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Microhabitat Variation in Feeding Places Shape Ant-Hemiptera Interactions Within Cocoa Agroecosystems

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ABSTRACT

Ant–hemiptera mutualisms are pivotal in tropical ecosystems, yet how these interactions respond to fine-scale microhabitat variation and management remains poorly understood. We investigated ant–hemiptera interactions across feeding microhabitats (flowers, leaves, pods) and contrasting management systems in Brazilian cocoa farms, comparing traditional agroforestry ("Cabruca," which retains much of the native shade) with intensified systems ("Total Suppressed," where native vegetation is removed). Across 934 interactions, leaves and pods supported larger and richer networks than flowers. Although Total Suppressed systems showed higher interaction frequency, network structural metrics such as nestedness and modularity remained stable across microhabitats and management types. This stability appears to be driven by dominant generalist ants acting as structural buffers. Core ant species were widely shared among plant structures, whereas core hemipteran species varied markedly across microhabitats, indicating ecological partitioning. In addition, interaction beta diversity was mainly driven by rewiring among persistent species rather than species turnover. Overall, while hemipterans respond to fine-scale microhabitat heterogeneity, dominant ants maintain network cohesion through behavioral plasticity, highlighting the resilience of mutualistic networks in cocoa agroecosystems.

RESUMO

Os mutualismos entre formigas e hemípteros são cruciais em ecossistemas tropicais, mas ainda é pouco compreendido como essas interações respondem à variação de micro-habitats em escala fina e ao manejo. Investigamos as interações entre formigas e hemípteros em diferentes micro-habitats de forrageamento (flores, folhas, frutos) e em sistemas contrastantes de manejo em fazendas de cacau brasileiras, comparando sistemas agroflorestais tradicionais ("Cabruca", que retém grande parte da sombra nativa) com sistemas intensificados ("Supressão Total", nos quais a vegetação nativa é removida). Ao longo de 934 interações, folhas e frutos sustentaram redes maiores e mais ricas do que flores. Embora os sistemas de Supressão Total tenham apresentado maior frequência de interação, métricas estruturais da rede, como aninhamento e modularidade, permaneceram estáveis entre micro-habitats e tipos de manejo. Essa estabilidade parece ser impulsionada por formigas generalistas dominantes que atuam como amortecedores estruturais. As espécies centrais de formigas foram amplamente compartilhadas entre as estruturas das plantas, enquanto as espécies centrais de hemípteros variaram acentuadamente entre os micro-habitats, indicando particionamento

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ecológico. Além disso, a diversidade beta de interações foi predominantemente determinada pela reorganização das interações entre espécies persistentes, em vez da substituição de espécies. De modo geral, enquanto os hemípteros respondem à heterogeneidade dos micro-habitats em escala fina, formigas dominantes mantêm a coesão da rede por meio de plasticidade comportamental, evidenciando a resiliência de redes mutualísticas em agroecossistemas de cacau.

1 | Introduction

Ecological interactions are characterized as fundamental components of the ecosystem processes that support biodiversity (Bascompte and Jordano 2007, Jordano 2016, Del-Claro and Torezan-Silingardi 2021). Among these interactions, ant mutualisms are especially notable, involving resource exchanges with a wide variety of organisms (Hölldobler and Wilson 1990; Ness et al. 2009; Nelson and Mooney 2022), and serve to protect their associated partners from their natural predators and parasites (Delabie 2001; Heil and McKey 2003; Rico-Gray and Oliveira 2007). A classic example is the mutualistic association between ants and hemipterans, especially species from the Auchenorrhyncha (e.g., membracids) and Sternorrhyncha (e.g., aphids, coccids, pseudococcids) suborders (Delabie 2001; Pringle 2021).

Hemipterans possess a distinctive trait among herbivorous insects: the ability to feed directly on plant sap extracted from the phloem and xylem tissues (Raven 1983; Douglas 2006). This feeding strategy is facilitated by their specialized mouthparts, which function like a straw, allowing them to pierce plant tissues and access internal fluids (Nelson and Mooney 2022). This feeding behavior results in the production of honeydew, a sugary excretion rich in carbohydrates, amino acids, and proteins, which is a key food resource for ants (Vilcinskas 2016). Honeydew is energy-rich, nutritionally valuable, and offers spatial and temporal stability since it is continuously produced by hemipterans that remain attached to their host plants, providing a reliable and spatially consistent food source (Blüthgen et al. 2000; Styrsky and Eubanks 2007) that arboreal ant populations largely use for their sustenance (Völkl et al. 1999). As a reliable trophic subsidy, honeydew supports ant colony growth and development (Davidson et al. 2003). In return, ants protect their hemipteran partners from predators and parasites and remove excess honeydew and other wastes, thereby maintaining the health and efficiency of their hosts (Delabie 2001; Billick et al. 2007; Nielsen et al. 2010; Banerjee et al. 2024).

However, these mutualisms are not evenly distributed among ant species. Dominant arboreal ants often monopolize honeydew resources through aggressive behavior and interspecific competition, excluding other ants through the assemblage organization called “mosaic of dominant ants” well known in a range of agroecosystems and forests (Room 1975; Majer et al. 1994; Ribeiro et al. 2013; Dejean et al. 2019) and shaping the interactions of both ants and hemipterans (Blüthgen et al. 2000; Fagundes et al. 2016; Camarota et al. 2016). Thus, dominant ants can affect the richness and distribution of both other ants and the hemipterans with which they interact (Costa-Silva et al. 2023). These food-for-protection mutualisms are prevalent in diverse habitats and form intricate networks involving numerous species of ants and hemipterans (Blüthgen and Fiedler 2004). In many systems, four to five dominant ant species may coexist, each associated with a distinct hemipteran species as a key nutritional resource (Costa et al. 2016; Koch et al. 2020). The intensity and outcomes of these interactions can vary significantly within species pairs, depending on environmental conditions and the life-history traits of the organisms involved (Rico-Gray and Oliveira 2007; Chamberlain et al. 2014). These factors support the idea that ant-hemiptera mutualisms are keystone interactions, meaning they have significant evolutionary and ecological implications for both groups and wide-ranging consequences for the ecosystems in which these interactions occur (Styrsky and Eubanks 2007; Schifani et al. 2024).

