



Urban *Lasius niger* ants more readily accept low concentration sucrose solution than rural ants

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Abstract

Urbanisation causes broad changes in biotic and abiotic factors, which are often detrimental to animals. While extensive attention has been focussed on food resources for pollinators, comparatively little research has examined resources for aphidophagous insects. Many ants, such as *Lasius niger*, belong to this group of insects and rely on honeydew secretions for the majority of their carbohydrate intake. Ants will also often reject sugar solutions that are of lower concentration than those they are used to consuming. Here, we ask whether *L. niger* ants from urban environments show differential acceptance to various sucrose solution molarities compared with rural populations. We offered outgoing ants on active foraging trails drops of sucrose solutions over a range of molarities (0.125, 0.25, 0.5, 1, and 2 M), and quantified acceptance. Acceptance was scored using a simple behavioural measure of whether the ant remained in contact with the sucrose drop for over 3 s (full acceptance), broke away from the drop within 3 s but remained in the area and eventually drank to satiation (partial acceptance), or did not drink to satiation and walked away (rejection). Urban ants showed a significantly higher acceptance of all sucrose molarities than rural ants, with this difference especially pronounced at lower molarities. This may indicate that they are under nutritional stress for carbohydrates, either in quality or quantity, as well as heightened motivation to exploit any available food source under the pressures of urban environments.

Keywords Urbanisation · Carbohydrate · Nutritional landscape · Ants · Honeydew · Plant production

Introduction

Urbanisation and land-use alterations are one of the main causes of the current global biodiversity crisis (Almond et al. 2022). Although the threats to biodiversity are diverse (e.g., ocean alteration, terrestrial land use, insecticides,

invasive species) (Hald-Mortensen 2023), these threats largely result from environmental changes caused by human activities. Among these, land use change represents one of the most important drivers of biodiversity loss (Oliver and Morecroft 2014), primarily due to the combined effects of multiple abiotic and biotic pressures, such as habitat loss, fragmentation (Zhang et al. 2024), and the introduction of invasive species (Mollot et al. 2017).

Urbanization represents one of the most extreme forms of land-use transformation, although its full impact on native biodiversity remains insufficiently understood. As a result, urban ecological research has gained increasing relevance in recent years, driven by the urgent need to understand the functioning of these novel ecosystems and to inform conservation strategies aimed at mitigating their widespread ecological consequences (McIntyre 2000). Urbanisation brings about profound physical and environmental changes, for example the conversion of natural meadows into impermeable surfaces. Less visible, yet equally important, are alterations in soil chemistry, including elevated levels of heavy metals and other toxic compounds (Swain 2024) as well as

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the presence of microplastics (Celis et al. 2025). Urbanization also induces shifts in environmental conditions, such as increased exposure to artificial light at night (Hopkins et al. 2018) and the urban heat island effect (MacLachlan et al. 2017). Together, these changes have triggered a wide range of responses within urban biotic communities, spanning from shifts in community composition and interactions in biological networks (e.g., Miles et al. 2019; Patterson et al. 2023; Marcacci et al. 2023; Stukalyuk and Maák 2023; Trigos-Peral and Reyes-López 2025) to behavioural and physiological adaptations at the individual level (e.g., Ditchkoff et al. 2006; Meillère et al. 2015; Brans et al. 2018; Minias 2023; Tougeron and Sanders 2023). For instance, urbanization has been linked to declines in epiphyte diversity (Becker et al. 2017), reduced the health and performance of bumble bee colonies (Theodorou et al. 2022), and intensified offspring defence in urban populations of the Black Kite *Milvus migrans* (Kumar et al. 2018). In addition, urbanization has been associated with the evolution of reduced attraction to light in moths and reduced light avoidance in spiders (Altermatt and Ebert 2016; Czaczkes et al. 2018), as well as alterations in animals phenology, such as diurnal spiders switching to hunt during the night facilitated by the artificial illumination in cities (Frank 2009) or changes in ant foraging activity and colony development (Trigos-Peral et al. 2024a). While some organisms have the capacity to adjust their behaviour and physiology in response to urban environmental conditions (Luniak 2004; Czechowski et al. 2012; McDonnell and Hahs 2015), enabling them to persist in these novel ecosystems, others – like those with low ecological plasticity – have faced more severe consequences, including the local extinction of their populations (Ancilotto et al. 2025; Dri et al. 2021; Duncan et al. 2011).

As previously mentioned, organisms respond to environmental changes in diverse ways, both in form and timescale, ranging from rapid behavioural adjustments that help overcome temporary conditions to slower evolutionary adaptations that persist across generations. Beyond the crucial role that both types of responses play in organisms' survival, rapid behavioural responses can also offer practical applications with potential benefits for humans. For example, bivalve mollusc response to changes in water quality, allowing real-time monitoring of water quality levels (Vereycken and Aldridge 2023). Like aquatic organisms, soil organisms can also display a rapid response to changes in habitat status and quality (Viana et al. 2011; Morelli et al. 2021). Alterations in their functional traits often reflect the close relationship between species' ecological requirements and habitat characteristics. This response is particularly pronounced in organisms with limited dispersal capacity, which are typically strongly adapted to local conditions and, consequently, more sensitive to environmental changes. As a result, shifts

in their traits, performance, or population dynamics can provide early insight into how soil communities are affected by habitat alteration (Andersen 1995, 1997, 1999; McGeoch 1998).

