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The preference for energetic resources is positively associated with predatory activity in ants

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Abstract

1. Land use changes can alter resource availability and microclimate variables in tropical ecosystems, generally altering community structure by decreasing species richness and changing its composition. These changes affect foraging activity, nutrient preferences and consequently ecosystem functions.
2. Our aim was to assess how foraging activity and nutrient preference are influenced by changes in land use and microclimate.
3. We sampled ants (Formicidae) at 32 sites undergoing conversion from natural habitats to coffee systems in two Neotropical biomes: the Atlantic rainforest and the Cerrado. We assessed nutrient preference (amino acids, carbohydrates, lipids and sodium) and predation using mealworm larvae, while also measuring temperature and humidity.
4. We found the same ants foraged for different resources, likely because generalist species can perform these activities on the ground. Furthermore, foraging for energetic resources (carbohydrates and lipids) positively correlated with foraging for larvae. This indicates that the limitation of energetic resources can contribute to an increase in foraging and predatory activity. Moreover, ant preference for amino

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acids decreases with increasing temperature, indicating that ants prefer to consume energetic resources to support metabolic processes.

5. In conclusion, foraging is primarily carried out by generalist species. In addition, the preference for energetic nutrients, driven by energetic limitations, is linked to predatory activity. Moreover, ant species richness increases foraging for larvae, while rising temperatures decrease the preference for amino acids. Thus, conserving species richness and mitigating temperature increases may enhance larval foraging and support the insect predation function in Neotropical habitats.

KEYWORDS
disturbance, ecosystem function, macronutrients, nutrient preference, nutritional ecology, temperature, tropical biodiversity

INTRODUCTION

Land use changes drive tropical biodiversity loss primarily through the conversion of forest to agriculture (Jayathilake et al., 2021; Williams & Newbold, 2020). This conversion alters environmental conditions (Machado et al., 2023) and decreases the resources that are available to resident species (Stein et al., 2014; Tews et al., 2004). This can decrease species richness (McKinney & Lockwood, 1999; Wilker et al., 2024b) and select for organisms with different ecological adaptations, such as modifications in their foraging activity and diet (Castillo-Guevara et al., 2019; Manlick & Newsome, 2021). In turn, changes in foraging activity and nutrient preference can alter ecosystem functions (Dudley et al., 2012; Maisey et al., 2021). Consequently, understanding how land use in the tropics affects foraging activity and nutrient preference would provide a better comprehension of the impacts of land use beyond community structure (e.g., species richness), laying the groundwork for future conservation practices.

The foraging activity of animals can be altered by microclimate alterations resulting from land use changes. For example, as forest vegetation is converted to open vegetation land uses, there is a reduction in available shade and an increase in solar radiation (Machado et al., 2023). This leads to an increase in maximum temperature and a decrease in minimum temperature and humidity (Alkama & Cescatti, 2016; Trancoso et al., 2022). Consequently, many animals tend to reduce their foraging activity to minimize thermal and desiccation risks (Parr & Bishop, 2022). On the other hand, increased temperatures may enhance foraging activity on average, especially in ectotherms. This happens because higher temperatures raise animals' metabolic rates, thus allowing them to forage for greater durations relative to when it is cooler (Riemer et al., 2018). Therefore, changes in foraging due to microclimatic changes can have opposite effects in tropical habitats.

The other way in which land use change impacts foraging activity and nutrient preference is by decreasing the quantity and variety of resources provided by plants and animals (Adkins et al., 2023; Tilman et al., 1996). This occurs because, according to the compensation hypothesis, animals tend to increase their foraging activity for nutrients that are scarce in their environment or diet (Kaspari et al., 2012; Kaspari & Yanoviak, 2001). In this sense, as agricultural systems reduce the productivity of native plant resources (Barnes et al., 2017), a scarcity of energetic nutrients occurs. This can lead both to a decrease in overall foraging activity due to smaller population sizes and to an increase in the search for specific limiting energetic nutrients (e.g., carbohydrates and lipids) compared to non-energetic nutrients (e.g., amino acids (AA) and sodium; Lasmar et al., 2021; Peters et al., 2014). Moreover, the decline in productivity commonly associated with anthropogenic land uses may lead to increased foraging for energetic resources (Lasmar et al., 2021), including a greater preference for lipids over AA among predatory groups due to energetic limitations (Lasmar et al., 2023; Mayntz et al., 2005). In contrast, species that forage on the ground in natural tropical environments are typically not constrained by sodium availability (Lasmar et al., 2021). Additionally, sodium availability may rise through practices such as fertilization and irrigation (Hopmans et al., 2021), which could reduce the preference for this nutrient. Thus, despite an expected decrease in foraging activity due to the low population sizes in agricultural land uses, animals may alter nutrient preference, focusing primarily on energetic resources, due to there being a greater number of limiting nutrients caused by the land use change.

Despite the negative impacts of land use on community structure, the effects on foraging activity and nutrient preference are still poorly evaluated (but see Lasmar et al., 2023; Moses et al., 2023). Several studies have identified a decline in species richness due to the local extinction of sensitive species and the survival of generalist species (e.g., Tabarelli et al., 2012). This may lead to a reduction in overall foraging activity due to the positive relationship between species richness and the intensity of foraging (Lasmar et al., 2021; Noriega et al., 2021). On the other hand, generalist species can forage for a variety of resources in anthropogenic land uses (Dehling et al., 2021; Manlick & Newsome, 2021), changing their patterns of nutrient preference. Additionally, the impact of land use changes can vary in magnitude depending on the type of natural habitat (Carvalho et al., 2022; López-Bedoya et al., 2022; Wilker et al., 2024b). For example, land use changes in different biomes may select for different species based on the original species pool (Corbelli et al., 2015). Consequently, these species may alter their foraging patterns in various ways, influenced by their response to changes in the microclimate and resource availability, as well as by the impacts of land use modifications on foraging activity and nutrient preferences. Thus, assessing the effects of land use changes on nutrient preference, considering the biome context and microclimatic variables, may contribute to conservation in both natural and anthropised habitats.

Ants (Hymenoptera: Formicidae) are excellent models for assessing the effects of land use changes (Andersen, 2019; Ribas et al., 2012) on foraging effort and nutrient preference (Lasmar et al., 2021, 2023; Peters et al., 2014). This is because ants exhibit a high diversity of species and life histories among animals (Feitosa et al., 2022). They also exhibit decreases in species richness and changes in community composition in response to anthropogenic impacts, including land use change (Andersen, 2019; Ribas et al., 2012). Furthermore, ants forage for various nutrients such as carbohydrates and lipids as energy sources, AA for body growth and sodium for metabolic processes (Riemer et al., 2018). For example, ants may exhibit increased predatory activity in anthropogenic land uses, driven by the heightened activity of generalist groups (Wilker et al., 2023). Moreover, the consumption of lipids has been linked to predatory activity in ants and ground-dwelling communities (Lasmar et al., 2023). Consequently, in predatory behaviour, which is most exhibited by generalist ants (Cerdá & Dejean, 2011), these arthropods may forage more for carbohydrates and lipids due to their limited availability at the trophic level (Kaspari et al., 2012; Lasmar et al., 2023; Wilder et al., 2013). Alternatively, the scarcity of these nutrients in their diet can lead to increased lipid intake from prey bodies (Mayntz et al., 2005). However, ant foraging activity and nutrient preferences may be affected by changes in land use. Due to ants being thermosensitive, microclimate changes in anthropogenic land uses can decrease their foraging activity (Parr & Bishop, 2022). Additionally, a lower number of species associated with intensified land use is linked to reduced foraging activity, likely due to a smaller number of foraging ants (Lasmar et al., 2021). Thus, ants may exhibit changes in foraging patterns with alterations in land uses in tropical ecosystems.

