparecida Hebling dared to soar, teaching all of us how to take flight. Through their research and legacy, they have encouraged and inspired other women to enter the world of ant studies, showing that despite men being more numerous and widely recognized, the women's


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contributions have been essential not only to the construction of knowledge about Brazil's ants but also to the building of our myrmecological community.

**Scenario over the years**

The following data were collected by the authors from a widely circulated survey within the myrmecological community, targeting women who currently work or have worked with myrmecology in Brazil. The questionnaire was distributed via email and social media to various laboratories and myrmecologist centers across Brazil, aiming for broad diversity coverage. The form is available as supplementary material (https://doi.org/10.6084/m9.figshare.29906423.v2). A total of 72 responses were obtained.

Regarding age, women over 35 are the majority (63.2%), while about one-third (36.8%) are between 18 and 34 years old. Most of them hold a doctorate (65.3%), with the rest still in some stage of their education, from undergraduate to doctoral studies. These numbers show that women have long played a significant role in ant studies in Brazil while also indicating a promising future for a new generation of female myrmecologists.

They are predominantly Brazilian (95.8%), and there are also representatives from Colombia (2.8%) and Argentina (1.4%) contributing to the study of Brazilian fauna. In Brazil, although all regions of the country are represented, the largest number of myrmecologists comes from South (39,6%) and Southeast (35,4%), while the Northeast (14,6%), Central-West (6,2%) and North (4,2%) regions have the lowest representation. Although part of this disparity may result from the survey's limited reach beyond the southern regions, it may also reflect the broader reality. These numbers align with the well-documented regional imbalance in the distribution of scientific and technological resources in Brazil, driven by historical investment patterns that have concentrated research institutions and public universities in the southern regions (Barros, 2000). This scientific centralization is likewise evident in myrmecology.

As for the region where these women's research activity is concentrated, the same pattern mentioned above can be observed, with the highest number of responses for Southeast (54.7%) and South (34.7%) regions, while Northeast (20%), North (18,7%) and Central-West (13.3%) regions have lowest

numbers. In terms of research areas, most women work in Ecology/Conservation (62.7%), followed by Taxonomy and Systematics (38.7%), Behavior and Natural history (28%), with the lowest representation in applied studies (16%). Both of these questions allowed for multiple responses, meaning women could have conducted their research in more than one Brazilian region and worked in more than one area.

Regarding ethnic-racial identity, 69.3% self-identify as White, 22.6% as Brown, 6.6% as Black, and 1.3% as Indigenous. For comparison purposes, the Brazilian population as a whole is predominantly Brown (45.3%), followed by 43.5% White, 10.2% Black, 0.6% Indigenous, and 0.4% East Asian (IBGE, 2023). We know that a number of reasons may be related to the low representation of non-White women in myrmecology. Some of them may even be related to the low career profitability. However, this pattern found in our form is reflected in data from Brazilian higher education, where White are the majority (25.8%), followed by Brown (12.3%) and Black (11.4%) (IBGE, 2022), indicating that beyond all the reasons, access to higher education (where most research is developed in Brazil) for non-white women needs to be expanded and maintained, as a way of expanding career possibilities.

All participants self-identify as cisgender women. Regarding sexual orientation, the majority (69.3%) identify as heterosexual, followed by bisexual (26.7%), homosexual (2.8%), and pansexual (1.4%) (the answers did not include other options). These numbers indicate low representation of sexual minorities in the sample of women who responded to the survey. We emphasize the need to incorporate the full spectrum of recognized gender identities and sexual orientations in future studies, enabling a more accurate assessment of diversity in Brazilian myrmecology. Additionally, we urge critical reflection on how the academic community ensures equitable access and fosters a sense of belonging in these spaces.

Our survey also collected data on the marital status of myrmecologists. About half of the women reported being single (53.3%), 38.7% are married, and 8% are divorced. Regarding motherhood, 39% of myrmecologists have children. Studies show that marital status, and especially motherhood, significantly impact women's careers (McIntosh *et al.*, 2012; Machado *et al.*, 2019; Torres *et al.*, 2024). This is because, in addition to dealing with all the challenges of the profession,


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at home they are still primarily responsible for domestic tasks and childcare. Ramalho *et al.* (2020b) emphasize the impact of parenthood on the lives of myrmecologists (both men and women), particularly in fieldwork, lectures, and participation in events. Although the study addresses both genders, the arrival of children has a much more negative impact on women's careers compared to men's (Machado *et al.*, 2019).

We also sought to understand the main obstacles faced by women during their careers in myrmecology. This question allowed for multiple responses. Among the most cited obstacles, mental health issues ranked first (41.3%), most likely influenced by one or more of the other challenges, such as harassment or uncomfortable situations (40%), social inequality (37.3%), sexism (25.3%), motherhood (14.7%), racism and xenophobia (5.3%), wage inequality (4%). These results highlight the persistence of well-known unsafe and hostile environments towards women in academia. For example, the high frequency of mental health issues may indicate the cumulative impact of these structural and interpersonal challenges throughout their careers.

This is the first step to assess the profile of female myrmecologists in Brazil. We acknowledge that the data are based on a preliminary survey with a limited number of respondents and therefore do not fully represent the entire myrmecological community. However, they provide an initial overview that may be refined and expanded as new data are collected. Our goal is not to discuss theoretical foundations or to propose affirmative policies, but to begin understanding who these women are and the challenges they face. We encourage and look forward to further research in this area, as well as deeper discussions advocating for women in STEM.

## VOICES IN THE ANTHILL: CONTEMPORARY WOMEN MYRMECOLOGISTS AND THEIR PATHWAYS

The presence of women in Brazilian myrmecology is advancing slowly but steadily, like some ants. A study by Lucky *et al.* (2020) identifies Brazil as one of the countries with the highest number of female authors in publications from 2008 to 2017. Additionally, the traditional Formigas do Brasil Course has consistently had more women as participants (CFB, 2024). While women are

active in symposia and conferences, their representation in leadership roles remains a key issue. A positive sign is the increasing participation of women as speakers at the world's largest myrmecology event, the International Symposium on Myrmecology, reached gender parity for the first time in the 2023 edition in Manaus. We know that small victories should be celebrated, but there is still much work to be done. That said, in the following texts we aim to honor and share the stories of some women in Brazilian myrmecology who have inspired the authors to reach where we are today, hoping to motivate more people to pursue and succeed in myrmecology, further advancing gender equity in science.

**Aline Machado de Oliveira**

Aline Machado de Oliveira, born in Campo Mourão, in the midwest region of Paraná. Grew up in São Paulo, in the city of Cruz das Posses, and as a child, she moved with her family to São José dos Pinhais, in the metropolitan region of Curitiba. Aline had the opportunity to take a free preparatory course for university admission exams and, in 2013, she began her journey in Biological Sciences at the Universidade Federal do Paraná (UFPR), in Curitiba. During her undergraduate studies in Biology, she became interested in several areas, but it was in myrmecology that she found her true vocation, in the recently opened Laboratório de Sistemática e Biologia de Formigas at UFPR. She began her career as a researcher at a very young age, carrying out her first scientific initiation with the ant fauna of the Cerrado State Park, in Jaguariaíva, Paraná, being a pioneer in the study of ants in this region. While still an undergraduate, Aline forged her path in taxonomy, revising the genus *Probolomyrmex* in the Neotropics and describing four new species (Oliveira & Feitosa 2019).

Always questioning and with a restless mind, Aline always knew, deep down, that she could change the world in her own way. In her dissertation defense, she broke with the technical standards of academic presentations and presented her results in a didactic and accessible way for everyone. Among the spectators were her students from the free preparatory course "Em Ação", the same program where she had once been a student herself, and to which she


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later returned as a volunteer teacher. The project seeks to promote equitable access to higher education for students from low-income backgrounds.

In 2018, she started her master's degree and dedicated herself to studying the genus *Cephalotes*, whose taxonomic revision had not been updated since the late 1990s. In this revision (Oliveira *et al.*, 2021), Aline described five new species and named them after women myrmecologists who are, or have been, admirable taxonomists. In fact, the reception to this work was so positive that the article became the model for formatting taxonomic papers by the Brazilian Journal of Entomology. During her time in the laboratory, Aline also actively participated in the project "Scientists at School," disseminating science and myrmecology to students from municipal schools in Curitiba. In all the spaces she has occupied, she always contributed to the strengthening and even creating a fairer and more inclusive scientific culture, promoting gender equity in science.

With great courage and determination, Aline has never stuck to her "comfort zone". During the uncertainties of the COVID-19 pandemic, she took on new challenges and moved to Hong Kong, where she held the position of curator of the Hong Kong Biodiversity Museum for four years. Today, with over 10 years of experience in myrmecology, she is a PhD candidate at George Washington University, in the Powell Lab, where she will continue her taxonomic research with her turtle ants (*Cephalotes*). Aline inspires us and shows that an academic career does not need to be linear, and that each path is unique. Her dedication and curiosity about life make her unique and fascinating, just like the ants she studies.

**Amanda Batista da Silva de Oliveira**

A brilliant Black scientist from Rio Branco, in the state of Acre, Amanda Batista da Silva de Oliveira is an inspiring example of how a passion for nature can transform one's journey. A master's graduate in Ecology from the Universidade Federal do Acre (UFAC), Amanda took her first steps in the study of ants during her master's program, where she investigated

the diversity of ant assemblages in the canopies of Brazil nut trees (*Bertholletia excelsa*) across different Amazonian environments (Oliveira & Schimidt, 2019).

Her interest in these tiny insects emerged during a graduate course. It was during this period that Amanda discovered the fascinating world of ants. The enthusiasm and passion conveyed during the lectures sparked a deep interest in her, and she became captivated by the complexity and importance of these creatures.

At that time, Amanda was facing challenges with her previous advisor, but upon discovering the captivating world of ants, she made the bold decision to change the direction of her studies. She chose to join a completely new research group, immersing herself fully in the study of ants. This decision not only defined her academic path but also opened doors to a profound understanding of the immense diversity of these small beings.

Amanda earned her PhD in Zoology from the Universidade Federal do Amazonas (UFAM), where she focused on the biogeography and evolution of ant assemblages in white-sand forests, one of the most unique environments in the Amazon. Her research has significantly advanced scientific knowledge about these ecosystems, highlighting the importance of preserving these singular areas (Oliveira *et al.*, 2023; Oliveira *et al.*, 2025). In addition to research, Amanda also dedicated herself to teaching.

For Amanda, the fascinating world of ants has not only provided her with valuable knowledge but also allowed her to meet incredible people and visit extraordinary places. Her scientific journey is marked by perseverance and curiosity, traits that make her a true professional in science and inspiring future scientists to follow in her footsteps.

**Amanda Martins Dias**

Amanda Martins Dias was born in Anápolis, Goiás. Born and raised in the heart of the Cerrado, she says that the first genus of ants she learned to recognize as a child was the imposing *Dinoponera*, abundant in the region. Motivated to be a biologist during her teenage years by the


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work of the Canadian NGO Greenpeace, she entered the Biology school at the Universidade Estadual de Goiás (UEG) in her hometown in 2013, and in her first year of college, she became a member of the laboratory of professor Dr. Hélida Ferreira da Cunha, a great termitologist who also guided students in research with other groups of insects.

Hélida suggested that she begin studying ants, being responsible for creating a myrmecological collection for the educational institution through a scientific initiation in 2014. The doubts and interest in the group generated by the development of the collection led Amanda to discover the Formigas do Brasil Course (CFB) through social networks, which she participated in 2014 through financial support from her scientific initiation scholarship and her tutor.

As she studied in a city far from the big myrmecology centers in the southeast and south regions, Amanda saw the course as a great opportunity to meet other researchers in the area and start a network of collaborations. After graduating as a biologist in 2016 and encouraged by Aline Oliveira, whom she met during the CFB, the researcher entered her master's degree in Entomology at UFPR, in Curitiba, where she developed the taxonomic review of the genus from her childhood memories, *Dinoponera* (Dias & Lattke, 2021).

Completing the review of the genus in 2019 and completely fascinated by Ponerinae, Amanda decided to pursue taxonomy in her doctorate, developing the taxonomic review of one of the most challenging genera of the subfamily in terms of identification and species delimitation: *Hypoponera*. Still at UFPR, but under different guidance, she reviewed the species of the genus that occur in the Brazilian Atlantic Forest, identifying and describing several new species.

Highlighting her brilliant performance in the taxonomic review of the largest and smallest Ponerinae and her collaboration in updating the identification keys for the subfamilies and genera of ants that occur in Brazil, the researcher is currently a Postdoctoral student at the California Academy of Sciences, in San Francisco, where she is combining her taxonomic knowledge with studies with molecular data to investigate a group of *Hypoponera* species from the island of Madagascar and also refine information about this and other groups of ants.

The challenges that the researcher decided to face throughout her career demonstrate the fearless and determined person that Amanda Dias is and did

not lead her to become a great Greenpeace activist, but they definitely made her a great inspiration as a scientist.

**Carla Rodrigues Ribas**

Carla Rodrigues Ribas is originally from São Paulo city, in the state of São Paulo, but her academic career led her to the state of Minas Gerais, where she made the Universidade Federal de Viçosa (UFV) her home. From 1995, when she began her studies in Biology, until 2006, when she obtained her Ph.D., her path deepened in different areas of ecology: mosaic vs. competition with arboreal ants, latitudinal gradient of species richness, and ants as bioindicators in different Brazilian biomes. Bit by bit, Carla became a recognized figure in the field of ant ecology.

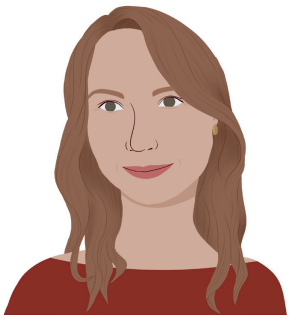
She is not only an admirable researcher, but also an excellent mentor to students. Many students who passed through her lab at the Universidade Federal de Lavras (UFLA) have gone on to become myrmecologists and are now professors and researchers in different regions of Brazil, fulfilling the same role that Carla once inspired in them.