Ants belong to a broader group of organisms that are sensitive to changes in environmental conditions and habitat quality, and they have therefore been frequently considered in studies assessing ecosystem change (Underwood and Fisher 2006). Ant species are often broadly classified according to their ecological preferences and tolerance ranges, distinguishing generalist species with flexible resource use from specialist species that rely on narrower ecological niches (Andersen 1999; Roig and Espadaler 2010; Vasconcelos et al. 2018; Trigos-Peral et al. 2020). While this classification is effective for assessing abiotic characteristics of habitats, it proves less efficient in detecting biotic changes, particularly in the availability and quality of nutritional resources. Still, nutritional constraints can directly influence ant physiology, behaviour, and colony performance, and persistent deficits in food resources may ultimately threaten population stability, as observed in many other organism groups.

The availability of abundant, high-quality food is crucial for organisms with limited nest mobility, such as ants. A scarcity of essential nutrients within their nesting niche can significantly impact ant populations, as a nutrient-rich diet is vital for colony development and the overall physiological status of ants and colonies (Csata and Dussutour 2019). For aphidicolous ant species like *Lasius niger*, aphid honeydew constitutes a key component of the diet. This sugary secretion offers a complex mixture of micronutrients important to the ants (Shik et al. 2014). Nevertheless, *L. niger* is a highly opportunistic species that exploits a wide range of alternative carbohydrate sources, including floral and extrafloral nectaries, fruit juices, and anthropogenic resources such as food waste or sugary residues, particularly in urban environments (Stadler and Dixon 2005; Seifert 2018; Buczkowski and Bennett 2008). However, in urban environments, pollutants and microplastics can impair plant health and nutrient uptake, reducing plant productivity and quality even under fertilization and, in turn, diminishing both the quantity and nutritional quality of honeydew and other carbohydrates sources (Gupta et al. 2024; Hashemi 2025; Wong and Taylor 2025; Manhas et al. 2025). Additionally, high urban temperatures can further reduce honeydew quality by inducing plant heat stress, which impairs root and shoot growth as well as root nutrients uptake (Mishra et al. 2023). As a result, ants – capable of detecting subtle nutritional changes – actively select the most nutritious honeydew available to them (Csata et al. 2020). However, food source selection is not determined solely by nutritional content; previous feeding experience also plays a role (Wendt and Czaczkes 2017; Wendt et al. 2019). Ants accustomed

to richer food sources may exhibit reduced acceptance of alternatives with comparatively lower nutritional quality as a result of a negative incentive contrasts (Flaherty 1996). As such, the willingness of aphidicolous to accept low molarity sucrose concentrations should be a direct function of the sugar concentration or general quality of the honeydew they have been collecting.

Ants are poikilothermic organisms; therefore, their activity is strongly shaped by prevailing environmental conditions. During foraging, in addition to meeting the colony's nutritional demands, workers are influenced by abiotic factors such as temperature and humidity. When these variables reach extreme levels, foraging activity typically declines – or may even cease – because of elevated risks of desiccation or heat stress (Chong and Lee 2009; Menzel et al. 2018). As a consequence, both the intensity of food collection and the precision of resource selection can be reduced or suppressed as colonies adjust their behaviour to minimize mortality at the colony level.

This study aims to investigate potential shifts in aphid honeydew quality between urban and rural habitats by using the aphidicolous ant *Lasius niger* as a model species. Specifically, we seek to assess whether urban environments may impose nutritional limitations on ants by comparing nutritional selection – measured as the acceptance of sucrose solutions of varying concentrations – between ant populations from highly urbanised and low urbanised environments. We hypothesized that urban ant populations would accept lower-quality carbohydrate solutions because they may be adapted to collecting nutritionally poorer honeydew produced by plants experiencing environmental stress in urban habitats. In addition, this study aims to assess whether temperature, humidity, or tree trunk size (used as a proxy for overall tree size and age) influence sucrose acceptance. We further predict that sucrose acceptance may decline under warm or dry environmental conditions due to their known physiological impacts on ants. Finally, we expect ant traffic to increase as tree size increases due to higher production or higher quality of sugar sources in mature trees.

Methods

Species and Localities

To assess whether ants can serve as reliable bioindicators of food quality in human-modified habitats, we used the generalist Holarctic ant species *Lasius niger* as model species. This aphidicolous species relies on honeydew produced by aphids as its main source of carbohydrates (Devigne and Detrain 2005; Novgorodova 2015). *Lasius niger* employs mass recruitment to food sources, so workers form stable

foraging trails from the nest entrance to the exploited source (Devigne and Detrain 2005; Novgorodova 2015) and foraging trails can reach up to 2.9 m long (Stukalyuk and Akhmedov 2022), making them particularly easy to find. Moreover, the ecological plasticity of *L. niger* enables them to colonize a wide range of biotopes (Seifert 2007; Czechowski et al. 2012; Radchenko 2016), including highly modified habitats such as urban areas (Stukalyuk and Maák 2023). In such urban habitats, the species exhibits a marked dominance (Trigos-Peral et al. 2020), representing nearly 50% of the observed ant workers (Stukalyuk et al. 2020).