Here, our aim was to assess whether changes in land use and microclimate explain the foraging activity and nutrient preference of ants. We considered foraging activity for the following resources: nutrients (lipids, carbohydrates, AA, sodium) and mealworm larvae (*Tenebrio molitor* Linnaeus, 1758). More specifically, we asked: (i) How similar is the species composition across land uses and resources? We expected that ant composition would differ across land uses due to species turnover but would be similar among ants that forage for larvae, carbohydrates and lipids, indicating limiting resources for predatory ants; (ii) Is foraging for larvae explained by nutrient preference? We expected that foraging for larvae would be positively associated with foraging for carbohydrates and lipids, as predatory ants should increase their foraging for energy sources; (iii) How are changes in foraging activity (foraging for larvae and nutrient preference) explained by ant species richness, land use and microclimate changes? We expected that foraging activity would be positively associated with increases in ant species richness and temperature but negatively associated with extreme temperatures and low humidity in agricultural systems. Moreover, we expected that foraging for lipids, carbohydrates (energetic resources) and larvae would increase in anthropogenic land uses due to resource limitations.

METHODS

Study site

We collected data on ant foraging activity in the state of Minas Gerais, Brazil. Minas Gerais has a territory of 586,528 km^2, mainly composed of the Atlantic rainforest (40%) and the Cerrado (54%) (Figure 1; Biomas, 2019). The Atlantic rainforest and Cerrado are considered global biodiversity hotspots due to their high species numbers, endemism and the significant threat by land use changes (Trew & Maclean, 2021). The Atlantic rainforest (tropical forest) extends into tropical and subtropical regions, generating diverse rainforest environments. On the other hand, the Cerrado (Brazilian savannah) features various vegetation types, ranging from open vegetation habitats to closed forests, including grasslands, shrublands, typical savannas and woodland savannah (cerradão). These regions are characterized by a wet summer (October to March) and a dry winter (April to September). In the winter, the Cerrado has an average precipitation of 23.50 mm and an average temperature of 18.25°C, while the Atlantic rainforest has an average precipitation of 26.75 mm and an average temperature of 18.97°C. In the summer, the Cerrado has an average precipitation of 212.87 mm and an average temperature of 22.16°C, while the Atlantic rainforest has an average precipitation of 134.54 mm and an average temperature of 20.41°C (INMET, 2024).

Experimental design

We sampled between January and March of 2022 and 2023. In total, we sampled 32 sites ($n = 32$). The sites are composed of six woodland savannahs (cerradão), six tropical forests in Atlantic rainforest, eight coffee plantations in Cerrado and 12 coffee plantations in Atlantic rainforest (Figure 1; Table S1). The collections in the Cerrado were conducted in the rural areas of the municipality of Patrocínio (14 sites), while the collections in the Atlantic rainforest were conducted in the rural areas in the municipalities of Lavras (4 sites) and Santo Antônio do Amparo (SAA) (14 sites). Each site had only one transect per sampling, and the sites were spaced at least 322 m apart.

We collected data from coffee plantations of the species *Coffea arabica* L. All plantations were unshaded and mechanized (e.g., use of tractors). In the Atlantic rainforest, all coffee plantations were conventional (12 sites). In the Cerrado, four sites were conventional coffee (with the use of fertilizers and insecticides), and four sites were organic coffee (without the use of fertilizers and insecticides). Before conducting our hypothesis tests, we assessed the possible influence of these variables on our analyses and found that the type of coffee management (conventional or organic) did not affect the results, allowing us to combine the data and disregard management type in the analyses.

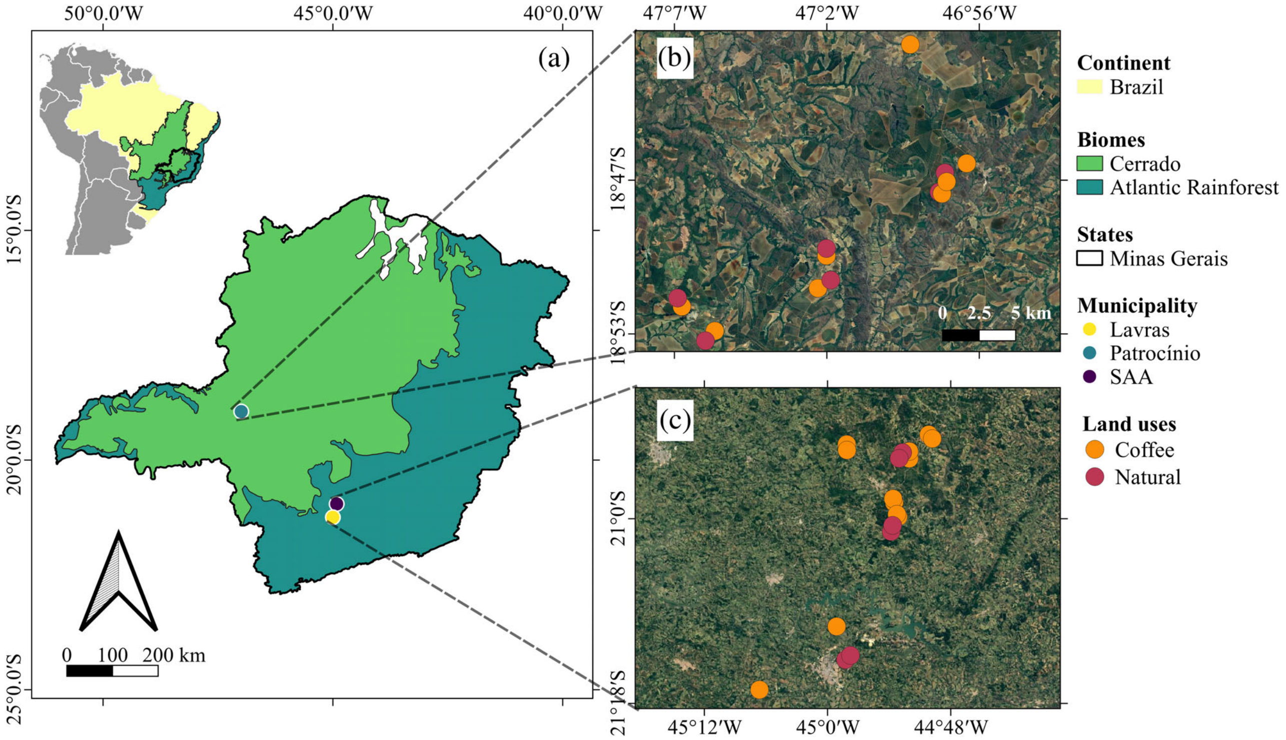

FIGURE 1 Panel A indicates the Brazilian state of Minas Gerais, including its position in South America and the location of the biomes and sampled municipalities. Panel B indicates some sampling points within the municipality of Patrocínio and panel C indicates the sampling points in municipalities of Lavras and Santo Antônio do Amparo (SAA). The figure was generated using QGIS version 3.32 (QGIS.org, 2023) and adapted biome and state data from Instituto Brasileiro de Geografia e Estatística (IBGE, 2019). The satellite image was from Google Satellite (2024).

Foraging activity for resources

In each transect, we assessed ant foraging activity for resources, including nutrients (AA, carbohydrates, lipid and sodium) and larvae. Nutrients were offered in liquid form, and we used water as a control. In each site, we created a transect with 25 sampling points spaced 10 metres apart (totalling 240 m). In each transect, we sampled ants between 7 a.m. and 8 a.m., using the nutrients in Fisher 50 mL tubes. Each tube contained 10 mL of an aqueous solution of each type of nutrient. The nutrients included 20% AA (made with Whey Protein Isolate and unflavoured containing L-glutamine and other AA such as leucine, isoleucine and valine), 20% carbohydrates (CHO, made with sucrose), lipids (100% extra virgin olive oil, without water), 1% sodium solution (NaCl, made with salt) and tap water (Lasmar et al., 2021, 2023). The tubes were placed horizontally on the ground and closed at the end of sampling, with the ants inside collected and stored in 70% alcohol for preservation.