Brazilian myrmecology has grown exponentially in the last decades, thanks to various initiatives in training, outreach and research. Carla has been one of the driving forces behind this growth, being one of the founders and organizers of the Formigas do Brasil Course (CFB), in addition to hosting and coordinating, together with Inara Leal, the organization of the XXVII Symposium on Myrmecology: An International Ant Meeting. These two major events are now a reference for anyone, inside and outside Brazil, who wants to study ants.

Carla has always made sure that her work serves the community. Now, she has decided to pursue one of her passions, ethnobiology, to have a more direct impact on the population outside of academia. In this new field, Carla has taken a fresh approach to scientific outreach, extending her knowledge beyond the walls of the university. Her experience and remarkable contributions give us confidence that the fruits of this new endeavor will soon be reaped.

The academic world presents many challenges, and Carla has faced some of them, such as being a mother while pursuing her Master's and PhD - commitments that required full dedication. Despite this, she has made significant contributions to Brazilian ecology. However balancing family and academic pursuit took a toll on her well-being. Embedded in a system of gender restrictions and unsustainable academic demands, Carla experienced first-hand the consequences of an environment that affects emotional, personal, and social well-being. As a result of her experiences, she has become a strong advocate for the mental health and well-being of students and researchers, pushing for greater equity for women and a healthier academic environment.

After getting to know Carla and her life, we can boldly say that she is a scientist, a mother, courageous and a fighter - fully aware of the challenges faced by women in science and supporting many others through her own experiences. She is undoubtedly an inspiration and a deserving figure to be written in the history of Brazilian myrmecology.



**Cintia Martins Perinotto**

Cintia Martins Perinotto is widely recognized for her contributions to the field of ant symbionts, where her passion for these tiny creatures has been evident since childhood. Influenced by her father, who worked with termites, Cintia developed a fascination for the world of insects at an early age.

Born in the state of São Paulo, Cintia graduated in Biological Sciences at Universidade Estadual Paulista Júlio Mesquita Filho (UNESP) in Rio Claro, where she delved into the study of ants. With determination and a burning desire to explore molecular biology, Cintia faced the structural limitations of the laboratory, forging partnerships with other research groups while her advisor worked to equip their own lab with the necessary tools.

Her passion for studying ant symbionts quickly inspired her colleagues, leading to the formation of a dedicated team that grew daily. Her academic journey is remarkable; after earning her degree, Cintia completed a master's in

Cellular and Molecular Biology at the same institution and, shortly after defending her master's dissertation, was hired through a competitive examination by the Universidade Federal of Delta do Parnaíba (UFDPar), where she now teaches her favorite courses, Molecular Biology and Evolution.

Alongside her work at UFDPar, Cintia pursued her PhD in Cellular and Molecular Biology at UNESP, supported by a Fulbright scholarship that allowed her to conduct research at the prestigious Field Museum of Natural History in Chicago, USA. In the meantime, Cintia made excellent contributions to the study of ants and symbionts (Martins & Moreau, 2020; Martins *et al.*, 2021).

Currently, in addition to being an associate professor at UFDPar, Cintia serves as the coordinator of the Programa de Ciências Biológicas and the Laboratório de Mirmecologia do Delta do Parnaíba, affectionately known as Martins Lab. She is also a permanent faculty member in the Programa de Graduação em Biodiversidade, Ambiente e Sáude. In 2020, she embraced a new and deeply rewarding challenge: balancing her professional accomplishments with the joys and responsibilities of motherhood.

Becoming a mother brought many changes for Cintia, influencing her academic pace and introducing new priorities into her life. However, myrmecology remains one of her greatest passions. The resilience with which she balances these two worlds demonstrates the strength and dedication of a researcher who is also a mother. She finds inspiration and inspires us in both motherhood and science, showing that it is possible to reinvent oneself without giving up on one's dreams.

**Gabriela Procópio Camacho**

Gabriela Procópio Camacho, or Gabi Camacho as she is known, was born in Belo Horizonte, in the state of Minas Gerais. She spent her childhood, adolescence, and early adult years in Uberlândia, a city about 500 km from the state capital. It was in Uberlândia that Gabi began her academic journey. In 2006, she enrolled in the Biological Sciences program at the Universidade Federal de Uberlândia (UFU).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It didn't take long for Myrmecology to gain a new member. In 2008, Gabi joined LEIS (Laboratório de Ecologia de Insetos Sociais). Working in an ecology-focused lab, her initial efforts centered on studying ant communities. As part of this process, she worked on processing, identifying, and curating ant collections. Gabi fell in love with these tasks... She adored naming species, using identification keys, and organizing collections. This was where her passion for taxonomy was born.

From that point on, Gabi became a prominent figure in the study of ants of the Ectatomminae subfamily. Combining her expertise in morphology with her exceptional skills in molecular biology, Gabriela led studies that updated the knowledge of the entire subfamily. Her work clarified the relationships within the group, described new species, and provided identification keys (Camacho *et al.*, 2020). But she didn't stop there. Gabriela has become a reference in studies utilizing UCEs (ultraconserved elements) and collaborates on numerous national and international projects in ant taxonomy and systematics, such as "Ants of the World" and research on patterns of endemism and diversity of Madagascar's ants (Camacho, *et al.*, 2025).

Beyond Gabriela the myrmecologist and researcher, Gabi the woman is a profound source of inspiration. Although she acknowledges her privileges, Gabi hasn't been immune to the challenges of academia, including sexism, xenophobia, and the mental health struggles that come with them. While managing her personal challenges, Gabi never stopped caring for others. She has always been an activist, engaged in social causes, from serving as a student representative during her postgraduate years to participating in lectures and panel discussions. Long before the idea of this chapter, Gabi was already sharing stories and highlighting the importance of women in Myrmecology through her lecture titled "Women in Myrmecology: Past, Present, and Future," presented at the International Symposium on Myrmecology in Curitiba in 2017.

Today, Gabriela Camacho is a professor at the Universidade de São Paulo and the first woman as a curator of the largest ant collection in Latin America, housed at the Museu de Zoologia (MZSP). Despite her relatively recent career, Gabi's journey in Myrmecology, along with her contributions and legacy, continues to move and inspire... from young girls to women, from undergraduates to advanced professionals...a whole generation of myrmecologists.

**Itanna Oliveira Fernandes**

Itanna Oliveira Fernandes was born in Riacho de Santana, Bahia, and moved to Rondônia at a young age, where she discovered her passion for myrmecology. A graduate in Biology from the Universidade Federal de Rondônia (UNIR), it was during the final years of her undergraduate studies that ants captivated her interest, marking the beginning of a career defined by dedication and pioneering efforts, solidifying her as one of the leading authorities in ant taxonomy in Brazil.

Early in her academic journey, Itanna embraced the challenge of revising the *foetida* complex of the genus *Neoponera* during her master's studies at Instituto Nacional de Pesquisas da Amazônia (INPA) (Fernandes *et al.*, 2014). In this work, she meticulously examined all castes of the ants, producing a detailed morphological analysis that quickly became a model study in the field. Expanding her horizons, during her doctoral studies, Itanna combined morphology and molecular biology to investigate the genera *Anochetus* and *Odontomachus* (Fernandes *et al.*, 2021). Her taxonomic revision of *Anochetus* and phylogenetic analysis of these genera, conducted in partnership with the Smithsonian Institution, brought groundbreaking contributions to myrmecology. During her time at the Smithsonian, she gained extensive experience in molecular phylogenetic tools and collection curation skills that continue to enrich her work today.

Itanna's journey is marked by overcoming unique challenges. Coming from a region outside the major taxonomic research hubs in southeastern Brazil and working in a field traditionally dominated by men, she faced the barriers of being a Northeastern Brazilian woman in this highly male-dominated environment. Her determination and expertise shattered these barriers, establishing her as a trailblazer and paving the way for other women in ant taxonomy, particularly in the Amazon region.

Itanna has consistently left a lasting impact wherever she has been, fostering close collaborations with numerous researchers and institutions. She is a prominent figure at scientific events and plays a crucial role in mentoring new


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researchers. After years of invaluable contributions as a postdoctoral researcher, she recently assumed a faculty position at the INPA, where she is poised to lead significant advancements in taxonomy and further strengthen Brazilian myrmecology. Her journey is a testament to excellence, talent, and dedication, serving as a professional and personal inspiration to countless young researchers.

**Laura Carolina Leal**

Laura Carolina Leal was born in Caruaru, in the interior of Pernambuco. She stayed in the state and completed her entire education at the Universidade Federal de Pernambuco (UFPE), from undergraduate to doctorate. Her master's and doctoral studies were in Plant Biology, with a focus on the interactions between ants and plants. Laura made major contributions to research on the costs of these mutualistic interactions (Melati & Leal, 2018) and to the study of myrmecochory in Brazil (Leal *et al.*, 2014). Her impact in the field was so significant that Laura Leal became known as a major myrmecologist, not only in Brazil but worldwide.

Throughout her journey, Laura faced significant challenges, including experiences of harassment that made her question whether to stay in academia. At the end of her doctorate, she felt fragile and uncertain about what her next step would be. Her first postdoctoral research, conducted at the State University of Feira de Santana (UEFS), marked a turning point in her career: there, she found the support she needed and reaffirmed her decision to continue in academia — determined to help build a more supportive and inclusive academic environment for those who would come after her.

She also had important international experiences, such as a joint PhD program in Australia and a second postdoctoral position at Clemson University in the United States. After returning to Brazil, Laura participated in her first academic selection process and was approved, becoming a professor at the Universidade Federal de São Paulo (Unifesp) in Diadema, in the postgraduate program in Ecology and Evolution.

As a researcher, Laura is admirable. In addition to her contributions to the study of insect-plant interactions, she also focuses on population and community ecology, ethology, evolutionary ecology, and scientific methodology. Moreover, she collaborates with other graduate programs, being accredited in three programs at the Universidade Federal do Paraná (UFPR). As a woman, she is even more inspiring. Through lectures and participation in academic events, she encourages women to occupy spaces in science and face the challenges of a field historically dominated by men. Laura openly discusses the impacts of impostor syndrome, sharing her own experiences and creating a welcoming and supportive environment.

Laura Carolina Leal represents the combination of scientific competence and dedication to building a fairer and more equal space for all women in science. She is undoubtedly a great inspiration for future generations of myrmecologists, showing that, in addition to being excellent scientists, we can also be active agents in transforming the structures that shape academia.

**Lívia Pires do Prado**

Lívia Pires do Prado was born in São Caetano do Sul, in the metropolitan region of São Paulo city. It was in the city of São Paulo that she began her remarkable journey in myrmecology. A biologist graduated from Universidade São Camilo, Lívia's path took a transformative turn during her undergraduate studies when she came across an open call at the Museu de Zoologia da Universidade de São Paulo (MZSP) for technicians to process and curate ant specimens. Without realizing the impact of this decision, she took her first step toward a brilliant career.

Lívia quickly stood out for her skill and agility, becoming a reference in processing materials for the MZSP collection and contributing to various projects. Her close interaction with the myrmecological collection, combined with the inspiration from her lab colleagues, ignited a strong passion for taxonomy. This passion led to her first project, focused on the taxonomy of the genus *Xenomyrmex*, which became the subject of her undergraduate thesis.


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Determined to deepen her studies, Lívia pursued a master's degree at the MZSP, revising the genus *Octostruma*. For her doctorate at Universidade Federal do Pará (UFPA), she turned her attention to the taxonomy and biology of the genus *Megalomyrmex*, collaborating with Rachelle Adams in Ohio (Prado *et al.*, 2022). Her connection with the Adams Lab marked her transition to a postdoctoral position, where she further expanded her expertise before returning to Brazil to take a position at the Museu Paraense Emílio Goeldi. There, she now contributes to the PPBio Eastern Amazon research network, pushing the boundaries of knowledge on Amazonian biodiversity.

From the beginning, Lívia demonstrated exceptional ability and unparalleled insight in taxonomic analysis, identifying critical traits for species delimitation with precision and establishing herself as an expert and significant contributor to ant morphology and taxonomy.

In addition to her work as a taxonomist, Lívia is a passionate historian. She often dives into old books, manuscripts, photographic records, and interviews, bringing to light the stories and achievements of prominent figures in Brazilian entomology and myrmecology. Her extensive knowledge of the history and development of Brazil's entomological collections is remarkable (Prado *et al.*, 2020).

Lívia is not only a talented myrmecologist but also a strong woman and an unforgettable personality, leaving her distinctive mark wherever she goes. Balancing her academic life with authenticity and dedication, Lívia is a transformative force in Brazilian myrmecology. From a shy girl to a prominent figure in the field, her journey exemplifies how passion, hard work, and courage can break barriers and inspire a new generation of scientists.

**Manuela Ramalho**

Manuela de Oliveira Ramalho Sanchez, known as Manu Ramalho, was born in Campinas and raised in Guaraci, in the interior of the São Paulo state. Manu came from a family that always encouraged her, since she was a little girl, to achieve her goals. At a very young age, she joined a scout group, where her passion for biology

began to blossom. In 2006, she enrolled in the Biological Sciences course at the Universidade Estadual Paulista Júlio de Mesquita Filho (UNESP). During her undergraduate studies, Manu studied the toxicity of plant extracts to workers of the ant *Atta sexdens rubropilosa*, popularly known in Brazil as "saúva-limão", and also investigated the mitochondrial DNA of *Camponotus textor* (weaver ants). While still at UNESP, she continued her academic career: during her master's degree, she continued her research on the DNA of weaver ants, and during her doctorate, she studied the microbiome of Camponotini ants. Becoming a reference in the area of symbiotic interactions, Manu always had the goal of internationalizing her career. It was then that she met Dr. Corrie Moreau, a partnership that took her to the Field Museum of Natural History and Cornell University, where she obtained part of the data for her doctoral research and later continued on to her post-doctoral studies.