The study was performed in two biotopes differing in the degree of urbanization: urban and rural areas. Urban areas were characterized by green spaces embedded within the cityscape, including courtyards with paved roads, tiled pavements, and lawns with the presence of a few trees; whereas rural areas were defined as areas of pastures, herbs, or spots surrounded by orchards. Both biotopes were sampled across five different cities within the Kyiv district of Ukraine: Bucha, Boyarka, Irpin, Gostomel, and Vishneve. The GPS coordinates of all sampled locations can be found in the raw data (S1).

Procedure

Active *L. niger* foraging trails were located by searching tree trunks for ants shuttling back and forth. Species identity was confirmed by examining samples of ants from each foraging trail under a stereo microscope, using identification keys in Radchenko (2016) and Seifert (2007).

Immediately after the trail was discovered, ant traffic was assessed by recording the number of ants moving in two directions (towards the nest and from the nest to the forage tree) was measured for one minute. The species of the tree and the diameter of its trunk at a height of 1.6 m above the ground were also recorded (Stukalyuk and Maak, 2023).

Air temperature and relative humidity were measured 5–10 cm above the forage trail in the shade before each test. The device (SHT35-DIS-B2.5KS, Sensirion, Switzerland) was held in place until the readings stabilised (30–60 s). The resulting values were assigned to the subsequent test.

At the start of each test, a 50 µl drop of sucrose solution was applied to a plastic substrate (see below) using a Pasteur pipette. The ants' responses were then recorded. Sucrose solutions of the specified concentrations were prepared in advance in the laboratory. After preparation, the solutions were placed in centrifuge tubes and labelled with letters of the Latin alphabet (A–E) to indicate their concentration. A separate person who was not involved in data collection prepared the solutions and assigned the concentration codes. Therefore, the experimenter was unaware of the correspondence between letters and concentrations, thus blind

to sucrose concentrations during the test. The solutions were prepared before each day of fieldwork. When visiting the colonies, tubes containing sucrose solutions were randomly selected from an opaque bag. This ensured randomisation of the concentration presentation. After taking measurements at each colony, the tubes were returned to the bag and mixed blindly. The experimenter was only informed of the code after field data collection was complete. This ensured a blind experimental design for the study.

To perform the behavioural assay, a small acetate sheet (c. 10 × 10 mm) was placed directly onto the trail. We tested the following sucrose molarities: 0.125, 0.25, 0.5, 1, and 2 M. Only one drop of one solution was presented at a time. After 20 ants encountered the solution, the acetate sheet was removed and a new sucrose solution drop of a different molarity was presented. While the experimenter was blind to solution type, high molarity (1 M, 2 M) sucrose is viscous and thus can be differentiated from the other molarities even when unlabelled. The response of outgoing ants (heading towards the tree) when encountering the solution was noted. We recorded one of three responses, following Wendt et al. (2019):

- Full acceptance (scored as 1): The ant maintains its mandibles in contact with the sucrose drop for 3 s upon first contact with the drop.
- Partial acceptance (scored as 0.5): The ant breaks contact with the drop within 3 s of initial contact, but remains in the vicinity (c. 2 cm radius) of the drop, returns to it frequently, or eventually drinks to satiation.
- Rejection (scored as 0): The ant breaks contact with the drop within 3 s, and continues on its outwards journey.

Solutions (all concentrations) were offered in patterned manner, so that all solutions were tested at each testing bout. All experiments were conducted in the shade, using a parasol to provide shade if necessary, and all data were collected between 9:00 and 12:00, between the 14th and 27th August 2024.

We studied 9 urban colonies and 9 rural colonies from each municipality, testing 20 ants from each colony on each molarity, resulting in a total of 9000 ants tested.

Statistical analysis

All code used in the analysis, and the code output, is provided in online supplement S1.

We analysed the data using Linear Mixed-Effect Models, with the ordinal package (Chistensen 2023) in R (R Core Team 2023) via Rstudio (RStudio Team 2015). Acceptance responses were predicted by an interaction of food concentration and biotope, with the addition of temperature and

humidity as independent variables. Colony ID was added as a random effect. Our main analysis model formula was:

$$\text{Acceptance score} (1, 0.5, 0) \sim \text{food concentration} * \text{biotope} + \text{random effect (colony ID)}$$

Differences in sucrose acceptance between biotopes were tested using an ordinal model (Cumulative Link model), in which the three acceptance scores (0=reject, 0.5=partially accepted, 1=accepted) were used as the three levels of the response variable. In the model, we explored the effect of environmental factors (humidity and temperature) and the ant traffic, on sucrose acceptance. Humidity and temperature were modelled using natural splines with the splines package (Bates and Venables 2025) to account for potential non-linear and non-monotonic effects, based on the hypothesis that acceptance peaks at intermediate environmental conditions and declines under extreme values as a result of reduced ant activity. We used the model formula:

$$\begin{aligned} \text{Acceptance_score} \sim & \text{sucrose_molarity} * \text{Biotope} \\ & + \text{Temperature} + \text{Humidity} + \text{ant_traffic} + \text{random effect (tree_species)} \\ & + \text{random effect (colonyID)} + \text{random effect (Location)} \end{aligned}$$

We also examined the three-way interactions with temperature and humidity using two modified versions of the above formula. In the first, the three-way interaction included Temperature; whereas in the second, Humidity was the included factor.