After the nutrient experiment, in the same transect but only at five sampling points spaced 50 m apart (totalling 200 m), we assessed foraging for larvae as a proxy measure for insect predation by ants. At each sampling point, we installed two beetle larvae (*Tenebrio molitor*). The larvae were attached with hook-and-loop fastener to an ethylene-vinyl acetate (EVA) surface to prevent them from escaping. At each sampling point, between 8 a.m. and 12 p.m., we observed foraging activity in four rounds of 5 min each. First, we attached the larvae to the ground at the first sampling point and immediately observed the foraging for larvae for 5 min. Then, we attached larvae at the second sampling point and observed the foraging for larvae for 5 min. We repeated this process until completing the transect and then started again for the second, third and fourth rounds. This totalled 20 minutes per sampling point and 100 minutes per transect. We considered the foraging activity by ants when they attacked the larvae, either by stinging or biting (Wilker et al., 2023). The ants that engaged in predation were collected and stored in 70% alcohol for later identification.

Microclimate measurements

We measured temperature and humidity alongside the larvae experiment. Using a digital thermo-hygrometer, we measured air temperature (°C) and humidity (%) at 5 cm from the ground at the sampling point. We took 20 temperature and humidity measurements per transect (five sampling points × four rounds) and used the average of them in our analyses.

Ant species richness and composition

After the larvae experiment, in the same transect with five sampling points spaced 50 metres apart (totalling 200 m), we installed pitfall traps to assess ant species richness and composition. The traps consisted of plastic pots with a diameter of 12 cm and a depth of 11 cm, installed at the ground level. We added an aqueous solution composed of 200 mL of water mixed with salt and detergent to capture and preserve the collected ants. Each trap was left sampling for a period of 48 hours. After this period, the captured ants were stored in 70% alcohol.

Ant species identification

We identified to the genus level based on Baccaro et al. (2015) and morphotyped them based on external morphological characters. Identification and confirmation of species and morphospecies were made by Rodrigo M. Feitosa and Ana Carolina A. Neundorf at the Laboratório de Sistemática e Biologia de Formigas at the Universidade Federal do Paraná (UFPR). Specific published descriptions were used to identify species in the genera *Acromyrmex* (Gonçalves, 1961), *Acropyga* (LaPolla, 2004), *Apterostigma* (Lattke, 1997), *Basiceros* (Probst & Brandão, 2022), *Brachymyrmex* (Ortiz-Sepúlveda et al., 2019), *Carebara* (Fernández, 2004), *Ectatomma* (Kugler & Brown Jr., 1982), *Gnamptogenys* (Camacho et al., 2020), *Labidus* (Watkins, 1976), *Linepithema* (Wild, 2007), *Neivamyrmex* (Watkins, 1976), *Odontomachus* (Brown Jr., 1976), *Pheidole* (Wilson, 2003), *Strumigenys* (Bolton, 2000) and *Wasmannia* (Longino & Fernández, 2007). Voucher specimens were deposited in the reference collection of Laboratório de Ecologia de Formigas at UFLA and the Coleção Entomológica Padre Jesus Santiago Moure at UFPR (DZUP).

Data analysis

Foraging activity for resources was computed in two distinct ways for nutrients and larvae. For nutrients, we used a measure of nutrient preference at each transect (relative resource use; Lasmar et al., 2021). As we are primarily interested in the preference between energy nutrients (carbohydrates and lipids) compared to AA, to calculate the nutrient preference, we excluded water (control) and sodium (NaCl) from computing nutrient preference. Moreover, as expected, the control and sodium tubes had lower ant occurrence (Figure S2). Nutrient preference was calculated as the number of tubes visited for a given nutrient at a transect, divided by the total number of tubes visited per transect. Thus, nutrient preference indicates the foraging for a specific nutrient in relation to all others. A nutrient foraging value of 1 indicates that all occurrences were on a single nutrient, and a nutrient foraging value of 0 means that no ant occurrences were recorded for a nutrient (Lasmar et al., 2021). To do this, we measured the nutrient preference between energy and AA, with energy being the combination of carbohydrates and lipids data. We transformed these proportional values using a logit transformation to meet Gaussian assumptions in our analyses (Lasmar et al., 2021; Warton & Hui, 2011). For larvae, foraging was calculated by the number of attacks on larvae, being a count data, and we used the Poisson family (Wilker et al., 2023).

To assess (i) whether the species composition is similar across land uses and resources, we calculated Sørensen dissimilarity using the betapart package version 1.6 (Baselga, 2010; Baselga et al., 2023). Sørensen dissimilarity ranges from 0 to 1, where 0 indicates assemblages with identical compositions and 1 indicates assemblages with completely different compositions. We had 32 sites with five resources (AA, carbohydrates, lipids, sodium and larvae), totalling 160 'assemblages'. However, in several sites, we collected only one or two ant species per assemblage. Due to the low number of species in each assemblage, we could not compute the dissimilarity between them. As an alternative, we merged the assemblages within the same land use type (woodland savannah, tropical forest, coffee plantation in Atlantic rainforest and coffee plantation in Cerrado). This reduced our sample size to 20 (five resources X four land use types) but increased the number of species for each sample unit. Moreover, we partitioned βsør-diversity into turnover (βsim) and nestedness (βsne). We used βsør, βsim and βsne to perform three non-metric multidimensional scaling (NMDS) analyses, using the function *metaMDS* (vegan package version 2.6-6; Oksanen et al., 2024). We then tested the difference in community dissimilarity with three permutational analyses of variance (PERMANOVA), using the function a*donis2* (vegan package version 2.6-6; Oksanen et al., 2024) with 9999 permutations. In all models, we used the predictor variables of resources and land use type. As a response variable, we used βsør, βsim and βsne, one for each model. When we found a significant result in PERMANOVA, we used the function *pairwise.adonis2* (pairwiseAdonis package version 0.4; Martinez Arbizu, 2020) to understand which pairs of assemblages were different.

To assess (ii) whether foraging for larvae is explained by nutrient preferences, we built two generalized linear models (GLM). As the response variable, we used the number of foraging for larvae per transect. As predictors, we used the nutrient preference per transect (foraging for a specific nutrient in relation to all others). In the first model, we used the nutrient preference for energetic nutrients, and in the second model, the nutrient preference for AA. We considered a result significant if $p < 0.05$. We used the Poisson family because the response variable is count data (number of ants foraging for larvae per transect). We evaluated the normality of the residuals using histograms and quantile–quantile plots and the heteroscedasticity using residuals by fitted value plots. Moreover, because the model was overdispersed, we changed the family to negative binomial, using the MASS package (Venables & Ripley, 2002).

To avoid multicollinearity between microclimate variables, we tested a correlation between temperature and humidity. The Spearman correlation coefficient between these variables was strongly negative ($\rho = -0.86$; $p < 0.001$; Figure S1). For this reason, we used only temperature as a microclimate variable.

To assess (iii) whether changes in foraging activity are explained by ant species richness, land use and microclimate changes, we calculated three GLMs. In all models, we used ant species richness, land use (natural habitat or coffee plantation) and temperature as predictor variables. We also used biome (Atlantic rainforest and Cerrado) with a predictor variable to assess whether the patterns were consistent across different geographic contexts. In one model, we used foraging for larvae as the response variable. In the other two models, we used nutrient preference for energy and nutrient preference for AA. For models with larvae, we used a negative binomial error family because of the overdispersion. For the models with nutrient preference, we used the gaussian family. In all models, we tested the residual normality and homoscedasticity. Moreover, in all models, we used the *dredge* function to select the best models and identified 'uninformative parameters' following Leroux (2019).

We used the *dredge* function (MuMIn package version 1.47.5; Bartoń, 2023) to run all possible models. The dredge function ranked the models based on the Akaike information criterion corrected for small sample sizes (AICc). We considered models to be equivalent if ΔAICc <2 (Burnham & Anderson, 2002). However, within our selected models, there may be 'uninformative parameters', leading to a Type I error (Leroux, 2019). We followed the approach proposed by Leroux (2019) for detecting these 'uninformative parameters'. We compared the log-likelihoods of the top model and those models within ΔAICc <2 that had additional parameters not in the top model. If the log likelihoods were different (log-likelihoods >1), we considered the additional parameters as informative. If the log likelihoods were similar (log-likelihoods <1), we checked to see if the 95% confidence intervals (CI) of the additional parameters overlapped zero, using the *confint* function (stats package; R Core Team, 2024). If the CI overlapped zero, we considered the parameters to be uninformative; if they did not overlap zero, we considered them to be informative. When the predictor overlaps zero, it probably does not explain the response variable (Leroux, 2019).