In recent years, Manu has dedicated herself to encouraging girls and women in STEAM (Science, Technology, Engineering, Arts and Mathematics) careers. In one of her works, Manu presents data that makes clear the limitations that women face in their education, which in turn prevent them from reaching prominent positions in academic careers, mostly occupied by men. Based on these statistics, Manu emphasizes the importance of support and opportunities for women to thrive in the field of Biological Sciences. Currently, Manu is an assistant professor at West Chester University (PA, USA) and, in addition to her line of research, RamalhoLab focuses on inclusion, diversity and outreach in science.

As well as being an excellent researcher, Manu is also a dedicated mother, and her activism extends to the area of mothers as researchers, a topic that is still little covered in academic society. Manu Ramalho's work is inspiring a new generation of researchers. As a woman, she is well aware of the challenges that women face, as highlighted by Ramalho *et al.* (2020). Committed to making a difference, her lab is mostly composed of women and encourages latina women, mothers, and first-generation college students to enter the field of science.


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**Maria Santina de Castro Morini**

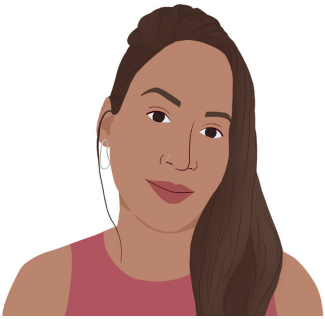
Maria Santina de Castro Morini was born in São Paulo state, where she built her scientific career. She completed her academic training entirely at Universidade Estadual Paulista Júlio de Mesquita Filho (UNESP). Initially, her main interest was in bees, but soon ants took over her research focus. Santina explored topics that were largely uncharted at the time, especially by women, making her one of the pioneers in myrmecology in Brazil. Since then, she has remained dedicated to this field, accumulating 25 years of experience.

Her passion for social insects guided her research in biodiversity, natural history, community ecology, public policies for conservation, urban insects, pest control, and environmental education. Despite her love for insects and their study, like many women in science, Santina was not immune to obstacles and challenges. Motherhood in academia demanded resilience. However, guided by her grandmother's teachings, Santina remained persistent. Her determination made her an inspiration for other women, mothers, researchers and undoubtedly, for her own son.

Her journey of achievements and perseverance led her to the Universidade de Mogi das Cruzes (UMC), where she currently works as a researcher and professor of Zoology in the Programa de Pós-Graduação em Biotecnologia e Políticas Públicas. In addition, Santina founded her own laboratory in 1999, the Laboratório de Mirmecologia e Abelhas do Alto Tietê, affectionately known as LAMAT.

Her contributions to myrmecology range from numerous scientific articles to book publications. Among them, some stand out as essential to Brazilian myrmecology, such as "Formigas em ambientes urbanos no Brasil" (Bueno *et al.*, 2017), "Serra do Itapeti: aspectos históricos, sociais e naturalísticos" (Morini *et al.*, 2012) and "Formigas do Alto Tietê" (Suguituru *et al.*, 2015). These inventories led to the creation of an ant collection for UMC, comprising 236 species. The richness of these works makes them essential for understanding the ant fauna of Atlantic Forest fragments and anthropized areas.

The vast quantity and quality of her work, the precision of her taxonomic data, and her mentorship of a generation of influential researchers makes Santina a great source of inspiration and a reference in the history of Brazilian myrmecology. As a pioneer, she has mentored more than 100 researchers, many of whom now stand out in the field, passing on their knowledge to new generations of scientists. Santina did not settle for merely opening doors, she widened them, ensuring that more women, like herself, can forge their own paths in myrmecology.



**Marília Maria Silva da Costa**

Marília Maria Silva da Costa was born in the municipality of Mamanguape, in the state of Paraíba, Brazil. Her academic journey began at the Universidade Federal da Paraíba (UFPB). Inspired by Brisa Lunar Tavares, it was during her undergraduate studies that Marília took her first steps into myrmecology. She joined Brisa's research group, the first in Paraíba dedicated to the study of ants and the training of myrmecologists. Within this context, her first contribution was a significant survey of the leaf litter myrmecofauna in Barra do Mamanguape.

After completing her undergraduate degree and seeking to expand her research, Marília pursued a master's degree at the Universidade Federal do Acre (UFAC), where she investigated the influence of forest cover on ant assemblages at a landscape scale. Completed in 2018, this research reinforced her ability to explore the intricate interactions between ants and their environment.

Continuing her academic career, she began her doctoral studies in 2020 at the Universidade Federal de Lavras (UFLA), Minas Gerais, under the supervision of Prof. Dr. Carla Ribas. Despite the geographic transition, Marília maintained strong ties with Paraíba. During her postgraduate studies, she began receiving requests for guidance from other students. By providing technical and scientific support and contributing to the training of new myrmecologists, Marília became a recognized figure in Brazilian myrmecology.

Her ability to effectively communicate knowledge ignited a passion for science outreach and popularization. Marília gained prominence by making information about ants accessible to the public, particularly to children. One of the most notable examples of this commitment is the book Formigas em Cores (Costa *et al.*, 2022). Developed in collaboration with various researchers, this educational material consists of a coloring book that presents information on different species of Brazilian ants, many of which were described by female taxonomists. Led by Marília, this work serves not only an educational role but also highlights and values the contributions of numerous women to Brazilian myrmecology.

Unfortunately, Marília was not immune to the challenges faced by women in academia. Throughout her career, sexism, xenophobia, and academic prejudice were obstacles that often discouraged her from continuing. Despite these adversities, with resilience, determination, and hard work, she overcame these challenges and remained steadfast in her path. She is currently a postdoctoral researcher at the Universidade Federal do Rio de Janeiro, establishing herself as one of the most promising scientists in Brazilian myrmecology. Her dedication to ant research and science outreach has been fundamental in bridging the gap between scientific knowledge and society, inspiring and encouraging new generations of scientists across Brazil.

**Mônica Antunes Ulysséa**

Mônica Antunes Ulysséa was born on the island of Florianópolis in Santa Catarina. During her undergraduate studies at the Universidade Federal de Santa Catarina (UFSC), which she completed in 2007, Mônica studied ethnoentomology. In 2012, during her Master's degree at the Universidade Estadual de Feira de Santana (UEFS), she focused on ecology and conservation, studying ant guilds in the Brazilian savanna (Cerrado). As we trace Mônica's path, we'll see how she learned from different fields of entomology and myrmecology to become the prominent researcher she is today.

The Museu de Zoologia da Universidade de São Paulo (MZSP) is a key institution in the study of Neotropical ants, with the largest collection in the region. Mônica first connected with the MZSP in 2005, when she was still a student, visiting the museum to identify ants collected from bromeliads. What seemed like a simple visit turned into a milestone, as 15 years later, Mônica would become one of Brazil's leading taxonomists, graduating from the same institution. Her descriptions of *Oxyepoecus regularis* Ulysséa & Brandão and the *O. browni* queen (Ulysséa & Brandão, 2012), as well as her first taxonomic revision of the genus *Hylomyrma* (Ulysséa & Brandão, 2021), were valuable contributions to the field.. Today, she is involved in several projects, including a revision of the genus *Eurhopalothrix*, as well as research on ant biodiversity and biological collections in Brazil.

Mônica has always been deeply interested in the relationship between people and nature, as well as in raising awareness about sustainability, social justice and gender equality. From an early age, she stood up against sexism and harassment, which led to many challenges. She served as a student representative at MZSP, advocating for more equitable and dignified spaces for women and students facing harassment. Today, she is one of the driving forces behind the campaign against harassment in myrmecology.

To understand Mônica, we must also mention her passion for art and agroecology. Her collection includes wonderful writings and photographs that highlight nature and our relationship with science and the world we live in. She has the sensitivity to transform an image that may seem "simple" into something poetic, as in the exhibition "How Clouds Are Born", which she created with Fabíola Fonseca. In this exhibition, a common image of ants covered in fungus tells the story of the discovery of a new species, the importance of a taxonomist's work and the value of biological collections, drawing a parallel between art and science.

Mônica's concern goes beyond detailed studies of the morphology, natural history and biodiversity of the creatures that fascinate us most: ants. She also actively demonstrates an awareness and affection for the value of women who serve as inspiration in various fields such as science, politics, sport and the arts, drawing attention to issues of female representation. In this spirit, she has named 14 new species of *Hylomyrma* in honour of women who have moved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her. Like them, we now share their stories, which serve as a mirror in which we and others can see ourselves.

**Natalia Maritza Ladino López**

Born in Villavicencio, the capital of Meta, in Colombia, Natalia Ladino is a black woman and the youngest of three sisters. Passionate about nature and science from an early age, Natalia graduated as a biologist at the Universidad de los Llanos in 2017, with a capstone project dedicated to the study of the ant fauna of a piedmont region in the transition between the Llanos and the Meta mountains, under the guidance of Prof. Dr. Claudia Lorena Yara Ortíz. Before graduating, Ladino had the opportunity to participate in the Amazon edition of the Formigas do Brasil Course (CFB) in Rio Branco, Acre. She met Rodrigo Feitosa at the course, who offered her a place in his laboratory at UFPR in Curitiba, where she developed her master's and Ph.D. projects.

In her master's degree, she chose to work with the most morphologically challenging genus of the Amblyoponinae subfamily, focusing on the taxonomic revision of Neotropical species of *Prionopelta* genus (Ladino & Feitosa, 2020). The highlights of this project are the creation of a glossary for sculpture, unprecedented in myrmecology, based on the depth of the foveae present in the ants' heads and the distance between them, and the description of the species *Prionopelta menininha*, a tribute to the Brazilian ialorixá Mãe Menininha do Gantois, an emblematic figure of Afro-Brazilian religions.

During her Ph.D., Natalia expanded her revision of *Prionopelta* geographically and methodologically. In addition to being the first person in her laboratory to conduct a worldwide taxonomic revision, the myrmecologist also used geometric morphology data to delineate her species and dedicated a chapter of her thesis to questioning, based on statistics, the traditional exhaustive measurement of specimens in taxonomy and how it is possible to sample all the variation of a group through an ideal - and much smaller - number of measurements.

Despite being a very discreet and reserved person, Natalia has always attracted the attention of her peers for her unique sensitivity and respect for the local communities she visited on field expeditions, making it part of her work to return to them with the results of her collections as a form of acknowledgment. The researcher also stands out for her exemplary discipline and professionalism, always being among the best students in postgraduate classes and other courses she participated in, thus earning the admiration and affection of professors and colleagues.

The taxonomist's endless list of qualities was not enough to prevent her from being hounded several times by racism, sexism, and xenophobia. From her existence as a black woman to her decision to pursue postgraduate studies in another country, Natalia faced many episodes in which her competence and capacity were questioned, to which she always responded by delivering nothing less than scientific excellence.

Currently, Natalia Ladino is a professor at the Universidade Federal de Pelotas, where she continues to develop projects in taxonomy and ecology innovatively and brilliantly and be an example of a person and professional for everyone who has the privilege of knowing her.

**Ronara de Souza Ferreira**

Ronara de Souza Ferreira is originally from Mantena, a town in the countryside of Minas Gerais. She began her academic journey at the Universidade Federal de Ouro Preto (UFOP), where she focused on the study of herbivorous insects in the canopy of forests. She continued her education with a master's degree at the Universidade Federal de Lavras (UFLA), concentrating on pest control through the study of flies. However, it was during her PhD that she discovered her true passion: the behavior of ants. This passion led her to Université Paris 13 in France, where she delved into the ethology of ants, a field that would become her specialty.

Ronara particularly stood out in the study of how stridulation can be used to separate species and understand the social dynamics of their communities


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(Ferreira *et al.*, 2010). Her research not only contributed new knowledge to ant biology but also highlighted the potential of acoustics as a tool to identify ecological and behavioral differences among them.

During her postdoctoral research, she explored other research models but returned to studying ants when she was hired in 2014 as a professor at UFES, Alegre *campus*, in Espírito Santo. She is currently a professor at the Instituto de Psicologia da Universidade de São Paulo (IPUSP), where she teaches in the field of ethology, specializing in ant behavior. She is known for being a welcoming professor with a strong commitment to inclusion, particularly for female students.

In addition to being an outstanding researcher, Ronara is the mother of Gael and Cecília, and her balance between professional and family life is an inspiration to many women. Ronara de Souza Ferreira is undoubtedly a central figure in scientific research on ant behavior, but she is also a symbol of courage, strength, and resilience, demonstrating that it is possible to be an excellent researcher, a dedicated mother, while also making a profound contribution to the development of a more inclusive and diverse academia.

## CLARIFICATION

The data about all women in here were extracted from the survey that we shared, Lattes CVs, personal communications, as well as from publicly available information in digital media, such as websites, newspapers and other online sources.

## FINAL CONSIDERATIONS

We hope that this chapter encourages other people to share inspirational stories about female contribution in myrmecology. We proudly acknowledge that there are many more women who are building and opening paths in myrmecology than those honored in these pages. Therefore, we hope that this project will transcend the present text, and the stories not included here will continue to be known and made visible. We reaffirm our intention to develop future works focused on female myrmecologists whose contributions have not only transformed their fields of study but also inspire young scientists.

## ACKNOWLEDGMENTS

We would like to thank all the women myrmecologists who came before us and paved the way for us to get here, as well as our colleagues from the new generation who are walking this journey with us, helping to make myrmecology an increasingly diverse and equitable space. Special gratitude goes to Rodrigo Feitosa for sharing his knowledge about the history of the honorees that he knew and for consistently supporting and encouraging girls aspiring to become women scientists. We also thank the organizers of the book *Formigas do Brasil* for giving us the opportunity to share these stories. Finally, we appreciate each person who helped us by responding to or sharing the form used in this chapter.