The proportional odds assumption was assessed using cumulative link models without random effects, as formal diagnostic tests are not available for cumulative link mixed models. The assumption was evaluated using nominal effects tests, which examine whether the effect of the Biotope varies across response categories.

We also examined the influence of the tree species. Prior to analysis, the dataset was subsetting and only observations from tree species occurring in both biotopes were used in the Biotope the model formula:

$$\begin{aligned} \text{Acceptance_score} \sim & \text{sucrose_molarity} * \text{Biotope} + \text{Temperature} + \text{Humidity} + \\ & \text{ant_traffic} + \text{tree_species} + \text{random effect (colonyID)} + \text{random effect (Location)} \end{aligned}$$

Finally, we explored the effect of tree characteristics on traffic with the glmmTBM package (Magnusson et al. 2020). For this, we excluded data from three tree species which were only sampled once, leaving three tree species. We used the following GLMM with a nbinom2 distribution:

$$\text{ant_traffic} \sim \text{tree_diameter} * \text{tree_species}$$

Model fit was evaluated using DHARMa residual diagnostics. Although the Kolmogorov–Smirnov test for uniformity was significant, residual plots showed no systematic

deviations, and tests for dispersion indicated appropriate model fit. Given the known sensitivity of the KS test in hierarchical count data, the model was considered suitable for inference.

P values were later corrected for multiple testing using a Benjamini-Hochberg correction (Benjamini and Hochberg 1995). Interactions were analysed using the functions `emmeans` and `emtrends` from the `emmeans` package (Lenth and Piskowski 2025). For graphical visualization, raw data figures were created using `ggplot2` (Wickham et al. 2020), while model predictions were visualized with `ggeffect` (Lüdtke 2018).

Results

The complete raw data on which the analysis was based is provided in online supplement S1. The complete analysis document, with all code and analysis results, is provided in online supplement S2.

We found a significant interaction between sucrose concentration and biotope on acceptance scores ($X^2=8.88$, $P<0.0001$). Overall, acceptance scores increased with sucrose concentration ($X^2=2871.67$, $P<0.006$) and ants from urban habitats exhibited higher levels of sucrose acceptance compared to the rural counterparts ($X^2=72.61$, $P<0.0001$). Moreover, the increase in acceptance with rising sucrose concentration was more pronounced in urban populations than the rural ones. At the highest concentration tested (2 M), acceptance level converged with no significant difference between urban and rural ant populations (see Fig. 1, Supplementary Table 1).

Results considering only the observations performed on ants foraging on the trees present in both biotopes follow the same pattern, also revealing a significant interaction between sucrose concentration and biotope on acceptance scores ($X^2=9.08$, $P=0.005$; Supplementary Table 2, Supplementary Fig. 1). We also found that while tree species did not show to have an important influence itself on the acceptance of the sucrose concentration ($X^2=0.11$, $P=0.730$), the tree species led to differences in the sucrose acceptance by ants in the different biotopes ($X^2=14.34$, $P<0.001$).

We found a positive correlation between tree diameter size and ant traffic ($X^2=6.94$, $P=0.008$), significant differences in traffic between different tree species ($X^2=7.19$, $P=0.007$), and a significant interaction between species and diameter ($X^2=5.16$, $P=0.022$), in which increasing diameter strongly increases traffic on *Acer platanoides* but only slightly increases traffic on *Populus nigra* (see Fig. 2; a plot showing the linear response without interaction can be found in the code and analysis supplement).

Finally, we found that humidity had no effect on sucrose acceptance, either alone or in a three-way interaction between humidity, sucrose concentration, and biotope (Humidity: $X^2=4.93$, $P=0.264$, three-way interaction: $X^2=0.068$, $P=0.992$). However, while temperature had no predictive power on sucrose acceptance alone ($X^2=1.48$, $P=0.686$), it did have influence on how ants in different biotopes respond differentially to different sucrose molarities (three-way interaction, $X^2=15.33$, $P<0.001$).

Exploring the three-way interaction by examining the predictions for the minimum, mean, and maximum temperatures (Fig. 3), we see that in urban environments at the lowest and highest temperatures, differences in sucrose acceptance is reduced compared to mean temperatures, especially for high sucrose levels.