However, the structure of these interaction networks is not static and can be strongly influenced by habitat complexity and management intensity. In tropical agroecosystems, such as cocoa (*Theobroma cacao*) plantations, management practices create a gradient of environmental heterogeneity ranging from diverse agroforestry systems to simplified monocultures (Philpott and Armbrecht 2006; Tscharntke et al. 2011). In the Atlantic Forest region of Brazil, the traditional system known as “Cabruca” involves cultivating cocoa under the thinned canopy of native forest trees, preserving high levels of structural complexity and shading (Sambuichi et al. 2012). In contrast, intensified management strategies, often referred to as “Total Suppressed” systems (where the native vegetation is removed and replaced by simplified shade), drastically reduce plant diversity and alter microclimatic conditions. Although the effects of shade simplification on ant species richness are well documented, often showing that complex habitats support more diverse ant communities while simplified ones favor behaviorally dominant species (Wielgoss et al. 2014), little is known about how these habitat changes cascade to affect the architecture of mutualistic networks, despite their potential impact on yield and ecosystem services in cocoa (Bisseleua et al. 2017). Theoretically, the structural complexity of shaded systems (e.g., Cabruca) offers more nesting sites and foraging trails, potentially reducing interspecific competition and allowing for more generalized interactions (nestedness). Conversely, simplified environments may exacerbate competition, leading to stronger compartmentalization (modularity) driven by dominant ants defending distinct resource patches (Blüthgen and Fiedler 2004; Chamberlain et al. 2014).

In addition to the macro-scale influence of the agroecosystem type, microhabitat variation at the plant scale plays a crucial role in structuring these interactions. Hemipterans often exhibit strong fidelity to specific plant structures, such as flowers, pods, or flushing leaves, depending on their feeding specialization and the spatial distribution of phloem quality (Campbell 1990; Cushman and Whitham 1991). This microhabitat partitioning is further shaped by plant phenology and tissue accessibility, which vary across the plant's architecture and developmental stages (Cushman and Whitham 1991; Stadler and Dixon 2005). Ants, in turn, selectively attend to hemipterans that excrete larger quantities of high-quality honeydew (Bristow 1991), often resulting in resource monopolization by dominant ant species in specific microhabitats (Room 1975; Shingleton et al. 2005). By defending these hemipterans, ants facilitate more continuous and deeper feeding on phloem, granting their partners access to structurally protected or high-yielding host tissues such as pods and woody branches (Davidson et al. 2003; Shingleton et al. 2005). Consequently, within-plant microhabitat variation acts as a finer filter for interaction specialization and spatial segregation (Blüthgen and Klein 2011; Stuble et al. 2013), potentially creating distinct interaction modules within the same agroecosystem. However, little is known about how this micro-scale heterogeneity interacts with the overarching management regime to modulate ant-hemiptera network architecture.

In this study, we employed network analysis to investigate how the architecture of ant–hemiptera interactions varies between two distinct cocoa management schemes (the structurally complex "Cabruca" vs. the simplified "Total Suppressed" system) and across different hemipteran feeding microhabitats (flowers, pods, and flushing leaves). We hypothesized that: (1) At the ecosystem level, network structure differs due to habitat complexity: we expected networks in the Cabruca system to exhibit higher nestedness and lower modularity. Mechanistically, the presence of native shade trees increases habitat heterogeneity and connectivity, facilitating the coexistence of species and promoting generalized interactions (resource overlap). In contrast, we anticipated that the Total Suppressed system would be more modular and specialized. Mechanism: The simplified structure and harsher microclimate favor the dominance of aggressive ant species, which monopolize hemipteran aggregations and compartmentalize the network. (2) At the plant level, feeding microhabitat filters interactions: we expected pod-based interactions to be more specialized and modular compared to leaves and flowers. Mechanism: Pods often support larger, stable hemipteran aggregations that produce high volumes of honeydew, making them prime targets for monopolization by dominant ants, whereas ephemeral resources like flowers promote more opportunistic and generalized visits.

2 | Material and Methods

2.1 | Study Area

The study was carried out in six cocoa plantations (*Theobroma cacao*) representing two distinct cocoa agroecosystems (three areas per system) in the municipality of Ilhéus, state of Bahia, Brazil: the "Cabruca" (CA) system and the "Total Suppressed" (TS) system. In the Cabruca system, the cocoa tree is cultivated under the thinned canopy of native Atlantic Forest trees, maintaining a complex and diverse multi-strata structure (Cassano et al. 2009; Schroth et al. 2011). Sampling in this system was carried out at Fazenda São Francisco (14°45′04″ S; 39°13′11″ W), Fazenda Primavera (14°47′34″ S; 39°12′44″ W), and Fazenda Nossa Senhora da Vitória (14°45′55″ S; 39°12′07″ W). In contrast, the Total Suppressed system represents an intensified management regime established through the clear-cutting of the original native forest vegetation. In these areas, the density of cocoa trees is approximately twice (~1100 trees/ha) as high as in the Cabruca system (500 to 600 trees/ha), and shading is provided exclusively by a monodominant canopy of the exotic tree *Erythrina* sp. (Delabie et al. 2007), resulting in a structurally simplified environment. Sampling for this agroecosystem was conducted in three areas on the grounds of the Centro de Pesquisas da Lavoura Cacaueira (CEPLAC), Ilhéus, BA, Brazil (14°45′ S; 39°13′ W) (Figure 1). The study region is located within the Atlantic Forest biome (Delabie et al. 2007), characterized by an AF climate type (hot and humid) according to the Köppen (1936) classification, with average annual temperatures varying from 20°C to 25°C (Rodrigues and Costa 2021).

2.2 | Data Sampling and Species Identification

We established three 50 × 25 m plots per site. Cocoa tree density varied between systems, with a mean of 79 ± 8 trees per plot in the Cabruca system and 138 ± 15 trees per plot in the Total Suppressed system. From January to December 2014, we performed monthly surveys (three sampling events per season) to capture seasonal variation. During each survey period (08:00–17:00 h), every cacao tree in the plots was inspected for 5 min, focusing on flowers, pods, and flushing leaves, where ant–hemiptera mutualisms most frequently occur. Whenever an ant was observed feeding on a hemipteran, we recorded both species and the specific plant organ involved and collected vouchers for subsequent identification at the laboratory. Subsequently, Hemiptera specimens were forwarded to taxonomic experts for identification. Specimens were identified to the genus or species level when possible; when immatures of Membracidae could not be resolved to species, they were retained under the family name "Membracidae" for subsequent analyses. All vouchers are deposited in the corresponding institutional collections. Ant and aphid specimens were identified using standard dichotomous keys and by comparison with the reference holdings of the CEPLAC/USFB/UESC Myrmecology Laboratory (CPDC, Delabie et al. 2020).