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# 23

# A QUICK BREAK FROM FIELDWORK TO TALK ABOUT BRAZILIAN ANTS - AN EXPERIENTIAL ACCOUNT

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# ABSTRACT

Ants, like most insects, are often viewed negatively by people. While science outreach efforts have aimed to shift this perception, communities near protected areas, where researchers frequently collect data, are often excluded due to logistical barriers. Motivated by frequent questions and curiosity from locals during fieldwork, we launched an outreach initiative as part of the project "Environmental factors and community structuring mechanisms upon ant community in distinct Brazilian Biomes." Traveling through the six Brazilian biomes, we engaged with people in discussions about the biology and ecology of ants. Our target audience comprised students from public schools. We chose these locations as they already serve as spaces for knowledge exchange and where we could find a greater number of people gathered together to listen to us. By asking students what they knew about ants, we uncovered mostly negative views and took the opportunity to explain the ecological roles of ants and their importance in the ecosystem. We also shared collected specimens and explained their relevance in simple, relatable language. Overall, we were met with a positive reception from both the students and the schools. Students and teachers expressed their surprise, noting that they were unaware of the diverse capabilities of ants. Based on that, we believe that this kind of outreach initiative plays a crucial role in bridging the gap between scientific research and public understanding, fostering appreciation for the ecological importance of ants while inspiring curiosity about biodiversity conservation.

**Keywords:** Ants; environmental education; scientific outreach; science communication.

## INTRODUCTION

Ants are widely present across all Brazilian biomes (SCHMIDT *et al.*, 2022; LASMAR *et al.*, 2021; 2023), both in natural and urban environments, and they play an important role in the cultures of different communities (KATZ, 2005; CARVALHO *et al.*, 2017; SILVESTRE; NETOL, 2020; ELLISON; GOTELLI, 2021; AGARWAL *et al.*, 2022). However, their ecological relevance often goes unnoticed by society, as they receive minimal attention in school curricula and are neglected in conservation efforts (ALONSO *et al.*, 2010; GUÉRNAD *et al.*, 2025). This is partly due to the negative association that people have with insects, including ants (QUEIROZ *et al.*, 2021), the lack of knowledge about their ecology (LEANDRO; JAY-ROBERT, 2019), and gaps in communication and dissemination of academic knowledge to the general society public.

Even with recent advancements in the interaction between academia and society, scientific research, its findings and its importance for societal development, remains largely inaccessible and difficult to understand for most people. To change this scenario, it is both essential and urgent that researchers dedicate themselves to presenting and sharing their knowledge and research beyond the walls of academia, using clear and accessible language to engage with society (TOOMEY, 2016). This task, however, is filled with challenges due to the complexity of scientific information, misinformation, science denialism, lack of resources and recognition, and communication barriers between different sectors and social actors (RUSSEL; BLACKBURN, 2017; NAGUMO *et al.*, 2022).

The popularization of science and scientific outreach are essential means to bring society closer to academia and make scientific knowledge more accessible and comprehensible, considering the characteristics of different audiences (BUENO, 2010; MEIJÁ *et al.*, 2024). The planning and integration of extension activities and scientific communication into research objectives enrich the impact of studies on society. By sharing the goals of their research and involving the public, researchers can spark curiosity about organisms and the ecological processes in which they participate, as well as the impact of human actions on ecosystem conservation (LUCKY *et al.*, 2014; LAPOLA *et al.*, 2021). This contributes to environmental awareness, the appreciation of diverse forms of knowledge, and empowers people to take action and become critical citizens.

One of the key moments of interaction between researchers and society outside academia occurs during fieldwork samplings in research areas. Yet, whenever we collect samples for our studies and extract data from a location, we contribute very little to the local communities. Many biologists, ecologists, and myrmecologists have certainly been questioned by local people during their fieldwork: "*But what are you doing in the woods?*"; "*Are you picking up trash?*" Specifically for myrmecologists, the most common questions include: "*Do you collect ants*? *My goodness, my house is full of them, why don't you collect there?*"; "*But you came all the way from Minas Gerais to collect ants here? Why?*"; "*Ants? How do I kill those tiny yellow ones that live in the sugar?*" These frequent questions, often accompanied by a sense of surprise, motivated us to carry out a scientific outreach activity as part of the research project "*Environmental factors and community structuring mechanisms upon ant community in distinct Brazilian Biomes*".

Thus, during our field works we made educational activities with society living around our sampling sites. We aimed to popularize scientific knowledge about ants, Brazilian biomes, biodiversity conservation, and our research project around protected areas (e.g., conservation units) while conducting our fieldwork samplings. Our target audience consisted of students from public schools.

## DETAILS OF THE EXPERIENCE

Our research project "*Environmental factors and community structuring mechanisms upon ant community in distinct Brazilian Biomes*" aimed to understand the environmental factors that determine ant diversity at different spatial scales and the main mechanisms of species coexistence in distinct Brazilian biomes, using ants as a model organism. For this purpose, we selected six protected areas, one in each biome: Humaitá Forest Reserve (Amazon; 9.762864° S, 67.642651° W), Catimbau National Park (Caatinga; 8.491198° S, 37.268901° W), IBGE Ecological Reserve and Brasília Botanical Garden (Cerrado; 15.936876° S, 47.878389° W), RPPN Sesc Pantanal (Pantanal; 16.521017° S, 56.406169° W), Intervales State Park (Atlantic Forest; 24.324395° S, 48.423595° W), and Espinilho State Park (Pampa; 30.184112° S, 57.499246° W). For field collections, we conducted extensive ant sampling in these protected areas using pitfall traps and baiting with specific


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nutrients (see details in LASMAR *et al.*, 2021; 2023), which allowed us to obtain a representative sample of the ant species in each region.

**A quick break to talk about ants**

During the project, we travelled across the six Brazilian biomes between 2016 and 2018. In addition to sampling biological material in the fieldwork, we dedicated extra time (one to three days) to engaging with communities and cities surrounding the protected areas where we conducted our samplings, in order to talk to people, answer their questions, listen to their experience with ants and show them what we actually do. Our target audience consisted of students from public schools in both urban and rural areas, ranging from elementary to high school, and included participants from 11 years old to senior citizens. We chose these locations because they already serve as centres of knowledge exchange and gathered a greater number of people willing to talk and listen to us.

Unfortunately, we were unable to visit any schools in the Amazon biome because the protected area was located in a remote and isolated region with no schools near the sampling site. Similarly, we could not visit schools in the Caatinga biome, as our collection period coincided with the start of the students' vacation, and rainy weather prevented students from attending classes during the final weeks of the school term.

In the Cerrado of the Federal District, we visited the Instituto Federal de Brasília – São Sebastião *Campus*, which served high school students. In the Pantanal, we visited the *Instituto Federal do Mato Grosso – Núcleo Avançado do Pantanal*, near Poconé – Mato Grosso, which served students of all ages, including adults, teenagers, and children. In the Atlantic Forest, we visited Escola Estadual Boa Vista, near the municipality of Ribeirão Grande – São Paulo, which also served elementary school students (Figure 1). Finally, in the Pampa, we visited *Escola Estadual Nilza Correa Pereira* in Barra do Quaraí – Rio Grande do Sul and the rural school *Manoel Imas dos Santos*, both of which served elementary school students. In total, we spoke to approximately 750 students and teachers.

**Figure 1 -** Science popularization work as part of the project "*Environmental factors and community structuring mechanisms upon ant community in distinct Brazilian Biomes*." The visits were conducted at the following institutions: *Instituto Federal do Mato Grosso – Núcleo Avançado do Pantanal*, near Poconé, Mato Grosso (a and c); *Escola Estadual Nilza Correa Pereira*, Barra do Quaraí, Rio Grande do Sul (d); *Escola Rural Manoel Imas dos Santos*, near Barra do Quaraí, Rio Grande do Sul (b); *Instituto Federal de Brasília – Campus São Sebastião*, Federal District (e); and *Escola Estadual Boa Vista*, near Ribeirão Grande, São Paulo (f).

**Source:** Authors (2025).

The aim of the activity was to create an environment for dialogue and knowledge exchange between us, the researchers, and the students and educators, in order to assess their perceptions, knowledge (SILVA *et al.*, 2014) and understanding of ants. We used guiding questions as a strategic framework for structuring and leading the activity (RABELO *et al.*, 2023). Thus, whenever we entered the classrooms, after introducing ourselves, we would pose the following question: "*What do you know about ants?*" From there, we received

a variety of responses. Most students associated ants with negative aspects, aligning with the findings of Queiroz *et al.* (2021), who reported a prevalent negative perception of ants in internet search results. However, in some rural schools, we heard a few positive responses, such as the idea that "*ants take care of plants*", which is in accord with Lapola *et al.* (2021). From this point, we began discussing ant biology and their ecological functions, emphasizing their importance to the environment in an informal and accessible language tailored to each grade level. At this stage, we also showed students the ants we had collected during our research in their region, which were stored in *Falcon* tubes with 90% alcohol. We chose to show the ants because they were readily accessible specimens we had on hand, and because they were collected from the same areas where the students and teachers live, helping to make the discussion more relatable and tangible. Although some individuals initially expressed fear of the ants, even when they were dead and preserved in *Falcon* tubes, we observed that this negative perception gradually diminished as we explained their biology and ecological significance.

Once the students had a discussion of the role of ants in the ecosystem, we introduced the topic of our research project. We explained what biomes are, their significance, and the importance of conserving each one. Many people tend to prioritise forest formations over savannas or grasslands in conservation efforts, including members of the local communities that we spoke with near the protected areas, so we addressed this misconception. Additionally, we discussed the objectives of our project in a simplified manner, explaining why we used ants as model organisms in our ecological assessments.

It is important to note that we did not apply any evaluation methodologies (SILVA *et al.*, 2014) to measure students' knowledge and perceptions of ants, their ecological importance, or their associated biomes. This decision was due to the project's focus and time constraints. However, we acknowledge and emphasize the importance of conducting pre- and post-intervention assessments to measure, track, and evaluate the impact of outreach activities on participants (MARQUES *et al.*, 2017; STEFANELLI-SILVA *et al.*, 2019; ZANELLA; ANDRADES, 2021).

## DISCUSSION

### Challenges and lessons learned from our scientific outreach activities

Overall, we received a positive reception from both students and schools. Students and teachers expressed surprise, stating that they had never realized that ants could do so many things beyond the negative aspects typically associated with them. This highlights the importance of outreach and science popularization activities like the ones we conducted, which facilitate knowledge exchange in educational environments. Therefore, we believe that our interaction with educators and students from the communities surrounding the protected areas where we conducted our samplings contributed to the demystification and popularization of science, encouraging scientific education and environmental awareness.

One of the main challenges we encountered in carrying out these outreach activities was coordinating the schedule for biological data collection with travel logistics and the school calendar. Since schools were contacted during our field campaigns, the time available to organize and engage local participants was limited. Additionally, while accessing communities in more remote areas was particularly challenging, these are likely the ones that suffer the most from a lack of information exchange and distance from academia. Therefore, we emphasize that achieving this goal requires strategic planning and sufficient time to ensure meaningful interaction and integration with these communities.

Another important challenge we identified, although indirectly, was related to the limited presence of ecological and biodiversity topics in school curricula. During our interactions, we perceived a clear knowledge gap among students regarding basic ecological concepts and the role of insects in ecosystems. This gap likely reflects a broader educational issue, as nature-related content, especially involving invertebrates and ecological interactions, has been increasingly reduced or simplified in official teaching materials (GANGWANI *et al.*, 2018). This context reinforces the relevance of outreach actions such as ours, which can help fill these gaps by providing direct and engaging contact with nature-related themes, fostering curiosity and critical thinking among students.

Although our efforts were limited in scope, we recognize their significance, not only in fostering an understanding of our role as researchers but also in initiating discussions about the ecological importance of ants in Brazilian biomes. Furthermore, during the activities, we noticed that our school discussions stimulated interest among students and the community in environmental issues, biodiversity monitoring, and conservation. They also fostered a sense of belonging and recognition of the importance of protected areas for both biodiversity conservation and quality of life. However, as that perception was not directly assessed, we emphasize the importance of incorporating evaluation methodologies during the development of these activities to track potential changes in the perceptions and behaviours of students, educators, and/or the local community (MARQUES *et al.*, 2017; STEFANELLI-SILVA *et al.*, 2019; ZANELLA; ANDRADES, 2021). Additionally, we suggest that, if time permits, the community be contacted beforehand to understand their interests and determine the most suitable format for addressing science popularization issues. This certainly can improve future science popularization activities in diverse educational environments.

During and after our activities, we also observed that integrating outreach, science communication, and popularization efforts into research projects is essential for breaking down communication, accessibility, and inclusion barriers between academia and society. However, achieving this requires a paradigm shift, both inside and outside academia, regarding the role and responsibility of researchers in science communication.

## FINAL CONSIDERATIONS

The main lesson we want to convey is that scientific research should not be confined to academic circles. Its findings must reach society, especially those directly affected by the studied ecosystems. Effective communication between researchers and local communities is essential for fostering mutual understanding, strengthening scientific literacy, and promoting environmental awareness. It is crucial then that research findings are shared with society, particularly with communities living within or near the areas where data collection takes place. Even though we acknowledge that limited funding and time constraints, both for us and other researchers, make it difficult to allocate additional

time for outreach beyond field data collection. However, valuing, encouraging, and financially investing in multidisciplinary research projects is crucial. These initiatives can potentially improve the involvement of diverse stakeholders and ensure that outreach efforts extend beyond isolated activities.

With this report, we also hope to encourage other researchers to plan financially and allocate time to create dialogue spaces with local communities beyond the walls of universities in the regions where their research is conducted. By communicating our research, we can contribute to scientific education and help shape people into critical-thinking citizens. This is urgently needed in times of scientific skepticism and denialism, which lead to phenomena such as '*flat-earthism*' and general ignorance about the environment.