Discussion

The sweeter a sucrose solution is, the more likely ants are to accept it, with ants generally rejecting low-molarity sucrose solutions (Wendt et al. 2019). However, we detected a marked difference in the response to low-molarity sucrose solutions between urban and rural populations: urban ants exhibited a greater acceptance for these lower-quality resources.

Sugary substances are particularly attractive to many ant species, especially aphidicolous species such as *L. niger*, as they constitute their primary carbohydrate –and thus energy– source (Wilson and Eisner 1957; Markin 1970). Under natural conditions, such ants primarily obtain carbohydrates from aphid honeydew, the composition of which varies significantly depending on factors such as soil chemistry, plant physiological state, and aphid species (Völkl et al. 1999).

One especially attractive component of honeydew for ants is the trisaccharide melicitose (Cornelius et al. 1996; Detrain and Prieur 2014). The concentration of melicitose in honeydew is strongly influenced by the environmental factors affecting the host plant's physiological condition, often increasing under conditions of thermal or hydric stress (Seeburger et al. 2022). It is plausible that honeydew produced by sap-feeding insects in urban environments contains elevated levels of melicitose compared to that from rural areas since urban vegetation commonly experience thermal or hydric stress (Zhou et al. 2017) due to the urban heat island and the restricted soil infiltration in impervious surfaces. On the other hand, urban environments also impose additional stressors that may reduce both the quantity and nutritional quality of honeydew, like presence of pollutants or reduced nutrients assimilation (see introduction). Our results, based on experiments using different sugar concentrations,

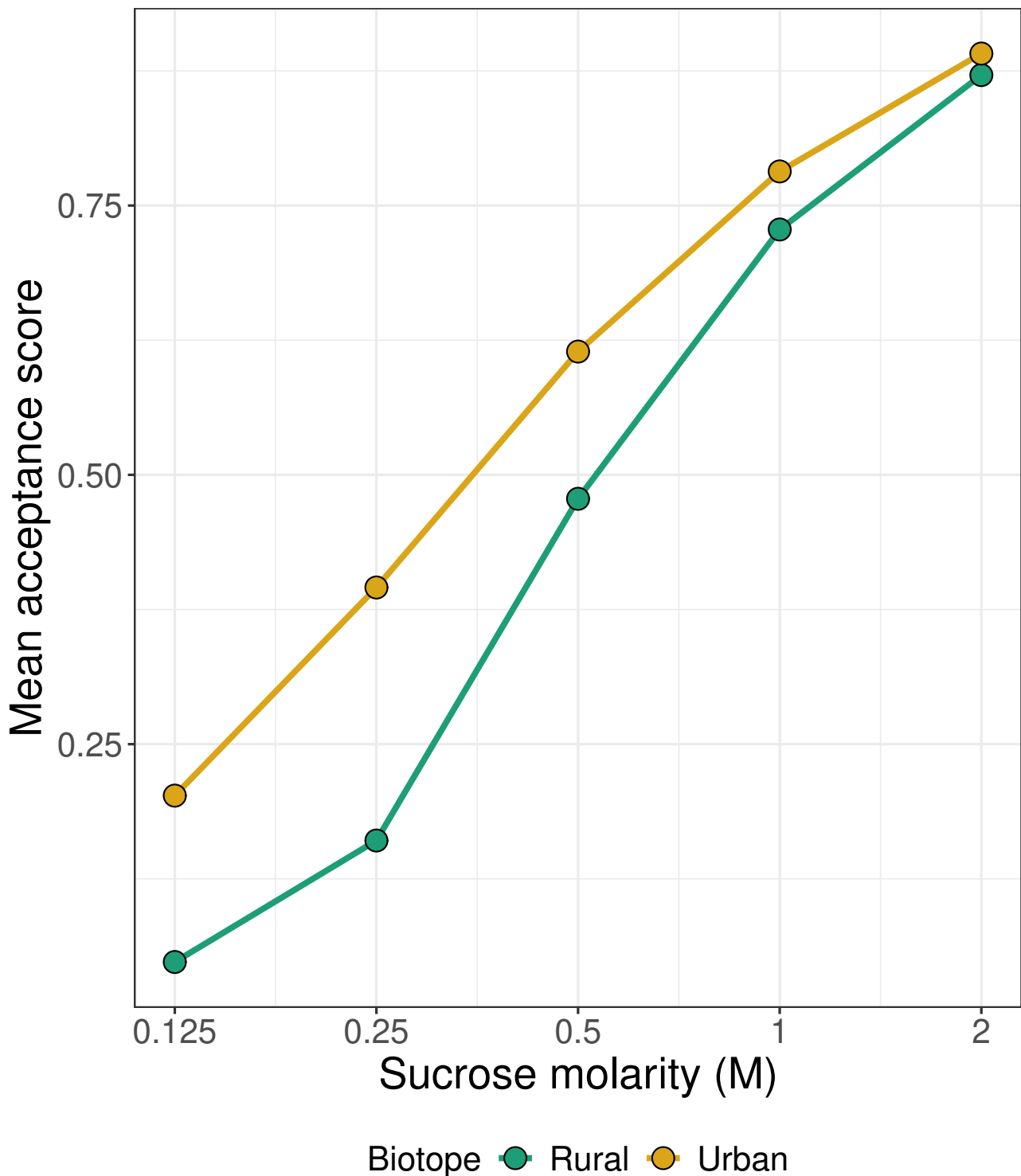


Fig. 1 Mean acceptance scores of ants from rural or urban areas in response to a range of sucrose solution molarities Symbols are means

support the second scenario. While foraging is essential for colonies to acquire the nutrients required for survival and development, foragers must confront various risks, which they are willing to endure only when the perceived quality

of the food source is sufficiently high (Nonacs 1990). However, ants' perception of food quality appears to be strongly shaped by prior experience – specifically, by the sugar concentrations to which they are accustomed (Wendt and