All analyses were completed in R 4.3.3 (R Core Team, 2024). All graphs were made with the ggplot2 package (Wickham, 2016).

RESULTS

We sampled 12,346 ant workers and 138 ant species, belonging to 124 ant species for pitfall data, 28 ant species foraging for larvae and 51 species for nutrient preference (more details in Tables S2–S6). Concerning nutrient preference, we found that ant foraging was higher for carbohydrates (ant presence in carbohydrate tubes: mean ± deviation standard = 0.50 ± 0.50) and lipids (ant presence in lipid tubes: 0.45 ± 0.49), intermediate for AA (ant presence in amino acid tubes: 0.19 ± 0.39) and sodium (ant presence in sodium tubes: 0.21 ± 0.41) and low for control tubes (ant presence in control tubes: 0.09 ± 0.29) across all transects (Figure S2; Table S6).

Regarding (i) whether the species composition is similar across land uses and resources, we found that the ant species composition differs between land uses (degrees of freedom (d.f.) = 3; F = 6.373; $p < 0.001$), and the principal beta diversity component is turnover (βsør = 0.918, βsim = 0.883, and βsne = 0.035; Figures S3 and S4). However, we did not find a different ant composition across different resources (Figure 2 and Table S7).

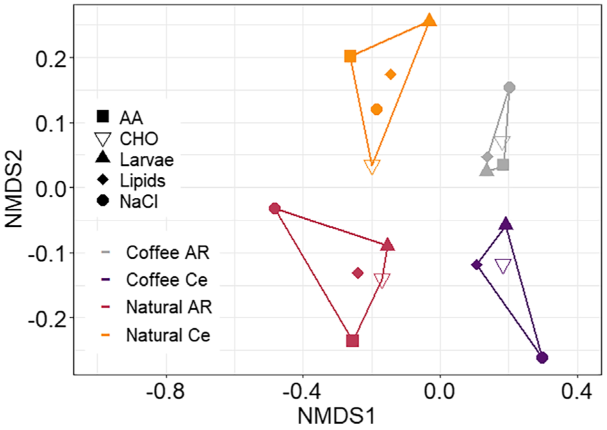

FIGURE 2 Ant species composition differs between land use types: Natural AR (forest in the Atlantic rainforest; medium pink), Natural Ce (woodland savannah in Cerrado; orange), Coffee AR (coffee plantation in the Atlantic rainforest; grey) and Coffee Ce (coffee plantation in Cerrado; purple). However, it does not differ significantly with respect to resource types: AA (amino acids; square), CHO (carbohydrates; empty triangle), Lipids (vegetable oil; diamond), NaCl (sodium; circle) and Larvae (predation experiment; full triangle). Species composition was measured using Sørensen dissimilarity (βsør).

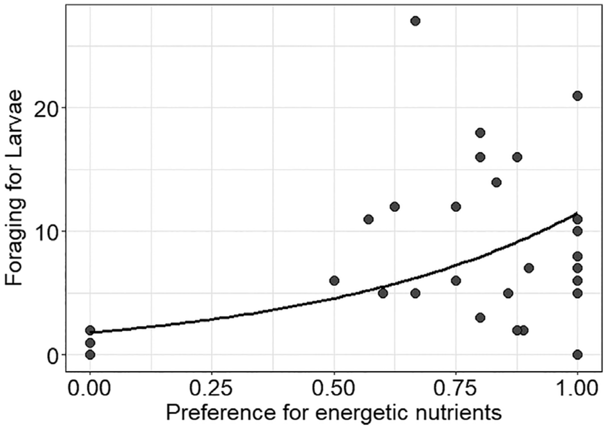

FIGURE 3 The y-axis indicates the number of foraging for larvae. The x-axis indicates the nutrient preference for energetic nutrients (carbohydrates and lipids) compared to amino acids. The increase in foraging for energetic nutrients, and consequently the decrease in foraging for amino acids, increases foraging for larvae.

Regarding (ii) whether foraging for larvae is explained by nutrient preference, we found that an increase in foraging for energy (carbohydrates and lipids combined), relative to AA, positively explained the foraging effort for larvae (d.f. = 30; F = 3.924; $p = 0.047$; $R^2 = 0.11$; Figure 3). However, we did not find an effect of nutrient preference for AA compared to energy (d.f. = 30; F = 0.956; $p = 0.328$).

Regarding (iii) whether changes in foraging activity are explained by ant species richness, land use and microclimate changes, we found predictors for both foraging for larvae and nutrient preference for AA (Table 1). As ant species richness increased, so did the number of foraging for larvae. Moreover, both foraging for larvae and preference for AA were greater in the Atlantic rainforest than in the Cerrado

TABLE 1 In the table, 'preference for AA' represents the preference for amino acids compared to energetic nutrients (CHO + lipids), while 'preference for energy' represents the preference for energetic nutrients compared to amino acid, 'Land use' are the land uses (natural habitat and coffee plantation), 'Temperature' is the mean of temperature in°C, 'Richness' is the ant species richness and 'Biome' are the biomes (Atlantic rainforest and Cerrado). Only models with ΔAICc ≤2 were considered. Degrees of freedom of the model (d.f.), differences in AICc values (ΔAICc), Akaike weight (ω), Log Likelihood (LogLik) and Adjusted coefficient of determination (Adj-R^2) were evaluated.

Question 3: How are changes in foraging activity explained by ant species richness, land use and microclimate changes?

	d.f.	**AICc**	**ΔAICc**	**ω**	**LogLik**	**Adj-R^2**
Model (larvae)						
Richness	3	198.0	0.00	0.21	−95.59	0.15
Biome + Richness	4	198.1	0.06	0.21	−94.31	0.21
Model (preference for AA)						
Biome + Temperature	4	125.0	0.00	0.31	−57.73	0.31
Temperature	3	126.4	1.47	0.13	−59.78	0.15
Model (preference for energy)						
Null model	2	151.4	0.00	0.22	−73.49	0.00
Biome	3	152.5	1.14	0.12	−72.84	0.04
Land use	3	152.7	1.28	0.11	−72.91	0.03
Temperature	3	152.8	1.42	0.10	−72.98	0.03
Richness	3	153.1	1.75	0.09	−73.14	0.02

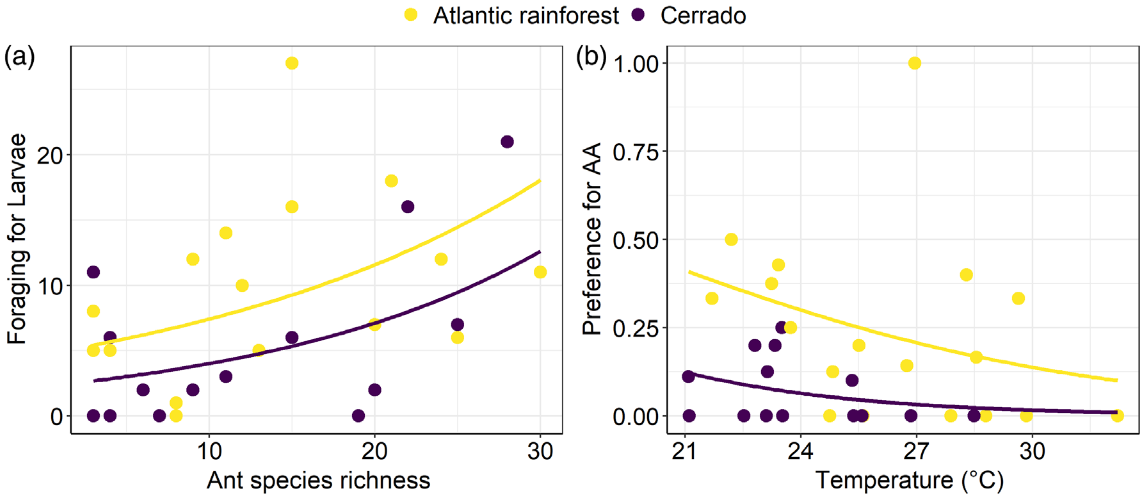

FIGURE 4 Foraging for larvae and preference for amino acids (AA) is greater in the Atlantic rainforest than Cerrado. However, ant species richness increases foraging for larvae (panel A), while temperature decreases preference for amino acids (panel B).