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# 24

# KEEPING ANTS IN THE ANTHILL: SEVEN EDITIONS OF THE *FORMIGAS DO BRASIL* COURSE

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# ABSTRACT

The states of Acre, Ceará, Espírito Santo, Mato Grosso do Sul, and Minas Gerais have served as official venues for the course offered by the *Formigas do Brasil* project in its teaching component. So far, five of the six Brazilian biomes have been represented: Amazon, *Caatinga*, *Cerrado*, Atlantic Forest, and *Pantanal*. With a mean of 23 institutions involved per edition, this introductory course to myrmecology has selected more than 270 participants for an in-depth learning experience primarily focused on collection techniques and sampling design, sample processing, scientific dissemination, morphology, taxonomy and systematics, ecology, behavior, biological control, patterns of diversity, and distribution of ants. Here, structured interviews and descriptive statistics are used to explore participants' perceptions of the course in terms of its impact on their training, career, network, learning experiences, and interests related to this initiative. The role of the course as a pivotal moment in early career students pursuing a future in myrmecology is highlighted.

**Keywords:** Ant fauna; Brazilian myrmecology; diversity; outreach; teaching.

## INTRODUCTION

Ants are among terrestrial environments' most diverse, abundant, and ecologically relevant organisms (SCHULTHEISS *et al.* 2022). More than 15.000 species inhabit or have inhabited Earth (BOLTON, 2025), and their diversity peaks in tropical regions (KASS *et al.* 2022). Brazil has the greatest ant richness worldwide, making it a strategic place for studying these insects (FEITOSA *et al.* 2022). Fortunately, with at least 69 research centers, the interest of researchers based in Brazil in the elucidation aspects related to morphology, physiology, ecology, behavior, evolution, biological control, and conservation of Formicidae has been a concomitant force (FORMIGAS DO BRASIL, 2025a).

Hence, it was only a matter of time, collaboration, and determination for a comprehensive project specifically focused on training future generations of myrmecologists studying the local ant fauna to emerge. In 2012, Dr. Fernando Schmidt (Universidade Federal do Acre, UFAC), Dr. Carla Ribas (Universidade Federal de Lavras, UFLA), and Dr. Rodrigo Machado Feitosa (Universidade Federal do Paraná, UFPR) created the *Projeto Formigas do Brasil* (Ants of Brazil Project, henceforth called FdB) inspired by initiatives of teaching, research, and outreach in myrmecology (See FORMIGAS DO BRASIL, 2025b for details). The teaching component is materialized in the *Curso Formigas do Brasil* (Ants of Brazil Course, hereinafter CFB). Over the course of a week, undergraduate and graduate students, as well as professionals interested in myrmecology, are encouraged to deepen their knowledge of biology, taxonomy, and ecology of Brazilian ants. The course provides academic resources such as talks by professors and specialists, and presentations by participants, ethical and responsible field collection of ants, and guidance through material processing and identification.

The pilot edition of the course was launched in 2012, in the city of Lavras, Minas Gerais state, using laboratory infrastructure and experimental units of the *Universidade Federal de Lavras*. A year later, the second pilot edition took place in the same state but a different institution, the *Instituto de Ciências Biológicas, Campus Pampulha*, of the *Universidade Federal de Minas Gerais* (UFMG) with field activities at the *Estação Ecologica da UFMG*, and local support of Dr. Frederico Neves. In 2014, the course began to move towards exploring the ant fauna of Brazilian biomes, starting with *Cerrado.* The academic activities were carried

out in the *Instituto de Biologia, Campus Umuarama* of the *Universidade Federal de Uberlândia*, Minas Gerais, and the field component at the *Reserva Ecologica do Panga*, counting on Dr. Heraldo Vasconcelos as local organizer. Subsequent editions were biannual, except in 2020, due to the restrictions imposed by the COVID-19 pandemic.

A long-awaited Amazon edition reunited the participants in 2016 at the *Universidade Federal do Acre, Centro de Ciências Biológicas e da Natureza* for talks and laboratory activities, while the field phase took place in the *Fazenda Experimental Catuaba*, with Dr. Fernando Schmidt as local organizer. In 2018, the *Instituto Nacional da Mata Atlântica* and the *Estação Biológica de Santa Lúcia* in the municipality of Santa Teresa, Espírito Santo state were venues for the talks and field components of the Atlantic Forest edition, with Dr. Tathiana Guerra Sobrinho as a local collaborator. Four years later, with the support of Dr. Ýves Quinet and his team work at *Universidade Estadual do Ceará*, the *Caatinga* edition was possible. It took place at the cities of Crateús and Pacotí, with field activities in the *Reserva Natural Serra das Almas*. Finally, a recent edition of the course in the *Pantanal* biome was held in November of 2024. This time, the institutions involved were the *Universidade Federal do Mato Grosso do Sul* and the *Base de Estudos do Pantanal*, in the cities of Campo Grande e Corumbá, Mato Grosso do Sul state and counted with the support of Paulo Robson de Souza, Suelen Sandim and Vivian Nacagava.

The first phase of the CFB, which involves exploring ants in Brazilian biomes within a teaching scenario, is coming to an end. With this, it is important to reflect on participants' perceptions from past editions. As the *Pampa* biome edition is on the horizon, expectations for its execution in 2026 as well as the prospects of this project' component are high. This text explores questions of this nature, with a focus on the participants' profile, career progression, learning experiences, and relevance of the course for them.


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## EXPERIENCE DETAILS

### Data acquisition

*Survey.* Participants (i.e., students, professors, and monitors) of the seven editions of the course were contacted via e-mail to voluntarily and anonymously answer a survey consisting of structured questions about their participation. Contact information was retrieved from the FdB website and filtered by CFB edition. The following questions ("Q") are addressed[1]:

1. What was the participation trend among different versions of the CFB?
2. What is the academic/professional profile of CFB participants?
3. What is the perception of learning on the main topics covered in the course?
4. How frequent are collaborations between course members in order to contribute to knowledge about ants of Brazil?
5. How relevant was the CFB for the academic career, professional trajectory, and network of participants?
6. There exists an interest in participating in a future CFB edition and in the replication of the FdB project?

*Additional information.* Consultations of the *Currículo Lattes*, a public academic data storage platform used by the *Conselho Nacional de Desenvolvimento Científico e Tecnológico* (CNPq), were made to track the career progression of those who attended the course more than once and to access updated email accounts when needed.

*Photos.* Images illustrating the course's academic activities, biomes, or ants were extracted from the public website of the FdB or provided by participants

[1] See Supplementary material S1 at https://doi.org/10.6084/m9.figshare.29914487.

and included in this text body. Additionally, given the success of the photographic exhibition held during the *Pantanal* edition of 2024 and headed by Dr. Esperidião Neto and Dr. Robson Paulo de Souza, a brief outreach catalog is provided[2]. This resource is a compilation of photos taken through the lenses of participants during different editions of the CFB. Image selection primarily considered the photo resolution, a focus on ants or landscapes of Brazilian biomes explored, authorization for public sharing, and the willingness to send them within a reasonable timeframe aligned with publication schedules.

### Data treatment

All data were processed with the R.4.4.0 programming language (R CORE TEAM, 2024). The map was elaborated with the packages *mapdata* (BECKER; BROWNRIGG, 2022), *maps* (BECKER; MINKA; DECKMYN, 2023), *ggrepel* (SLOWIKOWSKI, 2024), *sf* (PEBESMA; BIVAND, 2023) and *tidyverse* (WICKHAM *et al.*, 2019). Descriptive statistics was used to summarize and analyze data through *tidyverse*, *base* 4.4.0, *tibble* 3.2.1 (MÜLLER; WICKHAM, 2023), *treemapify* (WILKINS, 2023), *dplyr* (WICKHAM *et al.*, 2023), with *ggplot2* (WICKHAM, 2016) and *cowplot* (WILKE, 2024) for graphs. Plates were made in Adobe Illustrator 2020.

## DISCUSSION

A moderate number out of the 276 participants (considering as unique the participation of the same person in different editions) of the CFB (37.3%) voluntarily responded to the survey. Consequently, the results presented for questions three, four, six, and part of five may not fully represent the opinions of the entire course participant group and could be subject to bias (See Final Considerations section).

[2] See Supplementary material S2, at https://doi.org/10.6084/m9.figshare.29914748.


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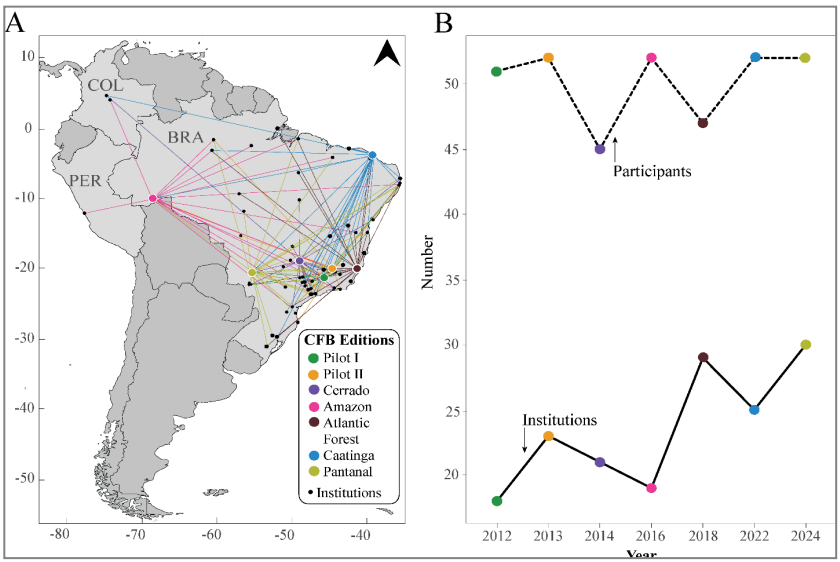
**Participation trends (Q1)**

The number of participants and institutions (mean of 50 and 23, respectively) interacting during different editions of the CFB has been variable (Figure 1). This might reflect a combination of an interest in the course, the quantity of ant research centers in the country that concentrate people already working on myrmecology or interested by this field, logistical difficulties for attending the course, and the Brazilian government's investment in science and technology over the last 12 years. After the pilot editions of CFB, which mainly reunited people from central and southern regions of Brazil, the participation network diversified. An increase in the proportion of participants from different country regions and based outside Brazil was perceptible, particularly since the Amazon edition of 2016. Also, there exist interesting issues in the last three editions that are worthy to mention. Most of the research centers on Brazilian myrmecology are located in the Atlantic Forest extension, which could explain the equilibrium between the number of participants and institutions involved in the edition for this biome in 2018. Therefore, the high number of participants recorded for the recent CFB versions of *Caatinga* and *Pantanal* could be interpreted as unexpected, considering the logistic or economic difficulties in attending scientific events in northeast or center-western states. Despite this, it is clear that a motivation for studying ants in Brazil exists beyond these barriers, a fact accompanied by the popularization of CFB. Furthermore, considering the academic and professional profile of participants (next section), it is probable that the support of funding agencies for attendance to scientific events strongly influenced what is observed in Figure 1.

**Figure 1 -** Seven editions of the *Curso Formigas do Brasil.* A. Location of the main venues of each edition, indicated by colored circles and lines, and participating institutions in black circles. B. Number of selected participants and institutions involved in each edition.




**Source:** The author (2025).

## Academic/professional profile, learning perception, and collaborations (Q2–4 and Q5 partial)

Several academic activities are conducted in the CFB (Figure 2). They can be summarized into three modules: talks, field collection, and material processing. The first is given by professors, monitors, and specialists in different fields of myrmecology (mainly ecology and taxonomy), and/or bridges knowledge about Formicidae and the biome in which the edition is being made. In addition, the students are encouraged to present their ongoing studies and interests. Secondly, the collection of ants in the field uses qualitative and quantitative techniques with the guidance of professors and monitors, framed in a sampling design. Last, the material collected is sorted, pinned, labeled, and identified by the students of the course, once again counting on the support of the scientific and organizing committee.

**Figure 2 -** Academic activities of the *Curso Formigas do Brasil* in a nutshell. A, H, L, O. Biomes; B. Leading team; C, I. Talks; D-F, M, N. Field; J. Certified participants; G, K. Ant processing and identification.

**Source:** Adapted from original contributor photographs, credits embedded in each photo.

During the development of the CFB, and particularly at the end of the activities, a space for open discussion is offered to participants to verbally discuss expectations and their alignment with the course outcomes. The feedback can be highly variable since it is influenced by the intrinsic characteristics of participants, their level of training and motivation for taking the course.

Among the people who answered the survey, less than 40% of the participants were not academically involved with ants at the moment of participating in

the course (Figure 3A). There was a balance between the perception of learning in the main areas of knowledge covered by the CFB, which included: (i) Introduction to myrmecology, (ii) Biological, morphological, ecological features and importance of ants, (iii) Introduction to ant taxonomy, (iv) Identification of ant subfamilies and genera in Brazil and morphospeciation, (v) Introduction to ant ecology and (vi) Sampling design, collection methods and material processing; here fitted into the three categories of Figure 3B.

Selected students of the CFB can become instructors, lecturers, or guest specialists in posterior editions. In the best scenario, members consolidate collaborations that allow them to contribute to Brazilian and worldwide myrmecology. Among the participants who answered the survey ~55% indicated some collaboration, whether through projects, affiliation with a laboratory, or at least one particular study with participants from different Brazilian institutions that also took the course (Figure 3C). The majority of those who participated in more than one edition of the CFB, followed an academic path in which ants were the protagonists of their main study topic, at least until their last participation in the course (Figure 3D). Influenced or not by the course content, this is a trend that should not be ignored. It implies that there is a growth of people in the country pursuing a career studying ants, and who had high-quality training provided by the CFB in at least one of its editions. Thus, the course could have a positive effect in keeping "ants" – referring to participants – in the "anthill", that is, actively studying Formicidae, which hopefully might lead to new laboratory leaders and principal researchers in myrmecology inside or outside Brazil. Here, a personal testimony is appropriate, since it is certainly not an exclusive, isolated case: my gateway to myrmecology and the pivotal moment in my academic career came thanks to the Amazon edition in 2016, where I entered as a foreign undergraduate student, with a fairly incipient experience in ant ecology in Colombia, but with an interest in other areas of knowledge in this group, particularly in systematics, biogeography and curatorship of biological data and collection specimens. Once in contact with the Brazilian myrmecological community, I did my master's and my doctorate in this country, during which I had the opportunity to elucidate various information about ants (mainly taxonomy and ecology). In 2022 I participated as a monitor in the *Caatinga* 2022 edition, this time much more prepared than when I entered this field nine years ago.