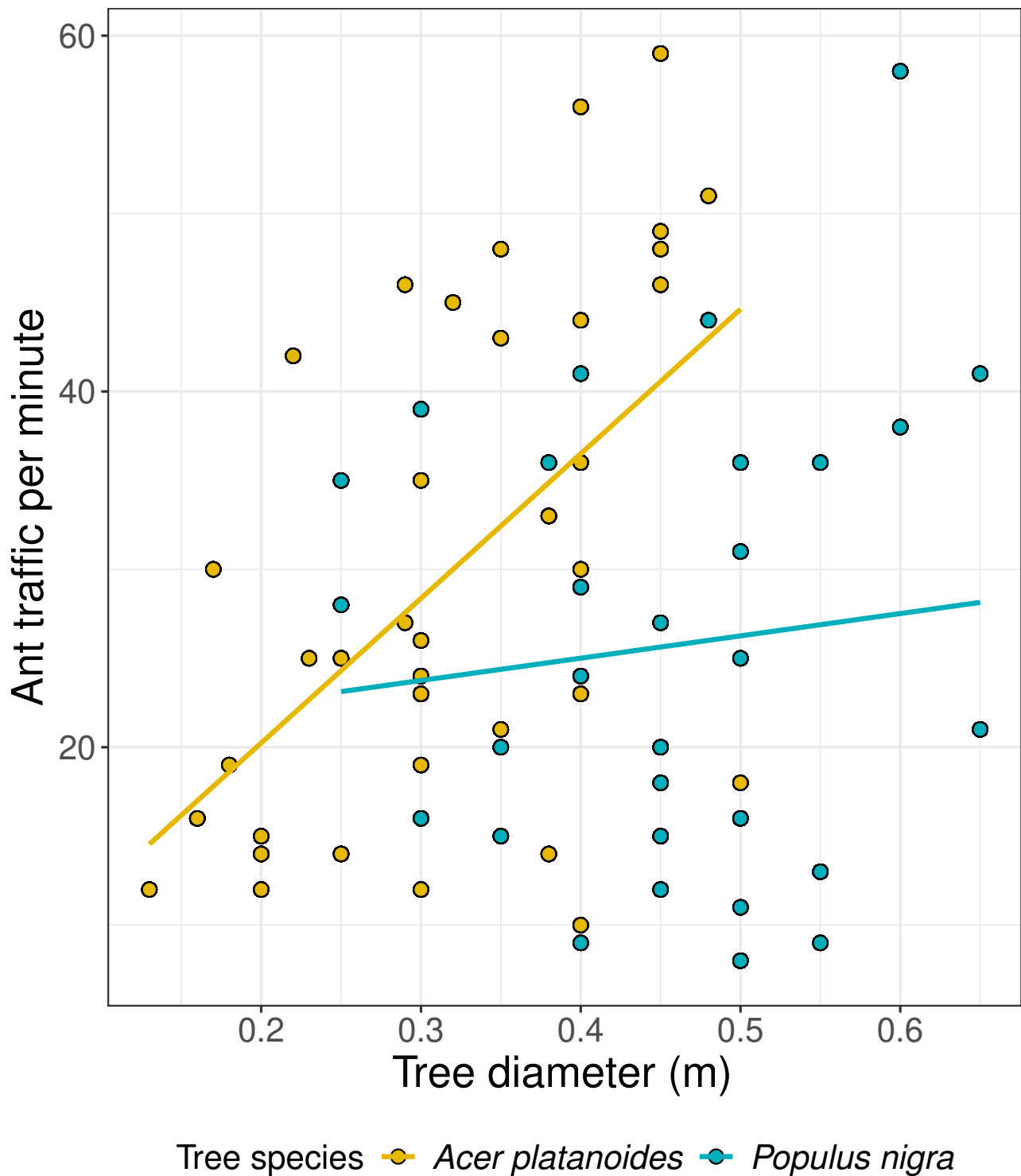


Fig. 2 Relationship between tree diameter and ant traffic. Traffic increases on larger trees, especially in Norway Maple (*Acer platanoides*). Lines are linear regressions, dots are individual values