2.3 | Network Analyses

In this study, we constructed quantitative bipartite matrices to describe interactions between ant and hemipteran species across distinct feeding microhabitats. Each matrix was organized with hemipteran and ant species in separate partitions, and the cell values represented the total number of independent interaction events, that is, the number of times a given ant species was observed feeding on honeydew produced by a particular hemipteran species within a specific plant structure. We built three separate matrices, corresponding to the three feeding microhabitats (flower, leaf, and pod), and an additional pooled matrix combining all records across microhabitats. This approach allowed us to quantify and compare network structural metrics both within and across microhabitats, and to examine differences between agroecosystem types (Cabruca vs. Total Suppressed). All interaction data were structured as quantitative bipartite adjacency matrices, where rows represented ant species and columns represented hemipteran species. Each cell in the matrix A_{ij} indicated the total frequency of interactions observed between ant species "i" and hemipteran species "j" in the corresponding microhabitat layer, while zeros denoted the absence of interactions. In this framework, the feeding place was treated as a network layer, enabling the comparison of interaction structures

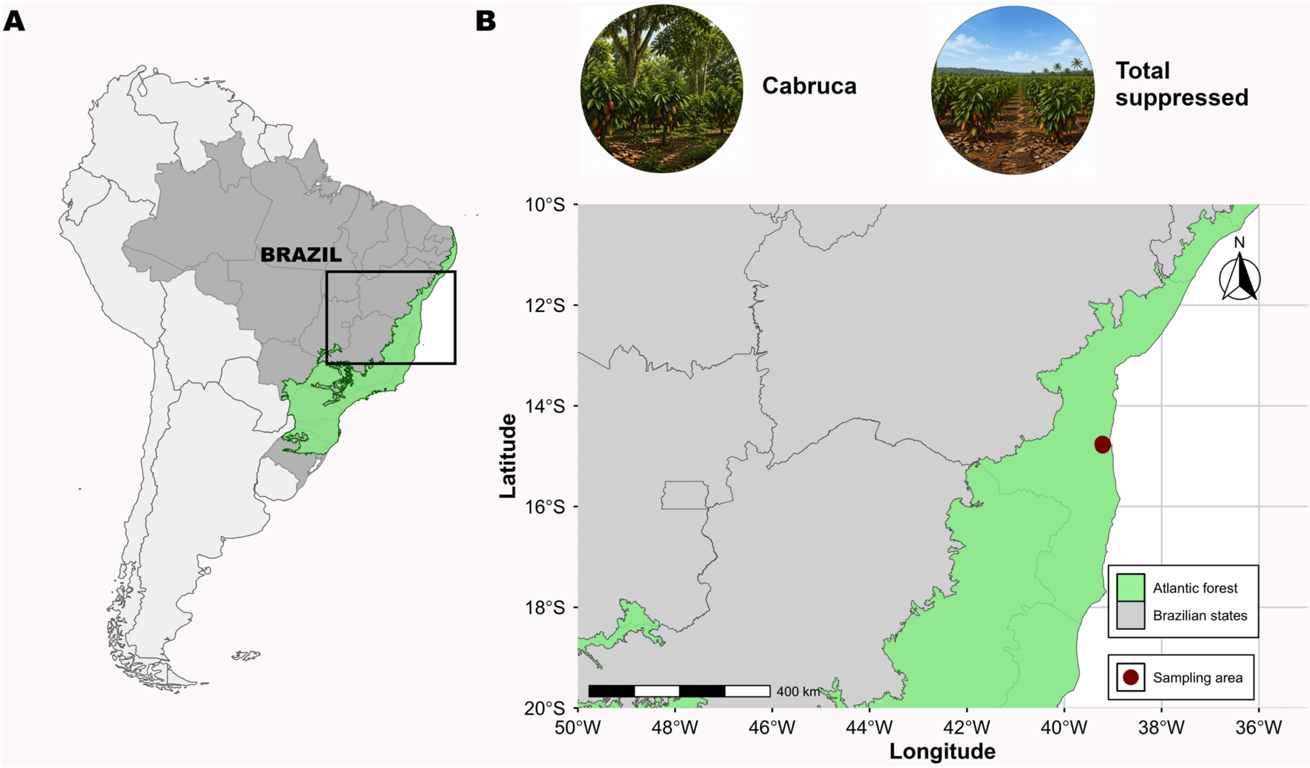

FIGURE 1 | (A) Map of South America highlighting Brazil and the Atlantic Forest biome (green), with the inset indicating the study region. (B) Detailed view of the study area in Bahia, northeastern Brazil, with the sampling site marked by a red point. Circular panels illustrate the two cocoa agroecosystems investigated: Cabruca (traditional agroforestry system with native shade trees) and Total Suppressed (intensified system with simplified canopy and reduced vegetation complexity).

among microhabitats while maintaining the classical bipartite ant-hemiptera interaction format within each layer. The networks were built using the 'circlize' package (Gu et al. 2014) in R version 4.4.1 (R Core Team 2025).

To investigate how the structure of ant–Hemiptera interactions varied among microhabitats, we calculated four widely used quantitative network metrics: (1) Connectance (C), defined as the proportion of realized interactions relative to all possible interactions, was calculated using the *networklevel* function; (2) Nestedness, defined as the degree to which the interaction partners of specialist species constitute subsets of those of more generalist species, was quantified using the Weighted Nestedness metric based on Overlap and Decreasing Fill (WNODF), which accounts for interaction frequencies in weighted matrices (Almeida-Neto and Ulrich 2011). Calculations were performed with the *networklevel* function using the WNODF method, which accounts for interaction frequencies in weighted matrices; (3) Complementary specialization (H2′) was calculated to assess the overall level of specialization in the network, providing a quantitative measure of interaction diversity based on Shannon entropy (Blüthgen et al. 2006, 2007). H2′ values close to 0 indicate high generalization and redundancy, while values closer to 1 indicate high specialization; and (4) Modularity (Q) was calculated using the QuaBiMo algorithm (Dormann and Strauss 2013), which was specifically developed for quantitative bipartite networks and is based on a stochastic simulated annealing approach. We used the *computeModules* function, retaining the highest Q value obtained after 1000 iterations as the modularity score for each network.

All metrics were calculated separately for each microhabitat network (i.e., flower, leaf, and pod), using quantitative bipartite matrices of interactions, where rows represented ant species, columns represented hemipteran species, and cell values indicated the frequency of interactions observed across plots. Network analyses were conducted using the package 'bipartite' (Dormann et al. 2025).