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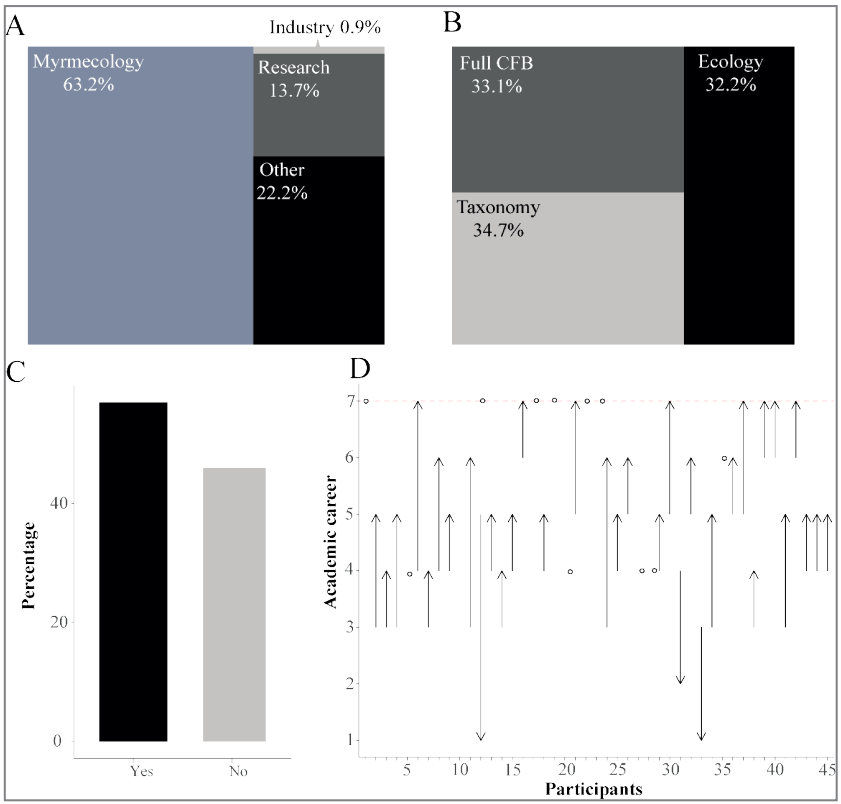
**Figure 3 -** Profile, learning perception and academic career progression of participants. A. Main occupation at the time of selection, B. Learning perception after course, C. Collaborations among participants, D. Career progression for those with more than one edition attended. The arrow indicates the current level of training recovered by consultation through *Lattes*: without information (1), non-researcher (2), undergraduate (3), master's fellow or degree (4), doctorate fellow or degree (5), postdoctoral fellow (6), principal investigator/professor (7). The dotted red line shows the higher position in the academic career.



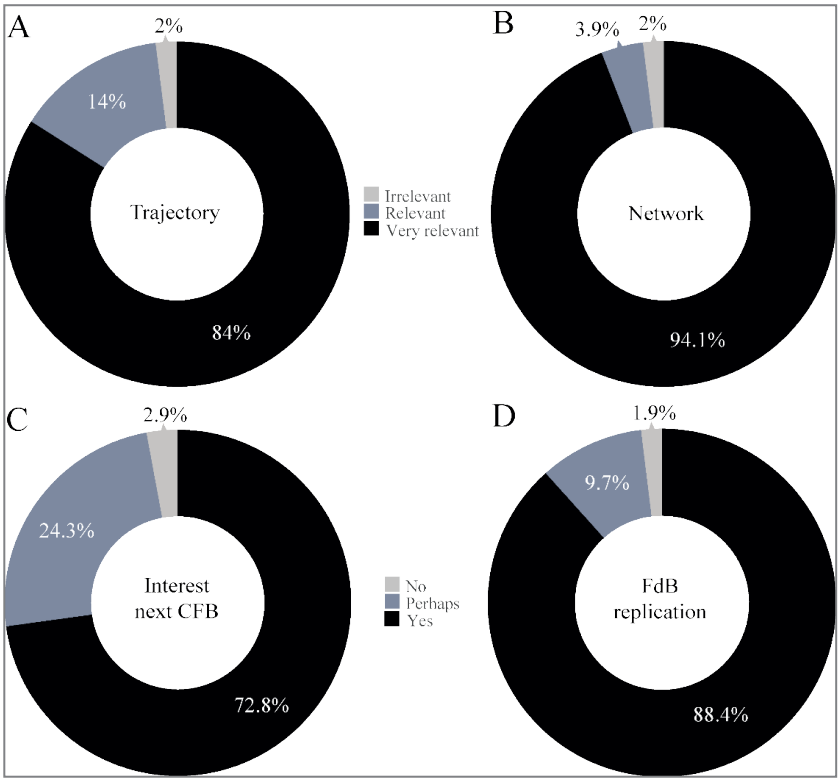

**Source:** The author (2025).

## Relevance of CFB and future interests (Q5 partial, and Q6)

Several generations were involved in the course, and after seven editions, the majority of surveyed participants considered that the CFB had a relevant role for their professional trajectory (84%) and network consolidation (94.1%) (Figure 4A, B). Following a similar path as other initiatives (e.g. *Ant Course* or the *Curso Internacional de Hormigas Neotropicales*) gathering people around an intense myrmecology workshop is a unique opportunity that has paid off in terms of the number of people who currently contributes to ant-related knowledge,

where the majority of former participants continue active, promoting research in myrmecology. The good reception of the course is also reflected in the interest of more than 70% to participate in a future edition of the CFB, be it the *Pampa* biome edition to be held in 2026, or an international one (Figure 4C). Likewise, it is not surprising that the percentage of people who consider that the FdB should not be replicated in other countries is practically negligible, with less than 2% (Figure 4D); in comparison to those who could consider the project a potential model for other regions (~98%).

**Figure 4 -** Relevance of the CFB for participants and future interests. Importance in A. Trajectory, B. Network. Interest in the C. *Pampa* edition and in D. replication of the FdB.




**Source:** The author (2025).

## FINAL CONSIDERATIONS

To mitigate biases, a higher response rate needs to be pursued in future studies. Strategies such as using communication channels that have a wide reach in the myrmecological community (e.g., social media) and implementing multiple follow-up emails could improve data collection. Furthermore, endorsement from all members of the organizing committee, professors, local organizers, and course alumni could encourage participation by emphasizing the importance of providing timely feedback for accurately reflecting the experiences of the CFB community. In addition, this study is only based in the participants selected. Thus, eventual withdrawals and changes in the number of people attending each edition must be taken into account. Despite this, valuable insights were gained regarding the course's relevance to myrmecology in Brazil. Several participants expressed interest in providing more detailed feedback and sharing their personal experiences, including suggestions for improvement. While this fell outside the scope of the current study, it highlights the need for a dedicated communication channel, such as an anonymous post-course feedback form, to capture these valuable perspectives.

In addition, could be convenient to furtherly explore the participation trend in the interval of 2018 to 2022 in relation to several factors as the investment in science and technology in Brazil, since the impact of such an atypical period as the COVID 19 pandemics could be strongly influencing the illustrated in Figure 1.

Myrmecology in Brazil continues to hold great promise, with a growing cohort of dynamic professionals eager to contribute actively and collaboratively. Initiatives like the FdB provide a valuable and accessible platform for individuals seeking education and training in this field, empowering them to proudly and responsibly embrace the challenge—and privilege—of studying the world's richest and fauna.

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# INDEX

## Symbols

16**S rRNA Gene:** 172, 191, 196

## A

**Alpha Taxonomy:** 53

**Amazon:** 10, 23, 34, 35, 55, 56, 59, 67, 69, 70, 108, 109, 119, 155, 160, 166, 173, 174, 176, 178, 180, 181, 199, 201, 209, 211, 227, 232, 233, 237, 238, 239, 240, 242, 244, 245, 272, 274, 275, 277, 279, 281, 284, 286, 289, 294, 315, 323, 324, 327, 329, 335, 336, 337, 339, 340, 341, 342, 343, 344, 350, 355, 363, 370, 423, 424, 425, 441, 442, 465, 466, 467, 468, 469, 472, 473, 474, 475, 476, 477, 478, 492, 509, 515, 518, 524, 529, 535, 536, 542, 545, 547, 550, 553

**Ant Diversity:** 8, 9, 11, 12, 33, 42, 45, 46, 47, 49, 50, 51, 54, 64, 67, 68, 70, 71, 73, 101, 103, 117, 176, 182, 190, 221, 224, 225, 242, 244, 253, 257, 258, 265, 266, 267, 285, 289, 294, 320, 327, 328, 329, 330, 337, 338, 340, 343, 346, 347, 350, 351, 352, 355, 356, 357, 359, 360, 362, 364, 365, 367, 368, 369, 370, 373, 376, 383, 384, 391, 393, 402, 410, 418, 419, 432, 433, 434, 437, 439, 444, 446, 448, 449, 450, 451, 452, 453, 454, 455, 456, 459, 463, 465, 466, 468, 473, 474, 475, 476, 478, 480, 495, 530, 535, 543

**ant Fauna:** 7, 9, 19, 37, 47, 55, 56, 57, 58, 73, 146, 148, 209, 211, 213, 216, 217, 218, 219, 223, 245, 314, 333, 336, 344, 345, 347, 348, 350, 363, 364, 366, 368, 369, 392, 400, 401, 402, 409, 414, 432, 439, 444, 446, 447, 448, 450, 453, 457, 458, 461, 463, 468, 470, 472, 478, 481, 491, 500, 507, 520, 524, 545, 546

**Anthropogenic Disturbance:** 145, 366, 397, 407, 411, 415, 417, 418, 419, 420, 487, 491, 529

**ant List:** 423

**ant-Plant Interaction:** 244, 272, 274, 275, 283, 292, 331

**Ant-Plant Interactions:** 93, 227, 228, 242, 243, 244, 275, 288, 290, 343, 368, 397, 403, 410, 449, 456, 457, 463, 484, 500

**Ants:** 7, 8, 9, 10, 11, 12, 22, 23, 24, 25, 29, 31, 32, 33, 34, 35, 39, 42, 44, 45, 46, 47, 49, 50, 51, 53, 54, 55, 56, 57, 58, 60, 61, 62, 63, 65, 66, 67, 68, 69, 70, 71, 72, 73, 74, 77, 78, 79, 80, 81, 82, 83, 84, 85, 86, 87, 88, 89, 90, 91, 92, 93, 94, 95, 96, 97, 98, 100, 101, 103, 105, 106, 107, 108, 109, 111, 112, 113, 114, 116, 117, 119, 120, 121, 123, 124, 125, 126, 127, 129, 131, 132, 133, 134, 135, 137, 138, 139, 140, 141, 142, 143, 144, 145, 146, 147, 148, 149, 150, 151, 152, 153, 154, 155, 156, 157, 158, 160, 162, 163, 164, 165, 166, 167, 168, 169, 170, 171, 172, 173, 174, 175, 177, 178, 179, 180, 181, 182, 183, 184, 186, 187, 188, 189, 190, 196, 197, 198, 199, 200, 201, 202, 204, 205, 207, 209, 212, 214, 215, 216, 217, 218, 219, 220, 221, 222, 223, 224, 225, 227, 228, 229, 230, 231, 234, 235, 237, 238, 239, 240, 241, 242, 243, 244, 245, 246, 247, 248, 249, 250, 251, 252, 253, 254, 255, 256, 257, 258, 259, 260, 261, 262, 263, 264, 265, 266, 267, 268, 269, 270, 271, 272, 273, 274, 275, 276, 277, 278, 279, 280, 281, 283, 285, 286, 287, 288, 289, 290, 291, 292, 293, 294, 295, 296, 299, 300, 302, 303, 304, 305, 306, 307, 308, 309, 310, 311, 312, 313, 314, 315, 316, 320, 322, 323, 326, 329, 330, 331, 332, 333, 334, 335, 336, 338, 340, 341, 342, 344, 346, 347, 348, 349, 350, 351, 354, 356, 357, 360, 361, 363, 364, 365, 366, 367, 368, 369, 370, 371, 372, 374, 375, 376, 377, 380, 381, 382, 383, 384, 385, 386, 387, 388, 390, 391, 393, 394, 395, 397, 398, 401, 402, 404, 406, 407, 408, 409, 410, 411, 412, 413, 414, 415, 416, 418, 419, 420, 421, 422, 423, 425, 426, 428, 429, 430, 431, 432, 433, 434, 435, 436, 437, 439, 440, 441, 442, 443, 444, 445, 446, 447, 448, 449, 450, 451, 452, 453, 454, 455, 456, 457, 458, 459, 460, 461, 462, 463, 464, 466, 469, 470, 471, 473, 476, 477, 479, 480, 481, 483, 484, 485, 491, 492, 493, 494, 495, 498, 499, 500, 501, 502, 503, 504, 506, 507, 508, 509, 510, 511, 512, 513, 514, 515, 516, 519, 520, 521, 522, 523, 524, 525, 526, 527, 528, 529, 530, 531, 533, 534, 535, 536, 537, 538, 539, 540, 542, 543, 544, 545, 546, 547, 548, 549, 550, 551, 552, 553, 556, 557, 558