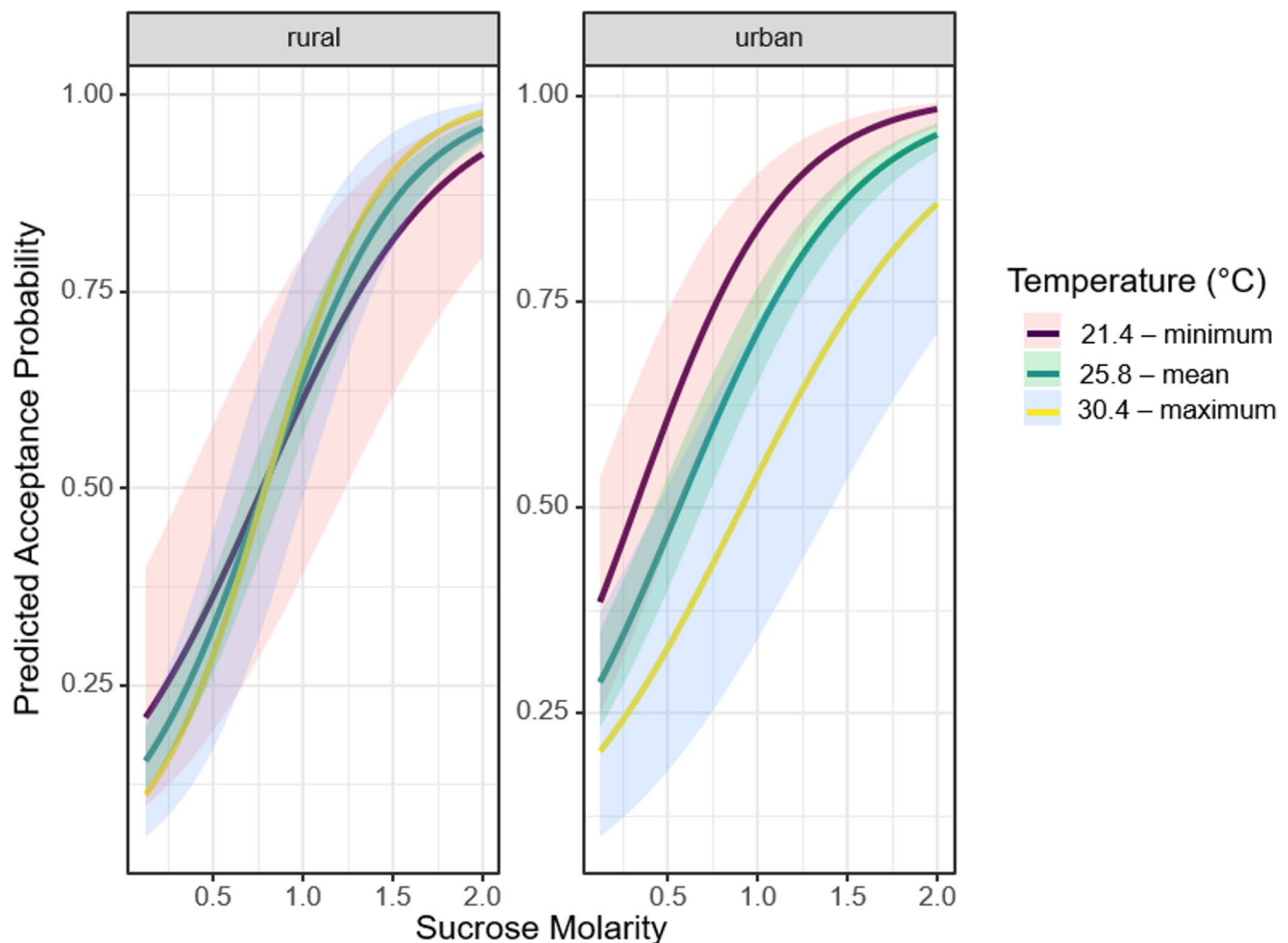


Fig. 3 Predicted acceptance scores of ants from rural or urban areas in response to a range of sucrose solution molarities, at the minimum, maximum, and mean temperatures. Lines are glmm model predictions, ribbons are the 95% confidence interval of each prediction

Czaczkies 2017; Wendt et al. 2019). Ants habituated to high-sugar diets tend to be less inclined to accept food sources with lower sugar concentrations. A comparable pattern was evident in our study: urban ants showed a higher acceptance of low-sugar solutions, whereas rural ants exhibited markedly lower acceptance, suggesting that urban ants may be more generally accustomed to lower-quality carbohydrate resources.

In addition to general differences in sugar source acceptance, rural populations of *L. niger* exhibited a more pronounced increase in interest in sugary solutions as concentration levels rose. Previous studies have shown that urban plants are more susceptible to aphid infestations than their rural counterparts (Lubiarz et al. 2011; Mackos-Iwaszko et al. 2015), potentially providing ants with a greater abundance of honeydew. However, the nutritional quality of this honeydew may be compromised by the physiological stress experienced by urban plants. Our findings support this interpretation: urban ants showed a consistent

interest in alternative sugar sources regardless of concentration, indicating a lower baseline quality of naturally available carbohydrates in urban environments. Consistent with the observations of Wendt et al. (2019), this pattern suggests that the more selective response of rural ants and their sharp increase in sugar consumption only at concentrations above 0.5 M might be linked to their access to higher-quality honeydew.