To assess whether the observed network metrics differed significantly from random expectations, we applied the Patefield null model, implemented via the *r2dtable* algorithm (Patefield 1981) using the *nullmodel* function of the 'vegan' package (Oksanen et al. 2025). This model generates quantitative randomized networks by constraining both row and column marginal totals, thus preserving the observed interaction frequencies per species (i.e., the marginal sums) while allowing the identity of the interacting partners to be randomized. Given the quantitative nature of our interaction data and the goal of comparing network patterns across microhabitat layers without introducing biases related to variation in interaction intensity or species marginal totals, the Patefield model was the most suitable choice for our analyses. For each network metric (i.e., WNODF, H2′ and Q), the observed value was compared to the distribution of values obtained from 999 randomized networks, and significance was inferred based on the proportion of null values equal to or exceeding the observed metric ($\alpha = 0.05$) (Manly 2018).

2.4 | Differences in Networks Structure Among Microhabitats

To test whether the structure of ant-hemiptera interaction networks differed among feeding microhabitats, we compared general descriptors of network structure across the three identified microhabitats: flowers, leaves, and pods. Specifically, we assessed network size (total number of interacting species), interaction richness (total number of unique ant-hemiptera interaction pairs), and interaction frequency (total number of interaction events). These metrics were calculated separately for each plot ($n = 3$) within each microhabitat ($n = 3$), resulting in independent replicates that accounted for spatial variability in the data.

We analyzed our data using generalized linear models (GLMs), with each interaction descriptor (i.e., network size, richness of interactions, and interactions frequency) set as response variables, with Microhabitat and Environment included as explanatory factors. Because these descriptors represent count data, models were initially fitted using Poisson error distributions. Model adequacy was evaluated using residual diagnostics. For interaction frequency, these diagnostics revealed substantial overdispersion; therefore, this response variable was subsequently analyzed using Negative Binomial GLMs (using the *glm.nb* function from the 'MASS' package), which appropriately accounted for the observed variance structure.

For the structural network properties, we used two distributions. Connectance is a bounded response variable ranging from 0 to 1. Since it represents a proportion derived from counts of links (realized) out of a known number of potential links (possibilities), we modeled connectance using a binomial GLM with a logit link function. This approach is appropriate for proportion data constrained between 0 and 1 and ensures that predicted values remain within this interval. For nestedness (WNODF), modularity (Q), and complementary specialization (H2′) we used Gaussian GLMs (i.e., normal error distribution with identity link). Although modularity (Q) and complementary specialization (H2′) are bounded, the observed values were not close to their limits and exhibited approximately symmetric distributions. For all models, visual inspection of residuals indicated no strong deviations from normality or homoscedasticity.

Given the balanced but limited number of sampling units per category, we used fixed-effect GLMs as a hypothesis-driven and interpretable framework. Each network metric was analyzed separately, with Microhabitat and Environment included as fixed predictors, and statistical significance was assessed using likelihood ratio tests based on comparisons with null models.

For all metrics, GLMs were fitted using the *glm* function, while Negative Binomial models utilized the 'MASS' package (Venables and Ripley 2002). Model adequacy was evaluated using residual diagnostics implemented in the 'DHARMa' package (Hartig 2024). Post hoc comparisons among microhabitats were conducted using Tukey-adjusted pairwise contrasts via the 'emmeans' package (Lenth 2017).

2.5 | Core-Periphery Species Composition

We used degree centrality to identify the core species within each interaction layer (i.e., flower, leaf, pod) and to assess whether the composition of these central species remained consistent across microhabitats. Among the various centrality indices proposed for ecological network analysis, degree centrality is the most direct and widely used, representing the number of direct interactions a species (node) has within the network (Lau et al. 2017; Rodrigues 2019). Degree centrality is also a key metric for revealing core–periphery patterns, where highly connected species (core) act as hubs linking less connected species (periphery) to the broader network structure (Lee 2016; Martín González et al. 2020; Miele et al. 2020). To control variation in network size and to allow fair comparisons, we used the normalized degree, calculated as the number of interactions per species divided by the number of possible interacting partners within the network, providing a standardized measure of a species' specialization relative to other species (Dunne et al. 2002). For each microhabitat and within each plot ($n = 9$), we used the *specieslevel* function from the 'bipartite' package (Dormann et al. 2025) to calculate degree centrality for all species. Species with a degree centrality above the network average were classified as core species, following approaches commonly used to delineate core–periphery structures (Costa et al. 2016; Lau et al. 2017; Martín González et al. 2020).

To evaluate whether the composition of core-periphery species varied among the different microhabitats, we compiled the occurrence of identified core-periphery species per site and microhabitat and conducted a permutational multivariate analysis of variance (PERMANOVA) using the *adonis* function in the 'vegan' package (Oksanen et al. 2025). Differences in core-periphery species composition among microhabitats were visualized using non-metric multidimensional scaling (NMDS) based on Bray–Curtis dissimilarity.

2.6 | Beta Diversity of Interactions

We evaluated the beta diversity of ant-hemiptera interactions across feeding microhabitats using the framework proposed by Poisot et al. (2012), which decomposes the dissimilarity of interactions (βWN) into two additive components: species turnover (βST) and interaction rewiring (βOS). In this framework, $\beta WN = \beta ST + \beta OS$, where βST accounts for dissimilarity due to species replacement between networks, while βOS captures changes in interaction patterns among shared species (Poisot et al. 2012; CaraDonna et al. 2017). This partitioning allows for the disentangling of whether changes in interaction networks are primarily driven by species turnover or by rewiring among persistent species. To allow this analysis, all matrices were converted to binary format to standardize the analyses and avoid biases due to variation in interaction frequency. The matrices were then aligned using the *webs2array* function to create a three-dimensional array of networks with consistent species pools, enabling accurate partitioning of beta diversity components. We calculated pairwise beta diversity of interactions between the three microhabitats using the *betalinkr_multi* function with Poisot partitioning (Poisot et al. 2012). For each pair of microhabitats, we obtained the overall dissimilarity of interactions (βWN), as well as the relative contribution of species turnover (βST) and rewiring (βOS), by expressing each component as a proportion of βWN (i.e., βST divided by βWN and βOS divided by βWN). The analyses were performed using the 'bipartite' package (Dormann et al. 2025) for the decomposition of interaction dissimilarity, and the 'vegan' package (Oksanen et al. 2025) for visualization and supporting analyses. All analyses were performed in R version 4.4.1 (R Core Team 2025).

3 | Results

3.1 | Ant–Hemipteran Community Composition and Interactions

A total of 562 ant-hemiptera interactions were recorded in the "Total Suppressed" and 372 in the "Cabruca" agroecosystems, totaling 934 interactions. Interactions were observed across different microhabitats, with 135 interactions in flowers, 398 in leaves, and 401 in pods. In the CA system, interactions involved 27 ant species (from 13 genera) interacting with 20 hemipteran species (from 11 genera). In contrast, the TS system featured 39 ant species (from 16 genera) interacting with 22 hemipteran species (from 15 genera). Specifically, in flowers, we identified 25 ant species and 10 hemipteran species; in pods, 25 ant species and 19 hemipteran species; and in pods, 37 ant species and 16 hemipteran species across both agroecosystems. We recorded a total of 135 unique pairs of interacting species (interaction richness) in the TS system, compared to 96 pairs in the CA system (Table 1).