(Table 1; Figure 4a; Figure 5). Additionally, an increase in temperature (°C) reduced the ants' preference for AA (Table 1; Figure 4b). On the other hand, we did not find any effect of microclimate or land use on nutrient preference for energetic nutrients (Table 1).

DISCUSSION

In our study, we identified important patterns regarding changes in foraging activity and nutrient preference caused by land use and microclimate changes. We found that ants preferred foraging for carbohydrates and lipids, indicating the ants' preference for energy resources (Lasmar et al., 2021, 2023; Peters et al., 2014). We also found that the ants foraging for different resources had the same species composition, probably due to the presence of generalist ants on the ground. Additionally, we found a positive relationship between ants foraging for energetic nutrients and larvae, suggesting that limitations in energetic resources (carbohydrates and lipids) an increase in ant foraging can contribute to higher insect predation, as it leads to more frequent foraging on larvae. Moreover, both foraging for larvae and preference for AA were higher in the Atlantic rainforest than in the Cerrado, suggesting greater predatory ant activity and amino acid consumption in this biome. Thus, although foraging for larvae was associated with amino acid preference in the same biome, it is possible that nutrient limitation for energetic resources leads to increased foraging activity for these nutrients, thereby enhancing predation events.

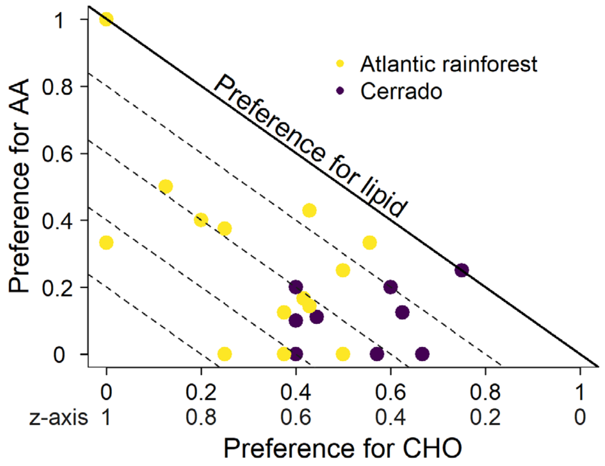

FIGURE 5 Right-angled mixture triangle (Raubenheimer, 2011), for AA (y-axis), carbohydrates (x-axis) and lipids (z-axis). This graph represents relative preference in three nutrients: AA, CHO and Lipids. For the x-axis, the higher the preference in CHO, the lower the preference in AA and Lipids. For the y-axis, the higher the preference in AA, the lower the preference in CHO and Lipids. For relative lipid preference, the points are graphically represented in relation to the diagonal lines, with the values indicated in relation to the z-axis. The lowest lipid preference occurs when the point touches the diagonal 0, and the highest occurs when the point touches the diagonal 1 for the z-axis. In the Atlantic rainforest, ant assemblages tend to forage more for amino acids than in the Cerrado.

In agreement with other studies, we found that the conversion of natural habitats to coffee systems decreases ant diversity (e.g., De la Mora et al., 2013; Escobar-Ramírez et al., 2020) and changes species composition (Perfecto & Snelling, 1995), making the communities more homogeneous in this type of land use. Sun coffee plantations, as observed in our study, tend to have more intense effects on ant assemblages compared to shaded coffee plantations, which have a more negative impact on ant diversity (Urrutia-Escobar & Armbrecht, 2013). Moreover, ants are important predators in coffee systems, contributing to the reduction of coffee berry borer (Aristizabal & Metzger, 2019; Philpott & Armbrecht, 2006). However, to the best of our knowledge, this is the first study to assess ant nutrient preference in coffee systems, making significant advances in the field, particularly by linking this nutrient search to insect predation, an important ecosystem function in this type of plantation.

How similar is the species composition across land uses and resources?

We found that ant composition differed across land use types but was similar across all resources. At a regional scale, it was expected that species composition would differ between biomes due to distinct species pools and geographic distance (Schmidt et al., 2017). Moreover, with land use changes, there is a loss of sensitive species and a gain of generalist and resistant ones, resulting in species turnover and changes in composition (Queiroz et al., 2020; Wilker et al., 2023). The similarity in ant composition across different resources is likely due to the presence of omnivorous and opportunistic species. Most ants in our study belonged to the genus *Pheidole* (Tables S2–S5), which is dominant in Brazilian biomes and forages broadly on the ground (Feitosa et al., 2022; Sarnat et al., 2015). Thus, while ant composition varies across land use types due to species turnover, it remains similar within each land use type because the same opportunistic species exploit available resources.

Is foraging for larvae explained by nutrient preference?

We found that an increase in foraging for energetic nutrients (carbohydrates and lipids) positively explained foraging for larvae. Energetic nutrients are scarce in prey, leading predators to increase foraging for carbohydrates and lipids despite the low energy gain from AA (Jensen et al., 2012; Lasmar et al., 2023; Wilder et al., 2013). Thus, our results suggest a positive link between the search for energetic nutrients (carbohydrates and lipids) and the predatory activity of ants compared to AA. Additionally, the lower correlation coefficient ($R^2 = 0.11$) can be explained by the greater number of generalist ants in our experiments, and this pattern could be stronger for strictly predatory animals.

(iii) How are changes in foraging activity explained by ant species richness, land use and microclimate changes?

Regionally, foraging for larvae and preference for AA were higher in the Atlantic rainforest than in the Cerrado. This may be due to a greater limitation of AA in Atlantic rainforest ecosystems compared to the Cerrado, leading predatory ants to seek these nutrients more in the bodies of their prey. The Cerrado is known for presenting high levels of AA that are present in extrafloral nectaries (Leal et al., 2017; Ribas et al., 2010). Although we collected data only from the ground, and extrafloral nectaries are found in arboreal strata, many ground-dwelling ants forage in both strata to search for resources (Passos & Leal, 2019; Rezende et al., 2024). Thus, ants are more limited by resources from nectaries, including AA, in the Atlantic rainforest than in the Cerrado, leading to increased predation in this biome. Therefore, the predatory activity of animals may depend on the biome context, where nutrient limitations can enhance this function.

We also found a positive effect of ant species richness on foraging for larvae. Several studies indicate a positive relationship between ant species richness and predatory activity (e.g., De la Mora et al., 2015; Philpott & Armbrecht, 2006). This occurs because ant predatory activity involves various species, including both specialists and generalists (Wilker et al., 2023). Thus, an increase in the number of species elevates foraging activity and, consequently, insect predation (Frizzo et al., 2020). Therefore, strategies aimed at conserving more species may consequently benefit the conservation of ecosystem functions such as predation.

In addition, we found that increasing temperature decreases the preference for AA compared to energetic nutrients. This is likely because, in ants and other ectothermic animals, rising temperatures lead to an increase in metabolic processes (Riemer et al., 2018). As metabolism increases, there is a greater demand for energetic resources such as carbohydrates and lipids, which are essential for energy production and metabolic function (Prather et al., 2018). On the other hand, the consumption of AA tends to be higher during periods of lower seasonality and cooler temperatures, which are typically associated with reproduction and body growth (Lasmar et al., 2021).