**Ants:** 7, 8, 9, 10, 11, 12, 22, 23, 24, 25, 29, 31, 32, 33, 34, 35, 39, 42, 44, 45, 46, 47, 49, 50, 51, 53, 54, 55, 56, 57, 58, 60, 61, 62, 63, 65, 66, 67, 68, 69, 70, 71, 72, 73, 74, 77, 78, 79, 80, 81, 82, 83, 84, 85, 86, 87, 88, 89, 90, 91, 92, 93, 94, 95, 96, 97, 98, 100, 101, 103, 105, 106, 107, 108, 109, 111, 112, 113, 114, 116, 117, 119, 120, 121, 123, 124, 125, 126, 127, 129, 131, 132, 133, 134, 135, 137, 138, 139, 140, 141, 142, 143, 144, 145, 146, 147, 148, 149, 150, 151, 152, 153, 154, 155, 156, 157, 158, 160, 162, 163, 164, 165, 166, 167, 168, 169, 170, 171, 172, 173, 174, 175, 177, 178, 179, 180, 181, 182, 183, 184, 186, 187, 188, 189, 190, 196, 197, 198, 199, 200, 201, 202, 204, 205, 207, 209, 212, 214, 215, 216, 217, 218, 219, 220, 221, 222, 223, 224, 225, 227, 228, 229, 230, 231, 234, 235, 237, 238, 239, 240, 241, 242, 243, 244, 245, 246, 247, 248, 249, 250, 251, 252, 253, 254, 255, 256, 257, 258, 259, 260, 261, 262, 263, 264, 265, 266, 267, 268, 269, 270, 271, 272, 273, 274, 275, 276, 277, 278, 279, 280, 281, 283, 285, 286, 287, 288, 289, 290, 291, 292, 293, 294, 295, 296, 299, 300, 302, 303, 304, 305, 306, 307, 308, 309, 310, 311, 312, 313, 314, 315, 316, 320, 322, 323, 326, 329, 330, 331, 332, 333, 334, 335, 336, 338, 340, 341, 342, 344, 346, 347, 348, 349, 350, 351, 354, 356, 357, 360, 361, 363, 364, 365, 366, 367, 368, 369, 370, 371, 372, 374, 375, 376,

377, 380, 381, 382, 383, 384, 385, 386, 387, 388, 390, 391, 393, 394, 395, 397, 398, 401, 402, 404, 406, 407, 408, 409, 410, 411, 412, 413, 414, 415, 416, 418, 419, 420, 421, 422, 423, 425, 426, 428, 429, 430, 431, 432, 433, 434, 435, 436, 437, 439, 440, 441, 442, 443, 444, 445, 446, 447, 448, 449, 450, 451, 452, 453, 454, 455, 456, 457, 458, 459, 460, 461, 462, 463, 464, 466, 469, 470, 471, 473, 476, 477, 479, 480, 481, 483, 484, 485, 491, 492, 493, 494, 495, 498, 499, 500, 501, 502, 503, 504, 506, 507, 508, 509, 510, 511, 512, 513, 514, 515, 516, 519, 520, 521, 522, 523, 524, 525, 526, 527, 528, 529, 530, 531, 533, 534, 535, 536, 537, 538, 539, 540, 542, 543, 544, 545, 546, 547, 548, 549, 550, 551, 552, 553, 556, 557, 558

## B

**Behavioral Approaches:** 77

**Behavioural Ecology:** 124, 294

**Biodiversity:** 7, 11, 12, 29, 31, 34, 36, 37, 38, 42, 43, 44, 45, 46, 47, 49, 50, 53, 54, 64, 68, 69, 71, 119, 122, 168, 170, 173, 174, 176, 189, 190, 191, 197, 198, 201, 205, 206, 220, 221, 222, 223, 225, 228, 238, 243, 244, 258, 259, 265, 266, 267, 268, 274, 276, 286, 289, 290, 292, 293, 294, 297, 306, 307, 311, 313, 314, 315, 316, 319, 320, 321, 322, 325, 326, 329, 331, 332, 333, 334, 336, 337, 338, 339, 340, 341, 342, 343, 344, 345, 346, 347, 358, 361, 365, 366, 367, 368, 369, 373, 374, 383, 390, 391, 392, 393, 394, 397, 398, 401, 403, 405, 406, 414, 415, 416, 417, 418, 419, 420, 421, 423, 424, 427, 431, 433, 436, 438, 439, 440, 441, 444, 445, 446, 447, 448, 450, 451, 452, 453, 454, 459, 460, 462, 463, 466, 467, 468, 474, 475, 476, 477, 478, 480, 482, 486, 487, 489, 490, 491, 492, 493, 494, 495, 508, 518, 520, 523, 529, 533, 535, 539, 540, 557

**Biodiversity:** 7, 11, 12, 29, 31, 34, 36, 37, 38, 42, 43, 44, 45, 46, 47, 49, 50, 53, 54, 64, 68, 69, 71, 119, 122, 168, 170, 173, 174, 176, 189, 190, 191, 197, 198, 201, 205, 206, 220, 221, 222, 223, 225, 228, 238, 243, 244, 258, 259, 265, 266, 267, 268, 274, 276, 286, 289, 290, 292, 293, 294, 297, 306, 307, 311, 313, 314, 315, 316, 319, 320, 321, 322, 325, 326, 329, 331, 332, 333, 334, 336, 337, 338, 339, 340, 341, 342, 343, 344, 345, 346, 347, 358, 361, 365, 366, 367, 368, 369, 373, 374, 383, 390, 391, 392, 393, 394, 397, 398, 401, 403, 405, 406, 414, 415, 416, 417, 418, 419, 420, 421, 423, 424, 427, 431, 433, 436, 438, 439, 440, 441, 444, 445, 446, 447, 448, 450, 451, 452, 453, 454, 459, 460, 462, 463, 466, 467, 468, 474, 475, 476, 477, 478, 480, 482, 486, 487, 489, 490, 491, 492, 493, 494, 495, 508, 518, 520, 523, 529, 533, 535, 539, 540, 557

**Bioindicators:** 205, 207, 208, 222, 299, 349, 364, 398, 449, 452, 461, 511

**Biology:** 12, 19, 33, 57, 61, 70, 79, 80, 91, 93, 97, 101, 102, 104, 111, 113, 120, 121, 129, 130, 136, 139, 142, 143, 145, 167, 168, 169, 170, 191, 196, 197, 199, 200, 201, 202, 221, 242, 243, 245, 292, 294, 311, 314, 315, 316, 334, 335, 340, 342, 343, 344, 375, 388, 392, 417, 419, 439, 441, 461, 477, 484, 493, 495, 500, 501, 503, 507, 510, 511, 512, 513, 514, 515, 516, 518, 526, 533, 538, 542, 546

**Bodyguard Ants:** 272

**Brazil:** 7, 8, 9, 10, 11, 12, 18, 19, 20, 21, 22, 23, 24, 25, 28, 29, 30, 31, 33, 34, 35, 36, 37, 38, 40, 41, 42, 43, 44, 45, 46, 47, 48, 50, 52, 53, 54, 55, 56, 57, 58, 59, 60, 62, 63, 64, 65, 66, 67, 68, 69, 70, 71, 72, 73, 74, 76, 77, 78, 79, 80, 81, 86, 88, 89, 90, 92, 94, 97, 100, 101, 102, 103, 105, 107, 108, 109, 110, 111, 113, 117, 119, 121, 123, 126, 127, 129, 130, 131, 133, 134, 135, 136, 137, 138, 139, 140, 143, 144, 146, 147, 149, 150, 152, 155, 156, 158, 159, 160, 161, 165, 166, 167, 168, 169, 171, 172, 173, 174, 175, 176, 177, 178, 179, 181, 183, 185, 187, 188, 189, 190, 191, 196, 197, 201, 204, 205, 206, 207, 208, 209, 213, 215, 218, 219, 220, 221, 223, 224, 226, 231, 232, 234, 243, 244, 246, 247, 249, 250, 252, 256, 258, 259, 261, 263, 264, 266, 267, 268, 269, 271, 272, 274, 275, 276, 277, 283, 286, 287, 288, 289, 290, 291, 292, 294, 295, 296, 299, 300, 301, 303, 304, 305, 306, 312, 315, 319, 321, 323, 324, 332, 333, 334, 340, 341, 342, 343, 345, 347, 348, 350, 352, 364, 365, 366, 367, 368, 369, 370, 371, 372, 373, 376, 377, 378, 379, 383, 384, 385, 389, 391, 393, 394, 395, 396, 399, 400, 418, 419, 420, 421, 422, 423, 424, 426, 432, 433, 434, 438, 439, 440, 441, 443, 445, 447, 448, 451, 452, 458, 460, 461, 462, 463, 465, 466, 467, 468, 471, 474, 477, 479, 480, 481, 483, 490, 491, 493, 494, 495, 497, 498, 499, 500, 501, 502, 503, 504, 505, 506, 509, 510, 511, 515, 516, 518, 519, 520, 521, 522, 523, 528, 529, 530, 531, 532, 543, 544, 546, 548, 550, 553, 556, 557

**Brazilian Behavioral Myrmecology:** 77

**Brazilian Myrmecology:** 7, 8, 9, 21, 24, 28, 30, 37, 45, 46, 48, 54, 62, 498, 501, 505, 506, 507, 511, 512, 516, 518, 520, 521, 522, 545, 550

## C

***Camponotus Femoratus*:** 227, 231, 232, 239, 240, 245

**Campos:** 11, 151, 168, 176, 220, 224, 340, 364, 365, 368, 378, 444, 458, 460, 461, 462, 464, 493, 501, 502, 527, 528, 543

**Charismatic Species:** 296, 298, 299, 300, 302, 303, 308, 314, 315

**Chemical Communication:** 150, 151, 152, 160, 165

**Chemical Ecology:** 94, 98, 145, 150, 152, 167, 168, 169, 170, 242, 243, 244

**Chronosequence:** 205, 208, 209, 210, 214, 215, 217, 418

**Climate Change:** 191, 198, 219, 273, 293, 322, 329, 337, 340, 341, 343, 344, 366, 397, 398, 399, 401, 403, 405, 406, 414, 416, 417, 418, 419, 438, 459, 480, 489, 490, 491

**Conservation:** 12, 44, 46, 49, 51, 54, 62, 63, 68, 69, 70, 71, 101, 103, 119, 120, 189, 191, 206, 221, 222, 223, 225, 229, 243, 245, 267, 283, 292, 294, 296, 297, 298, 299, 300, 301, 303, 304, 306, 307, 308, 309, 311, 312, 313, 314, 315, 316, 317, 320, 329, 335, 336, 337, 338, 339, 341, 342, 343, 344, 361, 363, 365, 367, 368, 369, 370, 372, 373, 374, 377, 383, 387, 388, 389, 390, 392, 393, 397, 403, 416, 417, 418, 419, 420, 421, 423, 425, 427, 431, 436, 437, 438, 440, 441, 442, 443, 444, 446, 448, 454, 459, 460, 461, 463, 467, 477, 478, 489, 492, 493, 494, 495, 503, 505, 520, 522, 529, 530, 533, 534, 535, 538, 540, 542, 546

***Crematogaster Levior*:** 227, 231, 232, 239, 240, 245

## D

**Decomposition:** 81, 132, 133, 134, 135, 222, 247, 248, 249, 251, 252, 254, 255, 256, 257, 258, 259, 260, 262, 263, 264, 265, 266, 267, 268, 269, 418, 424

**Descriptive Data:** 101

**Disturbance:** 67, 96, 145, 205, 206, 209, 213, 215, 217, 218, 219, 225, 344, 364, 365, 366, 397, 398, 399, 400, 402, 403, 404, 405, 406, 407, 408, 411, 412, 415, 416, 417, 418, 419, 420, 421, 449, 455, 487, 491, 529

**Diversity:** 7, 8, 9, 11, 12, 33, 39, 42, 45, 46, 47, 49, 50, 51, 53, 54, 64, 67, 68, 70, 71, 73, 77, 80, 88, 89, 92, 101, 102, 103, 107, 113, 114, 116, 117, 119, 127, 142, 143, 144, 150, 152, 154, 157, 158, 160, 161, 162, 166, 167, 168, 170, 172, 173, 174, 176, 178, 179, 180, 182, 183, 184, 185, 189, 190, 196, 197, 198, 199, 200, 202, 205, 209, 210, 214, 215, 216, 217, 218, 219, 221, 222, 223, 224, 225, 226, 227, 230, 234, 237, 238, 240, 242, 244, 245, 247, 250, 252, 253, 257, 258, 260, 261, 262, 263, 264, 265, 266, 267, 274, 275, 283, 285, 286, 289, 291, 292, 293, 294, 297, 299, 300, 316, 320, 321, 322, 323, 326, 327, 328, 329, 330, 331, 337, 338, 340, 341, 342, 343, 344, 345, 346, 347, 348, 350, 351, 352, 353, 354, 355, 356, 357, 359, 360, 362, 363, 364, 365, 366, 367, 368, 369, 370, 372, 373, 375, 376, 377, 379, 383, 384, 385, 388, 390, 391, 393, 394, 397, 399, 400, 401, 402, 405, 406, 410, 411, 414, 415, 417, 418, 419, 420, 424, 425, 431, 432, 433, 434, 435, 436, 437, 439, 441, 443, 444, 446, 448, 449, 450, 451, 452, 453, 454, 455, 456, 458, 459, 460, 461, 462, 463, 464, 465, 466, 467, 468, 469, 473, 474, 475, 476, 477, 478, 480, 481, 483, 485, 488, 489, 492, 493, 494, 495, 503, 504, 505, 509, 514, 519, 527, 530, 535, 542, 543, 545, 546, 557