3.2 | Network Characteristics and Properties Across Microhabitats

Consistent with our expectations, the characteristics of ant-hemiptera interaction networks differed among feeding microhabitats and between agroecosystem types (Table 1). Overall, leaf and pod networks supported larger network sizes, higher interaction richness, and greater interaction frequency compared to flower networks, with no differences detected between leaf and pod. Similarly, networks in the Total Suppressed system consistently exhibited higher values for all three metrics compared to Cabruca (Figure 2; Table 2). These patterns highlight the combined influence of feeding microhabitats and management practices shaping the organization of ant-hemiptera interactions (Figure 3).

However, contrary to our predictions, the structural metrics of the ant-hemiptera networks, including connectance, nestedness (WNODF), modularity (Q), and specialization (H2′), did not differ among feeding microhabitats or agroecosystem types (Table 3). These results indicate that, although some structural descriptors such as network size, interaction richness, and interaction frequency showed clear differences among microhabitats, the internal organization of interactions, as reflected by connectance, nestedness, modularity, and specialization, remained stable across feeding places and agroecosystems.

TABLE 1 | Descriptors of the ant-hemiptera networks across microhabitats (flower, leaf, pod) and the general network in Cabruca and Total Suppressed agroecosystems. Values include the richness of ant and hemipteran species, interaction pairs (number of unique ant-hemiptera pairs), interaction frequency (total number of interactions), connectance, nestedness (WNODF), specialization (H2′), and modularity (Q). The corresponding *p*-values indicate the significance of each metric compared to the null model. Bold values highlight significant values ($p < 0.05$).

	Microhabitat			
	Flower	**Leaf**	**Pod**	**General**
Cabruca				
Ant	13	21	19	27
Hemiptera	6	16	19	20
Interactions pairs	20	56	66	96
Interactions frequency	38	138	196	378
Connectance	0.256	0.166	0.182	0.177
Nestedness	23.297	18.762	32.279	38.015
p	0.585	0.981	0.795	0.693
Specialization	0.318	0.310	0.302	0.261
p	0.291	**< 0.001**	**< 0.001**	**< 0.001**
Modularity	0.45	0.426	0.367	0.363
p	0.152	**< 0.001**	**< 0.001**	**< 0.001**
Total suppressed				
Ant	23	33	24	39
Hemiptera	10	16	19	22
Interactions pairs	43	80	76	135
Interactions frequency	97	260	205	562
Connectance	0.186	0.151	0.166	0.157
Nestedness	26.426	27.895	21.646	36.161
p	0.782	0.967	0.998	0.796
Specialization	0.211	0.303	0.318	0.257
p	0.302	**< 0.001**	**< 0.001**	**< 0.001**
Modularity	0.432	0.392	0.429	0.351
p	0.228	**< 0.001**	**< 0.001**	**< 0.001**

3.3 | Core Species Composition

In both agroecosystems, the composition of core ant species did not differ among microhabitats (flower, leaf, pod). In the Cabruca system, PERMANOVA indicated no significant effect of microhabitat on the composition of core species ($F=0.293$, $p=0.921$, $R^2=0.0889$). Similarly, in the Total Suppressed system, the composition of core ant species was not structured by microhabitat ($F=0.353$, $p=0.907$, $R^2=0.1052$). The ants *Azteca chartifex spiriti, Crematogaster acuta* and *Dolichoderus bidens* dominated Cabruca, while *Cephalotes atratus, Dolichoderus bispinosus, Ectatomma tuberculatum, Dolichoderus bidens*, and *Solenopsis geminata* dominated the Total suppressed system. These results indicate a consistent pattern across both agroecosystems, suggesting that the dominant ants acting as network cores are widely shared across microhabitats and that no clear spatial differentiation occurs in the core-periphery structure within the microhabitats.

In contrast to ants, the composition of core hemipteran species differed among microhabitats in both agroecosystems. In the Cabruca system, PERMANOVA revealed a significant effect of microhabitat on the composition of core hemipteran species ($F=7.100$, $p=0.003$, $R^2=0.703$). Similarly, core hemipteran species composition in the Total Suppressed system varied across microhabitats ($F=11.202$, $p=0.004$, $R^2=0.789$). While the aphid *Toxoptera aurantii* was a core species broadly distributed across flowers and leaves in both systems, other abundant hemipterans showed stronger restrictions; for instance, *Planococcus minor* and Membracidae species were more frequently associated with pods and woody stems. These results indicate that, unlike ants, the composition of core hemipteran species is strongly structured by the microhabitat, highlighting a higher specialization or partitioning of core hemipterans across different feeding places within both agroecosystems.

3.4 | Beta Diversity of Interactions

In both agroecosystems, the beta diversity of ant-hemiptera interactions among microhabitats was consistently dominated by rewiring of interactions among shared species, rather than by species turnover. In the Cabruca system, interaction rewiring accounted for most of the interaction dissimilarity across all microhabitat pairs, representing 63.8% between flower and leaf, 73.2% between flower and pod, and 80.5% between leaf and pod of total dissimilarity (βWN). Similarly, in the Total Suppressed system, rewiring contributed 60.9%, 77.3%, and 74.9% for the same respective comparisons (Figure 4). These results indicate that, regardless of the agroecosystem, changes in interaction networks across microhabitats are primarily driven by interaction rewiring among persistent species, with species turnover playing a secondary role.