Study limitations and future directions

In our study, there are some methodological limitations and suggestions. The similarity in ant composition foraging for different resources may be due to our collection being limited to above-ground strata. These strata are dominated by omnivorous and opportunistic species that forage for a wide variety of resources. Therefore, it would be important to assess changes in species composition in other habitat strata, such as subterranean and arboreal (Lasmar et al., 2023). Moreover, we collected our data only during the summer, when temperature and humidity tend to be higher in the Atlantic rainforest and Cerrado biomes. Therefore, we encourage further studies to evaluate seasonal differences, as they may affect ant communities (Queiroz et al., 2023) and consequently influence the search for and use of resources. Additionally, although we found a positive relationship between foraging for energetic nutrients (carbohydrates and lipids) with larvae, we sampled these nutrients separately. However, arthropod prey typically contains these nutrients together in varying concentrations (Wilder et al., 2013; Wilder & Eubanks, 2010). Therefore, it may be important for future studies to evaluate combinations of these nutrients in relation to predation to understand this relationship more comprehensively (Wilder et al., 2019).

CONCLUSION

Here, we found that land use, species richness, biome and microclimate changes affect ant foraging activity and nutrient preference. Ant species composition varied with land use type but remained similar across different foraging resources. This suggests that generalist ants may forage on a variety of resources, helping to maintain ecosystem functions. More specifically, we observed a positive relationship between foraging for energetic nutrients (carbohydrates and lipids) and foraging for larvae, indicating that predatory ants are limited by energetic nutrients and forage for these nutrients, which can enhance predation. In addition, we found that both foraging for larvae and preference for AA were greater in the Atlantic rainforest than in the Cerrado, which may indicate higher predatory activity aimed at consuming AA in environments where these nutrients are less available. Moreover, species richness was positively associated with foraging for larvae, while higher temperatures reduced preference for AA. Therefore, we suggest that conserving species richness and mitigating high temperatures could help enhance predatory activity in tropical environments.

AUTHOR CONTRIBUTIONS

Icaro Wilker: Conceptualization; investigation; writing – original draft; methodology; validation; writing – review and editing; data curation; formal analysis; project administration; supervision; visualization. **Tom R. Bishop:** Conceptualization; writing – original draft; writing – review and editing; validation; supervision; methodology. **Chaim J. Lasmar:** Conceptualization; methodology; writing – review and editing; supervision; project administration; validation. **Dara Veiga:** Data curation; writing – review and editing; investigation. **Letícia G. Souza:** Writing – review and editing; data curation; investigation. **Antônio C. M. Queiroz:** Methodology; writing – review and editing; project administration. **Rodrigo M. Feitosa:** Data curation; writing – review and editing. **Ana C. A. Neundorf:** Data curation; writing – review and editing. **Mila F. O. Martins:** Writing – review and editing; investigation. **Guilherme P. Alves:** Data curation; writing – review and editing; investigation. **Luane K. Fontenele:** Data curation; writing – review and editing. **Marília M. S. Costa:** Data curation; writing – review and editing. **Carla R. Ribas:** Conceptualization; funding acquisition; methodology; writing – review and editing; project administration; supervision; resources.

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CONFLICT OF INTEREST STATEMENT

The authors declare that there is no conflict of interest.

DATA AVAILABILITY STATEMENT

Data used in this manuscript are available from Figshare https://doi.org/10.6084/m9.figshare.27089392.v1 (Wilker et al., 2024a).

ETHICS STATEMENT

Collect licence by SISBIO n° 19610-1.

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REFERENCES

Adkins, J., Hammill, E., Abdulwahab, U.A., Draper, J.P., Wolf, J.M., McClure, C.M. et al. (2023) Environmental variables drive spatial patterns of trophic diversity in mammals. *Ecology Letters*, 26, 1940–1950. Available from: https://doi.org/10.1111/ele.14306

Alkama, R. & Cescatti, A. (2016) Biophysical climate impacts of recent changes in global forest cover. *Science*, 351(6273), 600–604. Available from: https://doi.org/10.1126/science.aac8083

Andersen, A.N. (2019) Responses of ant communities to disturbance: five principles for understanding the disturbance dynamics of a globally dominant faunal group. *Journal of Animal Ecology*, 88(3), 350–362. Available from: https://doi.org/10.1111/1365-2656.12907

Aristizabal, N. & Metzger, J.P. (2019) Landscape structure regulates pest control provided by ants in sun coffee farms. *Journal of Applied Ecology*, 56(1), 21–30. Available from: https://doi.org/10.1111/1365-2664.13283

Baccaro, F.B., Feitosa, R.M., Fernandez, F., Fernandes, I.O., Izzo, T.J., Souza, J.L.P. et al. (2015) *Guia para os gêneros de formigas do Brasil*. Manaus: Editora INPA, p. 388.

Barnes, A.D., Allen, K., Kreft, H., Corre, M.D., Jochum, M., Veldkamp, E. et al. (2017) Direct and cascading impacts of tropical land-use change on multi-trophic biodiversity. *Nature Ecology & Evolution*, 1(10), 1511–1519. Available from: https://doi.org/10.1038/s41559-017-0275-7

Bartoń, K. (2023) MuMIn: Multi-Model Inference. R package version 1.47.5. https://CRAN.R-project.org/package=MuMIn

Baselga, A. (2010) Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography*, 19(1), 134–143. Available from: https://doi.org/10.1111/j.1466-8238.2009.00490.x

Baselga, A., Orme, D., Villeger, S., De Bortoli, J., Leprieur, F. & Logez, M. (2023) betapart: Partitioning Beta Diversity into Turnover and Nestedness Components. R package version 1.6. https://CRAN.R-project.org/package=betapart

Biomas, IBGE. (2019) Sistema costeiro-marinho do Brasil: compatível com a escala 1:250.000. Série Relatórios Metodológicos.

Bolton, B. (2000) *The Ant Tribe Dacetini*. Gainesville, Florida: Memoirs of the American Entomological Institute, Vol. 65, pp. 1–1028.

Brown, W.L., Jr. (1976) Contributions toward a reclassification of the Formicidae. Part VI. Ponerinae, tribe Ponerini, subtribe Odontomachiti. Section a. Introduction, subtribal characters. Genus *Odontomachus*. *Studia Entomologica*, 19, 67–171.

Burnham, K.P. & Anderson, D.R. (2002) *Model selection and multimodel inference: a practical information-theoretic approach*. New York: Springer.

Camacho, G.P., Franco, W. & Feitosa, R.M. (2020) Additions to the taxonomy of Gnamptogenys Roger (Hymenoptera: Formicidae: Ectatomminae) with an updated key to the New World species. *Zootaxa*, 4747(3), 450–476. Available from: https://doi.org/10.11646/zootaxa.4747.3.2

Carvalho, R.L., Vieira, J., Melo, C., Silva, A.M., Tolentino, V.C., Neves, K. et al. (2022) Interactions between land use, taxonomic group and aspects and levels of diversity in a Brazilian savanna: implications for the use of bioindicators. *Journal of Applied Ecology*, 59(10), 2642–2653. Available from: https://doi.org/10.1111/1365-2664.14270

Castillo-Guevara, C., Cuautle, M., Lara, C. & Juárez-Juárez, B. (2019) Effect of agricultural land-use change on ant dominance hierarchy and food preferences in a temperate oak forest. *PeerJ*, 7, e6255. Available from: https://doi.org/10.7717/peerj.6255

Cerdá, X. & Dejean, A. (2011) Predation by ants on arthropods and other animals. *Predation in the Hymenoptera: An Evolutionary Perspective (ed. by C. Polidori)*. Kerala, India: TransWorld Research Network, pp. 39–78.