**Dominance:** 84, 93, 97, 98, 107, 142, 227, 234, 239, 240, 265, 291, 292, 402, 407, 419, 434, 448, 453, 475, 500

## E

**Ecological Systems:** 444, 445, 446, 449, 450, 451, 459, 462

**Ecology:** 9, 25, 33, 41, 42, 46, 47, 51, 53, 54, 61, 62, 63, 64, 67, 69, 74, 77, 78, 79, 80, 82, 91, 93, 94, 96, 97, 98, 101, 102, 103, 117, 119, 120, 121, 122, 124, 129, 136, 140, 141, 142, 143, 144, 145, 146, 147, 150, 152, 167, 168, 169, 170, 172, 188, 190, 196, 197, 198, 199, 200, 201, 202, 208, 220, 221, 222, 223, 224, 225, 226, 242, 243, 244, 245, 247, 250, 254, 257, 258, 261, 262, 263, 265, 266, 267, 268, 269, 291, 292, 293, 294, 314, 316, 322, 324, 325, 335, 340, 341, 342, 343, 344, 348, 349, 354, 363, 364, 365, 366, 367, 368, 369, 370, 375, 379, 389, 390, 392, 393, 394, 411, 416, 417, 418, 419, 420, 421, 436, 438, 439, 440, 441, 460, 461, 463, 475, 476, 477, 478, 482, 484, 485, 491, 492, 493, 494, 495, 502, 503, 505, 508, 511, 512, 514, 516, 517, 520, 522, 525, 533, 534, 542, 543, 545, 546, 551, 553

**Ecosystem Functions:** 206, 207, 222, 238, 266, 346, 347, 397, 399, 400, 403, 407, 409, 410, 411, 414, 415, 416, 455

**Endangered Species:** 44, 296, 299, 303, 377

**Entomology:** 19, 29, 33, 39, 42, 44, 45, 50, 53, 57, 60, 62, 71, 72, 77, 80, 91, 92, 93, 94, 95, 96, 97, 98, 121, 142, 144, 146, 147, 168, 169, 170, 196, 197, 200, 223, 224, 243, 244, 245, 247, 249, 250, 253, 258, 260, 261, 262, 263, 264, 265, 266, 267, 268, 269, 270, 292, 294, 317, 320, 340, 341, 342, 343, 344, 365, 366, 367, 369, 370, 390, 419, 431, 439, 440, 441, 463, 485, 508, 510, 518, 522, 527, 528, 529, 530

**Entomology:** 19, 29, 33, 39, 42, 44, 45, 50, 53, 57, 60, 62, 71, 72, 77, 80, 91, 92, 93, 94, 95, 96, 97, 98, 121, 142, 144, 146, 147, 168, 169, 170, 196, 197, 200, 223, 224, 243, 244, 245, 247, 249, 250, 253, 258, 260, 261, 262, 263, 264, 265, 266, 267, 268, 269, 270, 292, 294, 317, 320, 340, 341, 342, 343, 344, 365, 366, 367, 369, 370, 390, 419, 431, 439, 440, 441, 463, 485, 508, 510, 518, 522, 527, 528, 529, 530

**Environmental Education:** 520, 533

**Equity:** 77, 90, 498, 507, 508, 512

**Ethology:** 54, 78, 79, 91, 92, 95, 97, 98, 124, 140, 141, 145, 146, 147, 375, 379, 517, 525, 526

## F

**Filling Biodiversity Gaps:** 320

**Fire Disturbances:** 346, 357, 362, 455

**Foraging Strategies:** 88, 93, 124, 129, 140, 147, 266, 410

**Forensic Entomology:** 170, 247, 249, 250, 253, 258, 260, 261, 262, 263, 264, 265, 267, 268, 269

**Formicidae:** 8, 36, 49, 50, 53, 55, 62, 64, 70, 71, 72, 73, 74, 91, 92, 93, 94, 95, 96, 97, 98, 101, 102, 119, 120, 121, 122, 142, 143, 144, 145, 146, 147, 148, 150, 152, 164, 167, 168, 169, 170, 172, 174, 196, 199, 200, 201, 221, 222, 223, 242, 243, 244, 247, 249, 250, 252, 261, 263, 264, 266, 267, 268, 269, 270, 292, 296, 300, 315, 316, 317, 320, 334, 340, 341, 342, 343, 344, 364, 366, 369, 372, 374, 377, 383, 389, 390, 393, 394, 417, 421, 423, 426, 431, 439, 440, 441, 442, 444, 445, 460, 461, 462, 463, 464, 477, 480, 491, 492, 493, 494, 495, 503, 527, 528, 529, 530, 542, 543, 546, 551, 553

**Formicidae:** 8, 36, 49, 50, 53, 55, 62, 64, 70, 71, 72, 73, 74, 91, 92, 93, 94, 95, 96, 97, 98, 101, 102, 119, 120, 121, 122, 142, 143, 144, 145, 146, 147, 148, 150, 152, 164, 167, 168, 169, 170, 172, 174, 196, 199, 200, 201, 221, 222, 223, 242, 243, 244, 247, 249, 250, 252, 261, 263, 264, 266, 267, 268, 269, 270, 292, 296, 300, 315, 316, 317, 320, 334, 340, 341, 342, 343, 344, 364, 366, 369, 372, 374, 377, 383, 389, 390, 393, 394, 417, 421, 423, 426, 431, 439, 440, 441, 442, 444, 445, 460, 461, 462, 463, 464, 477, 480, 491, 492, 493, 494, 495, 503, 527, 528, 529, 530, 542, 543, 546, 551, 553

**Friar Kempf:** 18, 19, 20, 45

## G

**Gender Disparity:** 498

**Generalized Mutualism:** 272

**Geographic Distribution:** 47, 153, 240, 252, 267, 292, 372, 375, 376, 385, 467

**Grasslands:** 176, 190, 219, 220, 221, 222, 223, 275, 317, 344, 346, 352, 359, 364, 433, 444, 445, 447, 448, 450, 451, 452, 453, 454, 455, 457, 458, 460, 461, 462, 463, 538

## H

**History of Science:** 29, 30, 48, 49, 69

**Hymenoptera:** 11, 23, 31, 48, 49, 50, 61, 63, 64, 70, 71, 72, 73, 74, 91, 92, 93, 94, 95, 96, 97, 98, 104, 119, 120, 121, 122, 142, 143, 144, 145, 146, 147, 148, 152, 167, 168, 169, 170, 196, 199, 200, 201, 221, 222, 223, 242, 243, 244, 264, 266, 267, 268, 269, 270, 292, 315, 316, 317, 340, 341, 342, 343, 344, 364, 366, 369, 372, 377, 383, 388, 389, 390, 393, 394, 417, 421, 439, 440, 441, 442, 460, 461, 462, 463, 464, 477, 485, 492, 493, 494, 495, 503, 527, 528, 529, 530, 542, 543

## I

**Interspecific Interactions:** 77, 80, 83, 84, 89

## M

**Microbial Ecology:** 172, 188, 190, 198, 200, 201

**Mutualism:** 57, 91, 94, 182, 184, 185, 200, 226, 227, 229, 242, 243, 244, 245, 272, 275, 276, 286, 289, 290, 291, 293, 343

**Myrmecofauna:** 24, 58, 62, 152, 319, 423, 425, 437, 459, 469, 480, 521

**Myrmecology:** 7, 8, 9, 12, 18, 20, 21, 24, 25, 28, 29, 30, 31, 33, 34, 37, 38, 41, 42, 43, 44, 45, 46, 48, 53, 54, 60, 62, 67, 68, 69, 77, 101, 102, 103, 104, 172, 174, 190, 249, 320, 322, 323, 324, 325, 326, 336, 339, 347, 348, 423, 432, 436, 437, 438, 481, 482, 483, 484, 486, 490, 497, 498, 499, 500, 501, 502, 503, 504, 505, 506, 507, 508, 510, 511, 512, 513, 514, 515, 516, 517, 518, 520, 521, 522, 523, 524, 526, 527, 528, 529, 530, 545, 546, 550, 551, 553, 554, 555, 556

**Myrmecology:** 7, 8, 9, 12, 18, 20, 21, 24, 25, 28, 29, 30, 31, 33, 34, 37, 38, 41, 42, 43, 44, 45, 46, 48, 53, 54, 60, 62, 67, 68, 69, 77, 101, 102, 103, 104, 172, 174, 190, 249, 320, 322, 323, 324, 325, 326, 336, 339, 347, 348, 423, 432, 436, 437, 438, 481, 482, 483, 484, 486, 490, 497, 498, 499, 500, 501, 502, 503, 504, 505, 506, 507, 508, 510, 511, 512, 513, 514, 515, 516, 517, 518, 520, 521, 522, 523, 524, 526, 527, 528, 529, 530, 545, 546, 550, 551, 553, 554, 555, 556

## N

**Natural History:** 49, 51, 56, 60, 62, 63, 64, 65, 66, 67, 69, 73, 94, 95, 97, 101, 102, 103, 104, 107, 115, 117, 118, 119, 120, 121, 122, 139, 140, 143, 144, 146, 243, 250, 311, 324, 344, 367, 375, 393, 500, 503, 505, 513, 519, 520, 523, 530

**Natural Regeneration:** 205, 206, 208, 209, 212, 217, 219

**Neotropical Insects:** 172

**Neotropical Savanna:** 143, 291, 294, 346, 348, 363, 364, 365, 366, 367, 368, 369, 418, 420, 463

## O

**Outreach:** 8, 41, 64, 66, 511, 519, 522, 533, 534, 535, 538, 539, 540, 541, 545, 546, 549

## P

**Pampa Biome:** 444, 447, 448, 449, 450, 451, 452, 455, 456, 458, 459, 547, 555

**Parabiosis:** 227, 232, 233, 234, 238, 239, 240,

245

**Predatory Behaviour:** 124, 135, 142

**Priority Collection Areas:** 480

**Protection Mutualisms:** 242, 272, 273

## R

**Regeneration:** 205, 206, 208, 209, 212, 216, 217, 219, 222, 224, 225, 241, 331, 339, 397, 401, 409, 410, 411, 413, 414, 415, 416, 418

## S

**Sampling Efficiency:** 466, 469, 470, 472

**Science Communication:** 9, 47, 533, 540

**Scientific Outreach:** 511, 533, 534, 535, 539

**Scientific Research:** 19, 29, 31, 33, 45, 191, 500, 526, 533, 534, 540

**Social Behavior:** 77

**Social Insects:** 40, 45, 124, 125, 142, 151, 167, 169, 266, 286, 315, 343, 348, 391, 436, 520

**Socio-Academic Profiles:** 77

**Species:** 7, 8, 11, 22, 23, 24, 25, 33, 34, 35, 36, 44, 46, 47, 49, 50, 53, 54, 55, 56, 57, 58, 59, 60, 61, 62, 63, 64, 65, 66, 70, 71, 72, 74, 77, 79, 80, 83, 84, 86, 88, 89, 90, 93, 96, 98, 101, 102, 104, 105, 107, 108, 109, 111, 112, 113, 114, 115, 116, 117, 118, 119, 121, 122, 124, 125, 126, 127, 128, 129, 130, 131, 132, 133, 134, 135, 136, 137, 138, 139, 140, 141, 143, 144, 145, 148, 150, 152, 153, 154, 157, 160, 161, 162, 163, 164, 165, 166, 167, 168, 169, 170, 172, 173, 174, 175, 176, 177, 178, 180, 182, 183, 185, 186, 189, 190, 191, 192, 196, 197, 198, 199, 200, 201, 206, 208, 209, 210, 212, 216, 217, 218, 219, 221, 224, 227, 229, 230, 231, 232, 233, 234, 235, 236, 237, 238, 239, 240, 241, 242, 243, 244, 245, 247, 248, 249, 250, 251, 252, 253, 254, 255, 256, 257, 258, 259, 260, 261, 262, 263, 264, 266, 267, 268, 269, 272, 273, 274, 276, 277, 278, 279, 281, 283, 285, 286, 287, 288, 289, 290, 291, 292, 293, 294, 295, 296, 297, 298, 299, 300, 301, 302, 303, 304, 305, 306, 307, 308, 309, 310, 311, 312, 313, 314, 315, 316, 320, 322, 323, 324, 326, 327, 328, 329, 330, 331, 332, 333, 334, 335, 336, 337, 338, 340, 341, 344, 346, 347, 350, 351, 352, 353, 354, 355, 356, 357, 358, 359, 360, 361, 362, 363, 364, 365, 368, 369, 370, 372, 373, 374, 375, 376, 377, 378, 381, 382, 384, 385, 386, 387, 388, 390, 391, 392, 393, 397, 398, 399, 401, 402, 404, 405, 407, 408, 409, 410, 411, 412, 413, 414, 415, 416, 417, 419, 421, 423, 424, 425, 426, 427, 428, 429, 433, 434, 436, 437, 440, 441, 442, 444, 445, 446, 447, 448, 449, 450, 452, 453, 454, 455, 457, 458, 459, 460, 466, 467, 468, 469, 470, 471, 472, 473, 474, 475, 476, 478, 480, 481, 482, 483, 485, 486, 487, 489, 490, 492, 499, 507, 508, 510, 511, 514, 518, 520, 522, 523, 524, 525, 527, 528, 529, 530, 535, 536, 542, 543, 546

**Symbiosis:** 172, 188, 196, 198, 199, 202, 243, 244, 331, 343

**Systematic Review:** 12, 51, 123, 124, 125, 149, 152, 153, 174, 175, 176, 190, 201, 211, 225, 246, 247, 249, 272, 274, 283, 294, 370, 372, 374

## T

**Teaching:** 8, 9, 102, 503, 509, 539, 545, 546, 547

**Tropical Forest:** 92, 274, 320, 350, 399, 421

**Tropical Forests:** 105, 125, 164, 222, 227, 337, 350, 372, 411

## U

**Umbrella Species:** 296, 298, 308, 316

## V

**Vegetation Heterogeneity:** 346, 352, 369

**Vertebrate Carcass:** 247, 250, 268

**Vertical Stratification:** 328, 346, 353, 355, 356, 362, 369, 370

## W

**Wallacean Shortfall:** 466, 467, 473

**Woman in Science:** 498

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