4 | Discussion

Our study demonstrates that while feeding microhabitats strongly shape the intensity and composition of ant-hemiptera interactions in cocoa agroecosystems, the overall network architecture remains remarkably invariant. This structural stability is driven by a small set of numerically and behaviorally dominant ants, specifically from the genera *Azteca*, *Solenopsis*, and *Dolichoderus* which function as flexible network hubs. These species maintained central roles across flowers, leaves, and pods, effectively buffering the network against

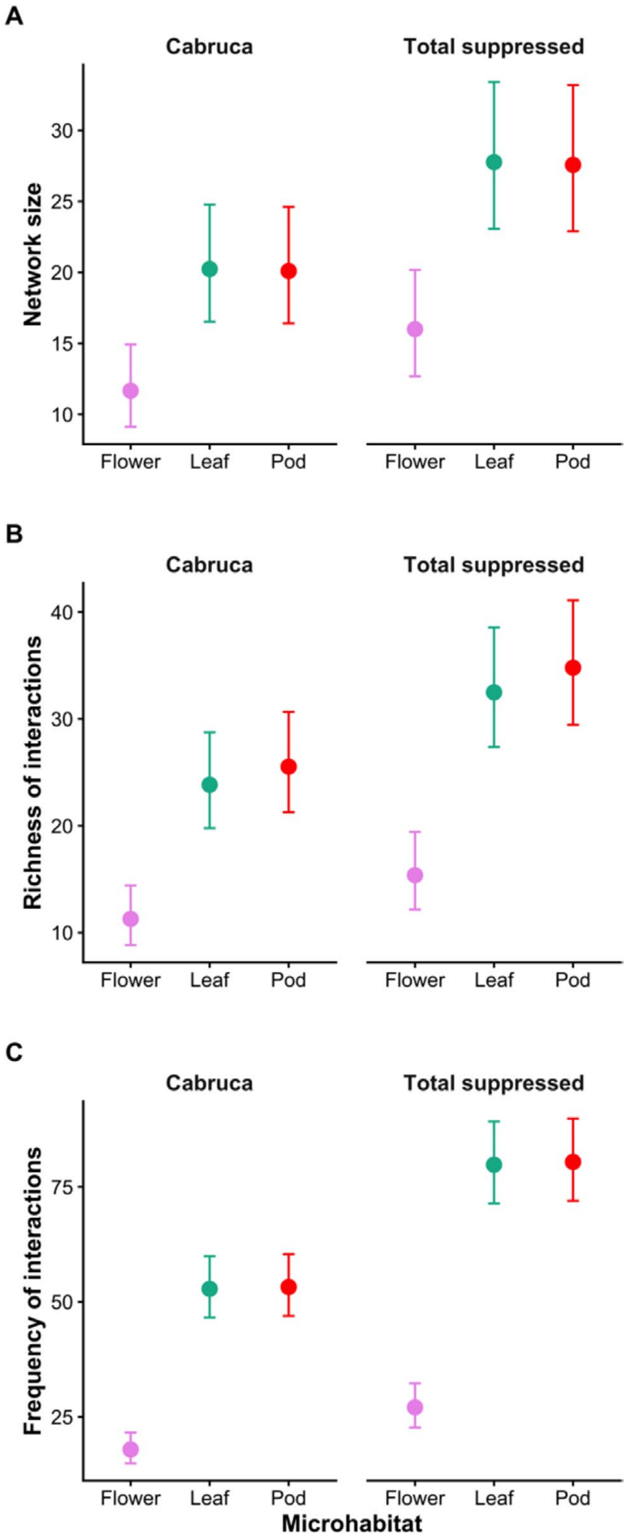

FIGURE 2 | Interaction patterns across microhabitat (flower, leaf, pod) and agroecosystem type (Cabruca, Total Suppressed) on general descriptors of ant-Hemiptera interaction networks. (A) network size (total number of interacting species), (B) interaction richness (number of unique ant-Hemiptera pairs), and (C) interaction frequency (total number of observed interactions).

TABLE 2 | Generalized linear models (GLMs) results showing the effects of microhabitat (flower, leaf, pod) and agroecosystem type (Cabruca, Total Suppressed = TS) on network size, interaction richness, and interaction frequency of ant-hemiptera interaction networks. Estimates are presented on the log scale. Tukey post hoc pairwise comparisons were conducted for the microhabitat factor. Significant values ($p < 0.05$) are highlighted in bold.

	Effect	Estimate	SE	z value	p	Tukey comparison	p
Network size	Microhabitat (leaf vs. flower)	0.551	0.1378	3.998	< 0.001	Flower/Leaf	**0.0002**
	Microhabitat (pod vs. flower)	0.544	0.1380	3.942	< 0.001	Flower/Pod	**0.0002**
	Microhabitat (leaf vs. pod)	—	—	—	—	Leaf/Pod	0.9981
	Environment (TS vs. Cabruca)	0.316	0.1053	3.003	0.0026	—	—
Interaction richness	Microhabitat (leaf vs. flower)	0.748	0.1357	5.511	< 0.001	Flower/Leaf	**< 0.0001**
	Microhabitat (pod vs. flower)	0.816	0.1343	6.081	< 0.001	Flower/Pod	**< 0.0001**
	Microhabitat (leaf vs. pod)	—	—	—	—	Leaf/Pod	0.7973
	Environment (TS vs. Cabruca)	0.309	0.0976	3.170	0.0015	—	—
Interaction frequency	Microhabitat (leaf vs. flower)	1.101	0.2054	5.36	< 0.001	Flower/Leaf	**< 0.0001**
	Microhabitat (pod vs. flower)	1.171	0.2049	5.72	< 0.001	Flower/Pod	**< 0.0001**
	Microhabitat (leaf vs. pod)	—	—	—	—	Leaf/Pod	0.9286
	Environment (TS vs. Cabruca)	0.502	0.1629	3.079	0.0021	—	—

environmental heterogeneity. In contrast, hemipteran assemblages exhibited marked microhabitat partitioning, with species restricted to specific feeding sites. These findings refine our understanding of mutualistic networks by showing that while "bottom-up" resources (microhabitats) filter the identity of partners, "top-down" biotic forces (dominant ants) homogenize the global network structure (Lee and Inouye 2010; Costa et al. 2016; Fagundes et al. 2016).

4.1 | Microhabitat-Driven Variation in Interaction Intensity and Richness

Our results confirmed that leaves and pods consistently supported larger networks, higher interaction richness, and greater frequency than flowers. These differences align with the "resource concentration hypothesis," where pods and flushing leaves provide more stable and voluminous phloem resources, sustaining larger hemipteran aggregations and, consequently, attracting more intense ant attendance (Blüthgen and Fiedler 2004; Shingleton et al. 2005; Banerjee et al. 2024). Similar microhabitat partitioning has been reported in cocoa (Way 1963; Koch et al. 2020), suggesting that the spatial distribution of phloem quality acts as a primary filter for interaction establishment. Furthermore, the Total Suppressed system supported higher interaction intensity than the Cabruca system. This likely reflects the denser planting density and simplified canopy of the intensified system, which may facilitate foraging trails and support larger populations of open-habitat dominant ants (Styrsky and Eubanks 2007; Philpott and Armbrecht 2006). Thus, while management intensity boosts the quantity of interactions, often affecting potential ecosystem services or disservices (Bisseleua et al. 2017), microhabitat quality determines their spatial distribution within the plant.