Corbelli, J.M., Zurita, G.A., Filloy, J., Galvis, J.P., Vespa, N.I. & Bellocq, I. (2015) Integrating taxonomic, functional and phylogenetic beta diversities: interactive effects with the biome and land use across taxa. *PLoS One*, 10(5), e0126854. Available from: https://doi.org/10.1371/journal.pone.0126854

De la Mora, A., García-Ballinas, J.A. & Philpott, S.M. (2015) Local, landscape, and diversity drivers of predation services provided by ants in a coffee landscape in Chiapas, Mexico. *Agriculture, Ecosystems & Environment*, 201, 83–91. Available from: https://doi.org/10.1016/j.agee.2014.11.006

De la Mora, A., Murnen, C.J. & Philpott, S.M. (2013) Local and landscape drivers of biodiversity of four groups of ants in coffee landscapes. *Biodiversity and Conservation*, 22, 871–888. Available from: https://doi.org/10.1007/s10531-013-0454-z

Dehling, D.M., Bender, I.M., Blendinger, P.G., Böhning-Gaese, K., Muñoz, M.C., Neuschulz, E.L. et al. (2021) Specialists and generalists fulfil important and complementary functional roles in ecological processes. *Functional Ecology*, 35(8), 1810–1821. Available from: https://doi.org/10.1111/1365-2435.13815

Dudley, R., Kaspari, M. & Yanoviak, S.P. (2012) Lust for salt in the Western Amazon. *Biotropica*, 44(1), 6–9. Available from: https://doi.org/10.1111/j.1744-7429.2011.00818.x

Escobar-Ramírez, S., Tscharntke, T., Armbrecht, I., Torres, W. & Grass, I. (2020) Decrease in β-diversity, but not in α-diversity, of ants in intensively managed coffee plantations. *Insect Conservation and Diversity*, 13(5), 445–455. Available from: https://doi.org/10.1111/icad.12417

Feitosa, R.M., Camacho, G.P., Silva, T.S., Ulysséa, M.A., Ladino, N., Oliveira, A.M. et al. (2022) Ants of Brazil: an overview based on 50 years of diversity studies. *Systematics and Biodiversity*, 20(1), 1–27. Available from: https://doi.org/10.1080/14772000.2022.2089268

Fernández, F. (2004) The American species of the myrmicine ant genus *Carebara* Westwood (Hymenoptera: Formicidae). *Caldasia*, 26(1), 191–238. Available from: http://www.jstor.org/stable/23641795

Frizzo, T.L., Souza, L.M., Sujii, E.R. & Togni, P.H. (2020) Ants provide biological control on tropical organic farms influenced by local and landscape factors. *Biological Control*, 151, 104378. Available from: https://doi.org/10.1016/j.biocontrol.2020.104378

Gonçalves, C.R. (1961) O gênero *Acromyrmex* no Brasil (Hym. Formicidae). *Studia Entomologica*, 4, 113–180.

Google. (2024) *Google Satellite Imagery*. https://www.google.com/maps

Hopmans, J.W., Qureshi, A.S., Kisekka, I., Munns, R., Grattan, S.R., Rengasamy, P. et al. (2021) Critical knowledge gaps and research priorities in global soil salinity. *Advances in Agronomy*, 169, 1–191. Available from: https://doi.org/10.1016/bs.agron.2021.03.001

IBGE. (2019) *Biomas e Sistema Costeiro-Marinho do Brasil – 1:250,000*. Instituto Brasileiro de Geografia e Estatística https://www.ibge.gov.br/geociencias/informacoes-ambientais/vegetacao/15842-biomas.html

INMET. (2024) Instituto Nacional de Meteorologia. Banco de Dados Meteorológicos para Ensino e Pesquisa – BDMEP. Brasília, DF, Brazil. http://www.inmet.gov.br/

Jayathilake, H.M., Prescott, G.W., Carrasco, L.R., Rao, M. & Symes, W.S. (2021) Drivers of deforestation and degradation for 28 tropical conservation landscapes. *Ambio*, 50(1), 215–228. Available from: https://doi.org/10.1007/s13280-020-01325-9

Jensen, K., Mayntz, D., Toft, S., Clissold, F.J., Hunt, J., Raubenheimer, D. et al. (2012) Optimal foraging for specific nutrients in predatory beetles. *Proceedings of the Royal Society B: Biological Sciences*, 279(1736), 2212–2218. Available from: https://doi.org/10.1098/rspb.2011.2410

Kaspari, M., Donoso, D., Lucas, J.A., Zumbusch, T. & Kay, A.D. (2012) Using nutritional ecology to predict community structure: a field test in neotropical ants. *Ecosphere*, 3(11), 1–15. Available from: https://doi.org/10.1890/ES12-00136.1

Kaspari, M. & Yanoviak, S.P. (2001) Bait use in tropical litter and canopy ants—evidence of differences in nutrient limitation. *Biotropica*, 33(1), 207–211. Available from: https://doi.org/10.1646/0006-3606(2001)033[0207:BUITLA]2.0.CO;2

Kugler, C. & Brown, W.L., Jr. (1982) Revisionary and other studies on the ant genus *Ectatomma*, including the description of two new species. *Agriculture*, 24, 1–8.

LaPolla, J.S. (2004) *Acropyga of the World*. Gainesville, Florida: Contributions of the American Entomological Institute, Vol. 33, pp. 1–130.

Lasmar, C.J., Bishop, T.R., Parr, C.L., Queiroz, A.C., Schmidt, F.A. & Ribas, C.R. (2021) Geographical variation in ant foraging activity and resource use is driven by climate and net primary productivity. *Journal of Biogeography*, 48(6), 1448–1459. Available from: https://doi.org/10.1111/jbi.14089

Lasmar, C.J., Bishop, T.R., Parr, C.L., Queiroz, A.C., Wilker, I., Feitosa, R.M. et al. (2023) Testing the context dependence of ant nutrient preference across habitat strata and trophic levels in neotropical biomes. *Ecology*, 104(4), e3975. Available from: https://doi.org/10.1002/ecy.3975

Lattke, J.E. (1997) Revisión del género *Apterostigma* Mayr (Hymenoptera: Formicidae). *Arquivos de Zoologia*, 34, 121–122.

Leal, I.R., Lopes, A.V., Machado, I.C. & Tabarelli, M. (2017) Plant–animal interactions in the caatinga: overview and perspectives. In: da Silva, J.M.C., Leal, I.R. & Tabarelli, M. (Eds.) *Caatinga: the largest tropical dry forest region in South America*. Cham: Springer, pp. 255–278.

Leroux, S.J. (2019) On the prevalence of uninformative parameters in statistical models applying model selection in applied ecology. *PLoS One*, 14(2), e0206711. Available from: https://doi.org/10.1371/journal.pone.0206711

Longino, J.T. & Fernández, F. (2007) Taxonomic review of the genus *Wasmannia*. In: Snelling, R.R., Fisher, B.L. & Ward, P.S. (Eds.) *Advances in ant systematics (Hymenoptera: Formicidae): homage to E.O. Wilson – 50 years of contributions*. Gainesville, Florida: Memoirs of the American Entomological Institute, pp. 271–289.

López-Bedoya, P.A., Bohada-Murillo, M., Ángel-Vallejo, M.C., Audino, L.D., Davis, A.L., Gurr, G. et al. (2022) Primary forest loss and degradation reduces biodiversity and ecosystem functioning: a global meta-analysis using dung beetles as an indicator taxon. *Journal of Applied Ecology*, 59(6), 1572–1585. Available from: https://doi.org/10.1111/1365-2664.14167

Machado, N.G., Biudes, M.S., Mützenberg, D.M.D.S. & Angelini, L.P. (2023) Effects of deforestation on microclimate in a Cerrado-Amazonia transition area. *Ciência Florestal*, 33(2), e70199. Available from: https://doi.org/10.5902/1980509870199

Maisey, A.C., Haslem, A., Leonard, S.W. & Bennett, A.F. (2021) Foraging by an avian ecosystem engineer extensively modifies the litter and soil layer in forest ecosystems. *Ecological Applications*, 31(1), e02219. Available from: https://doi.org/10.1002/eap.2219

Manlick, P.J. & Newsome, S.D. (2021) Adaptive foraging in the Anthropocene: can individual diet specialization compensate for biotic homogenization? *Frontiers in Ecology and the Environment*, 19(9), 510–518. Available from: https://doi.org/10.1002/fee.2380