Other studies also suggest nutritional constraints of urban areas. For example, Garber et al. (2024) report that urban *L. niger* colonies defended aphid clusters more fiercely than their counterparts in rural areas, suggesting a potentially greater reliance on this resource due to increased food scarcity in cities. In line with these findings, Penick et al. (2015) also found that ants from urban areas fed on human waste, which is an abundant, energy-rich, and accessible dietary alternative in urban environments. Similarly, Trigos-Peral et al. (2024b) found that urban ant populations of *L. niger* in Warsaw, Poland, consumed more carbohydrate-rich

(sugar-water) solutions and less protein than their rural counterparts.

This interpretation is consistent with observations of ant mobilisation strategies in habitats with varying levels of resource availability (Stukalyuk and Akhmedov 2022). In habitats with abundant food resources, ants typically mobilise fewer workers over shorter average distances to food sources, reflecting higher local resource density. Conversely, in environments with limited resources, workers are recruited from greater distances, indicating scarcity. While direct comparisons across urban-rural gradients were not the focus of the aforementioned study, the greater acceptance of dilute sucrose by urban *L. niger* in our experiments suggests an adaptation to environments where high-quality carbohydrates are less reliably available, resulting in more opportunistic foraging behaviour and that urban gynes had lower body fat content. These studies should, however, be interpreted cautiously, as such patterns may reflect behavioural responses to altered nutritional landscapes rather than intrinsic differences between urban and rural colonies. Notwithstanding, a recent study (Ammaturo 2025) focused on this topic, supports the existence of nutritional constraints in urban environment. This study shows that urban *L. niger* populations adopted a more generalist diet when offered artificial diets of varying quality immediately after collection, whereas rural populations were initially more selective. Over the following weeks, when both groups were maintained on the same artificial diet, rural ants became less selective while urban ants retained stable preferences. Similar reductions in food discrimination have been observed in other urban ant species, where shifts in foraging behaviour reflect adaptation to resource variability in human-dominated habitats (Chen and Neoh 2023).

Our study also shows how ant foraging activity increased accordingly to the tree size; however, this linear relationship was only observed in *A. platanoides* (Norway Maple) but not in *P. nigra* (Poplar). These patterns indicate that ant-plant-hemipteran interactions are strongly context and species-dependent. While larger trees generally offer more resources, the extent to which ants respond depends on how tree species mediate resource quantity and quality. Higher honeydew availability and improved nutritional quality can support greater ant recruitment and sustained foraging activity (Del-Claro et al. 2016) in Norway Maple, whereas Poplars are also known to invest heavily in chemical defences, such as phenolic compounds, which can influence herbivore performance and, indirectly, the nutritional value of honeydew for ants (Donaldson and Lindroth 2007; Mooney et al. 2012). This supports the idea that ant foraging behaviour is shaped not only by resource abundance but also by nutritional payoff and host-plant traits, particularly

under environmentally stressful conditions such as urban habitats (Stadler and Dixon 2008; Trigos-Peral et al. 2020).

Finally, we also examined whether environmental temperature and humidity influenced sugar acceptance in ants. Although both factors can affect worker physiology (Menzel et al. 2018), humidity levels in both habitats remained within suitable ranges and did not impact acceptance. In contrast, temperature had a clear effect, reducing differences in sucrose acceptance across concentrations at both low and high temperatures in urban populations. The strong temperature dependence observed in urban ants – particularly their reduced acceptance under high temperatures – may be linked to temperature-driven task allocation related to worker body size. Okrutniak et al. (2024) showed that, at elevated temperatures, foraging is increasingly carried out by smaller workers, likely as a strategy to reduce colony overheating. Because smaller workers typically collect smaller loads, this shift – together with evidence of evolved plasticity in thermal tolerance in urban ant populations (Diamond et al. 2018) – may account for the reduced differences in sugar consumption we observed under suboptimal temperatures. Overall, the acceptance curves indicate that urban ants adjust their foraging behaviour to balance energetic demands with the heightened thermal constraints characteristic of urban environments.

To conclude, our results support previous studies suggesting the presence of nutritional constraints in urban biotopes. Although more targeted studies are needed to accurately quantify nutritional resources across different biotopes, our findings clearly reveal differences in the acceptance across sugar solution concentrations, as well as contrasting responses to local temperatures between urban and rural ant populations. Together, these results highlight the need to deepen our understanding of urbanization as a global change driver in order to improve the effectiveness of biodiversity conservation measures in this rapidly expanding process.

Supplementary information The online version contains supplementary material available at <https://doi.org/10.1007/s11252-026-01907-7>.

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Author contributions TJC conceived of the project. TJC and SS planned the methodology. SS, MK, and YS collected the data. TJC, SS, and GT carried out the statistical analysis. TJC and GT wrote the manuscript. GT and SS edited the manuscript. All authors reviewed the manuscript.

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Data availability Data is provided in the supplementary information files.

Declarations

Competing interests The authors declare no competing interests.

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