4.2 | Stability of Network Structure Metrics Across Microhabitats

Contrary to our initial expectations, network-level structural properties (connectance, nestedness, modularity, and specialization) did not vary among microhabitats or agroecosystem types. This consistency suggests a high degree of structural resilience mediated by dominant ant species (defined here as core species with high network centrality and local abundance). Species such as *Azteca chartifex spiriti*, *Dolichoderus bidens* (in Cabruca system), and *Solenopsis geminata* (in Total Suppressed system) acted as generalist hubs. Their behavioral

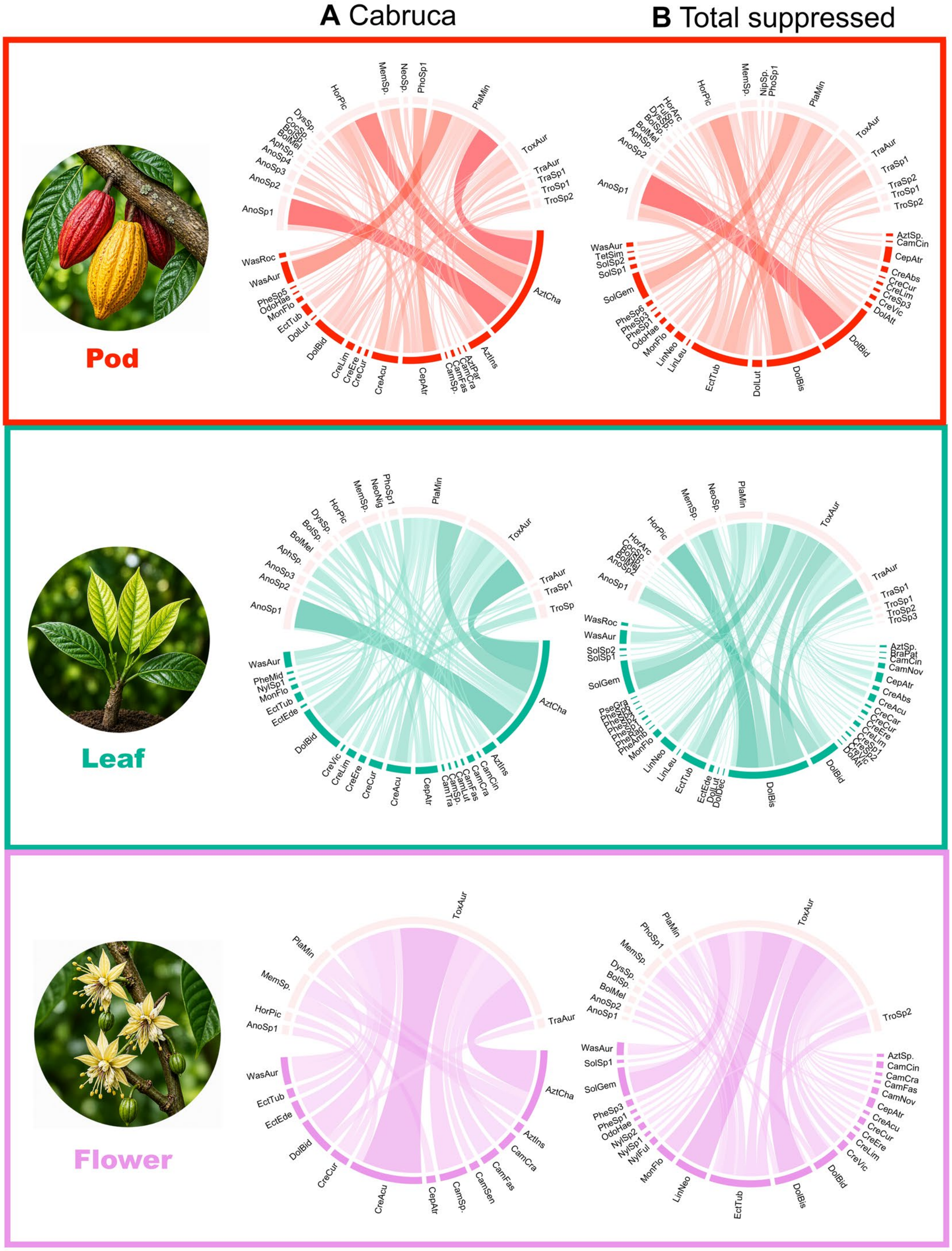

FIGURE 3 | Interaction networks of ants and hemipterans across different plant structures in Cabruca (A) and Total Suppressed (B) agroecosystems. The figure illustrates the interactions between ant species (dark colors), hemiptera species (light colors), and their occurrence in different plant structures (pod, leaf, flower). Species codes are available in Table S1. The images of the plant structures were produced using the Adobe AI Image Generator.

plasticity allows them to switch partners opportunistically based on resource availability rather than species identity (Spiesman and Gratton 2016; Costa-Silva et al. 2023). This pattern supports the "dominance-diversity" trade-off often observed in ant mosaics (Majer et al. 1994; Dejean et al. 2019), where a few aggressive species monopolize resources across the entire tree, effectively "gluing" the network modules together. Consequently, the internal organization of these networks is less sensitive to environmental variation because the central nodes (the ants) remain constant, even if the peripheral nodes (the hemipterans) change (Dáttilo et al. 2014; Cagnolo and Tavella 2015).

4.3 | Asymmetry in Core Species Composition

A striking contrast emerged in the core–periphery structure: core ant species were broadly shared across all microhabitats, whereas

TABLE 3 | Generalized linear models (GLMs) results showing the effects of microhabitat (flower, leaf, pod) and agroecosystem type (Cabruca, Total Suppressed = TS) on network connectance, nestedness (WNODF), modularity (Q), and specialization (H2′) of ant-Hemiptera networks. Estimates are presented on the logit (for connectance) or linear scale (for other metrics). Significant values ($p < 0.05$) are highlighted in bold.

	Effect	Estimate	SE	*z*/*t* value	*p*
Connectance (logit)	Microhabitat (leaf vs. flower)	−0.817	1.3182	−0.619	0.536
	Microhabitat (pod vs. flower)	−0.727	1.2997	−0.560	0.576
	Environment (TS vs. Cabruca)	−0.573	1.0929	−0.524	0.600
Nestedness (WNODF)	Microhabitat (leaf vs. flower)	−5.948	6.7714	−0.878	0.395
	Microhabitat (pod vs. flower)	−0.996	6.7714	−0.147	0.885
	Environment (TS vs. Cabruca)	−8.051	5.5288	−1.456	0.167
Modularity (Q)	Microhabitat (leaf vs. flower)	0.087	0.0588	1.487	0.159
	Microhabitat (pod vs. flower)	0.094	0.0588	1.601	0.132
	Environment (TS vs. Cabruca)	0.036	0.0480	0.753	0.464
Specialization (H2′)	Microhabitat (leaf vs. flower)	0.007	0.0870	0.079	0.938
	Microhabitat (pod vs. flower)	0.009	0.0870	0.108	0.915
	Environment (TS vs. Cabruca)	0.018	0.0710	0.249	0.807

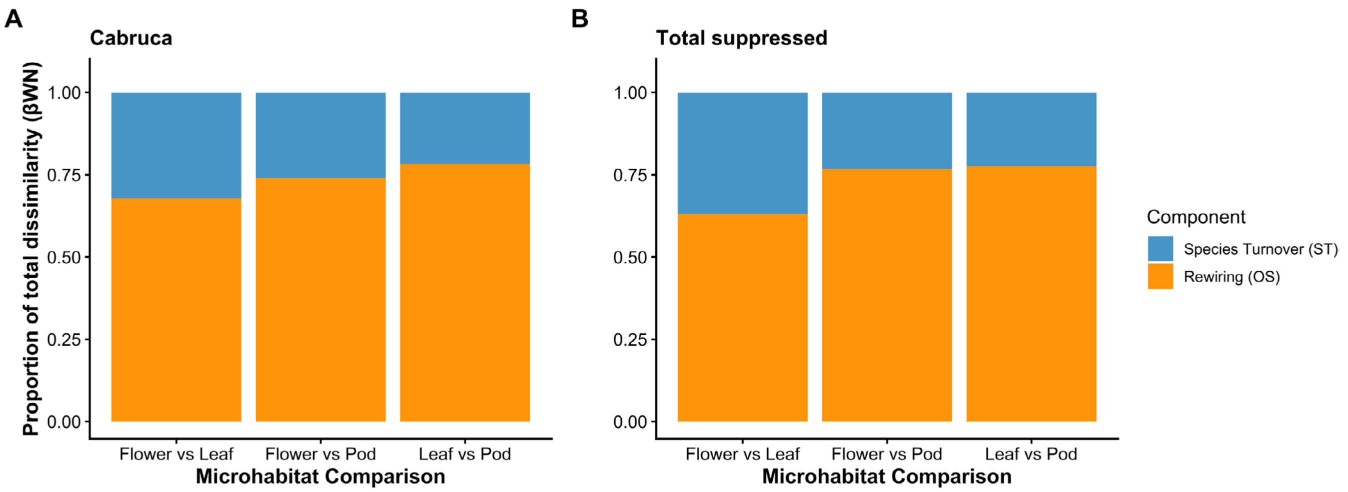

FIGURE 4 | Additive partitioning of beta diversity of ant-Hemiptera interactions among microhabitats (flower, leaf, pod) in Cabruca (A) and Total Suppressed (B) agroecosystems. Bars represent the proportion of total interaction dissimilarity (βWN) explained by species turnover (βST, in blue) and interaction rewiring among shared species (βOS, in orange).

core hemipteran species were highly partitioned. This asymmetry highlights distinct ecological constraints for each group. For dominant ants, the plant is a single foraging territory; for hemipterans, specific plant organs represent distinct ecological niches defined by physiological constraints (e.g., stylet length vs. tissue depth) and nutritional requirements (Shingleton et al. 2005; Banerjee et al. 2024). For instance, while the aphid *Toxoptera aurantii* was a core species across multiple microhabitats, other hemipterans were restricted to specific tissues. This supports the view that hemipterans are the "specialist" partners responding to fine-scale plant architecture (Cushman and Whitham 1991; Koch et al. 2018), while ants act as the "generalist" partners integrating these spatially separated resources. This integration is crucial for network cohesion, as the spatial consistency of dominant ants prevents the network from fracturing into disconnected modules (Martín González et al. 2020; Cuautle et al. 2022).

4.4 | Interaction Rewiring as the Main Driver of Beta Diversity

Our analysis of beta diversity revealed that interaction rewiring, rather than species turnover, was the primary driver of network dissimilarity across microhabitats (contributing 60.9%–81% of βWN). This aligns with findings from other mutualistic systems involving generalist partners (Poisot et al. 2012; CaraDonna et al. 2017). In our system, this high rewiring reflects the opportunistic nature of the mutualism: dominant ants “rewire” their connections to whichever hemipteran species is most abundant or productive in a given microhabitat. This plasticity has important implications for ecosystem stability. If networks were driven primarily by species turnover, the loss of a specific hemipteran could destabilize the system. Instead, the dominance of rewiring suggests that these networks can reorganize rapidly in response to spatial or temporal changes in resource availability (Mello et al. 2019; Tavella and Cagnolo 2019).

5 | Conclusion

Our findings reveal that ant–hemipteran networks in cocoa agroecosystems maintain a remarkably stable internal organization despite strong environmental variation. This resilience is not an intrinsic property of the network but an emergent outcome of the behavior of a few dominant ant species (*Azteca*, *Solenopsis*, *Dolichoderus*). These biological “super-connectors” bridge spatially distinct microhabitats, overriding the compartmentalizing effects of hemipteran specialization. For management, this implies that maintaining the ecological functions of these mutualisms depends less on preserving specific pairwise interactions and more on maintaining habitat conditions that support these key functional groups (Schifani et al. 2024). Future research should explore how this dominance-driven stability interacts with temporal dynamics, particularly under changing climate scenarios in tropical agroforestry.

Author Contributions

T.E.D.M., C.S.F.M. and J.H.C.D. conceived the ideas and designed methodology; E.B.A.K. and T.E.D.M. collected the data; E.L.S.B. and W.D. analyzed the data; E.B.A.K. and E.L.S.B. led the writing of the manuscript. All the authors contributed significantly and critically to the drafts and gave final approval for publication.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data and code that support the findings of this study are openly available in Figshare at https://doi.org/10.6084/m9.figshare.32050599.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Figure S1:** Rarefaction and extrapolation curves of species diversity for ant (top row) and hemipteran (bottom row) communities in (Cabruca, orange) and suppressed (Total suppressed, blue) agroecosystems. Diversity is presented at three Hill numbers: q = 0 (species richness), q = 1 (Shannon diversity), and q = 2 (Simpson diversity). Solid lines represent rarefied diversity, and dashed lines represent extrapolated estimates based on sample size. Shaded areas indicate 95% confidence intervals. **Table S1:** Number of observed interactions for each ant and hemipteran species in Cabruca and Total suppressed agroecosystems. Species names and their corresponding codes are presented. Values represent the total number of recorded interactions per species in each agroecosystem.