Martinez Arbizu, P. (2020) PairwiseAdonis: Pairwise multilevel comparison using adonis. R package version 0.4. https://github.com/pmartinezarbizu/pairwiseAdonis

Mayntz, D., Raubenheimer, D., Salomon, M., Toft, S. & Simpson, S.J. (2005) Nutrient-specific foraging in invertebrate predators. *Science*, 307(5706), 111–113. Available from: https://doi.org/10.1126/science.1105493

McKinney, M.L. & Lockwood, J.L. (1999) Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends in Ecology & Evolution*, 14(11), 450–453. Available from: https://doi.org/10.1016/S0169-5347(99)01679-1

Moses, J., Peters, M.K., Tiede, Y., Mottl, O., Donoso, D.A., Farwig, N. et al. (2023) Nutrient use by tropical ant communities varies among three extensive elevational gradients: a cross-continental comparison. *Global Ecology and Biogeography*, 32(12), 2212–2229. Available from: https://doi.org/10.1111/geb.13757

Noriega, J.A., March-Salas, M., Castillo, S., García-Q, H., Hortal, J. & Santos, A.M. (2021) Human perturbations reduce dung beetle diversity and dung removal ecosystem function. *Biotropica*, 53(3), 753–766. Available from: https://doi.org/10.1111/btp.12953

Oksanen, J., Simpson, G., Blanchet, F., Kindt, R., Legendre, P. & Minchin, P. (2024) vegan: Community Ecology Package. R package version 2.6–6. https://CRAN.R-project.org/package=vegan

Ortiz-Sepúlveda, C.M., Van Bocxlaer, B., Meneses, A.D. & Fernández, F. (2019) Molecular and morphological recognition of species boundaries in the neglected ant genus Brachymyrmex (Hymenoptera: Formicidae): toward a taxonomic revision. *Organisms Diversity & Evolution*, 19, 447–542. Available from: https://doi.org/10.1007/s13127-019-00406-2

Parr, C.L. & Bishop, T.R. (2022) The response of ants to climate change. *Global Change Biology*, 28(10), 3188–3205. Available from: https://doi.org/10.1111/gcb.16140

Passos, F.C. & Leal, L.C. (2019) Protein matters: ants remove herbivores more frequently from extrafloral nectary-bearing plants when habitats are protein poor. *Biological Journal of the Linnean Society*, 127(2), 407–416. Available from: https://doi.org/10.1093/biolinnean/blz033

Perfecto, I. & Snelling, R. (1995) Biodiversity and the transformation of a tropical agroecosystem: ants in coffee plantations. *Ecological Applications*, 5(4), 1084–1097. Available from: https://doi.org/10.2307/2269356

Peters, M.K., Mayr, A., Röder, J., Sanders, N.J. & Steffan-Dewenter, I. (2014) Variation in nutrient use in ant assemblages along an extensive elevational gradient on Mt Kilimanjaro. *Journal of Biogeography*, 41(12), 2245–2255. Available from: https://doi.org/10.1111/jbi.12384

Philpott, S.M. & Armbrecht, I. (2006) Biodiversity in tropical agroforests and the ecological role of ants and ant diversity in predatory function. *Ecological Entomology*, 31(4), 369–377. Available from: https://doi.org/10.1111/j.1365-2311.2006.00793.x

Prather, R.M., Roeder, K.A., Sanders, N.J. & Kaspari, M. (2018) Using metabolic and thermal ecology to predict temperature dependent ecosystem activity: a test with prairie ants. *Ecology*, 99(9), 2113–2121. Available from: https://doi.org/10.1002/ecy.2445

Probst, R.S. & Brandão, C.R.F. (2022) A taxonomic revision of the dirt ants, Basiceros Schulz, 1906 (Hymenoptera, Formicidae). *Zootaxa*, 5149(1), 1–75. Available from: https://doi.org/10.11646/zootaxa.5149.1.1

QGIS.org. (2023) QGIS Geographic Information System. QGIS Association. http://www.qgis.org

Queiroz, A.C., Marques, T.G., Ribas, C.R., Cornelissen, T.G., Nogueira, A., Schmidt, F.A. et al. (2023) Ant diversity decreases during the dry season: a meta-analysis of the effects of seasonality on ant richness and abundance. *Biotropica*, 55(1), 29–39. Available from: https://doi.org/10.1111/btp.13158

Queiroz, A.C., Rabello, A.M., Braga, D.L., Santiago, G.S., Zurlo, L.F., Philpott, S.M. et al. (2020) Cerrado vegetation types determine how land use impacts ant biodiversity. *Biodiversity and Conservation*, 29(6), 2017–2034. Available from: https://doi.org/10.1007/s10531-017-1379-8

R Core Team. (2024) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Raubenheimer, D. (2011) Toward a quantitative nutritional ecology: the right-angled mixture triangle. *Ecological Monographs*, 81(3), 407–427. Available from: https://doi.org/10.1890/10-1707.1

Rezende, F.D.M., Schmidt, F.A., Jesus, R.S., Ribas, C.R. & Schoereder, J.H. (2024) Beyond beta: diversity partitioning reveals different underlying patterns in ant assemblages along two small scale gradients in a Brazilian neotropical forest. international journal of tropical insect. *Science*, 44, 1–10. Available from: https://doi.org/10.1007/s42690-024-01244-2

Ribas, C., Oliveira, P., Sobrinho, T., Schoereder, J. & Madureira, M. (2010) The arboreal ant community visiting extrafloral nectaries in the neotropical cerrado savanna. *Terrestrial Arthropod Reviews*, 3(1), 3–27. Available from: https://doi.org/10.1163/187498310X487785

Ribas, C.R., Campos, R.B., Schmidt, F.A. & Solar, R.R. (2012) Ants as indicators in Brazil: a review with suggestions to improve the use of ants in environmental monitoring programs. *Psyche: A Journal of Entomology*, 2012(1), 636749. Available from: https://doi.org/10.1155/2012/636749

Riemer, K., Anderson-Teixeira, K.J., Smith, F.A., Harris, D.J. & Ernest, S.M. (2018) Body size shifts influence effects of increasing temperatures on ectotherm metabolism. *Global Ecology and Biogeography*, 27(8), 958–967. Available from: https://doi.org/10.1111/geb.12757

Sarnat, E.M., Fischer, G., Guénard, B. & Economo, E.P. (2015) Introduced Pheidole of the world: taxonomy, biology and distribution. *ZooKeys*, 543, 1. Available from: https://doi.org/10.3897/zookeys.543.6050

Schmidt, F.A., Ribas, C.R., Sobrinho, T.G., Ubaidillah, R., Schoereder, J.H., Clough, Y. et al. (2017) Similar alpha and beta diversity changes in tropical ant communities, comparing savannas and rainforests in Brazil and Indonesia. *Oecologia*, 185, 487–498. Available from: https://doi.org/10.1007/s00442-017-3960-y

Stein, A., Gerstner, K. & Kreft, H. (2014) Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. *Ecology Letters*, 17(7), 866–880. Available from: https://doi.org/10.1111/ele.12277

Tabarelli, M., Peres, C.A. & Melo, F.P. (2012) The 'few winners and many losers' paradigm revisited: emerging prospects for tropical forest biodiversity. *Biological Conservation*, 155, 136–140. Available from: https://doi.org/10.1016/j.biocon.2012.06.020

Tews, J., Brose, U., Grimm, V., Tielbörger, K., Wichmann, M.C., Schwager, M. et al. (2004) Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *Journal of Biogeography*, 31(1), 79–92. Available from: https://doi.org/10.1046/j.0305-0270.2003.00994.x

Tilman, D., Wedin, D. & Knops, J. (1996) Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature*, 379(6567), 718–720. Available from: https://doi.org/10.1038/379718a0

Trancoso, R., Syktus, J., Salazar, A., Thatcher, M., Toombs, N., Wong, K.K.H. et al. (2022) Converting tropical forests to agriculture increases fire risk by fourfold. *Environmental Research Letters*, 17(10), 104019. Available from: https://doi.org/10.1088/1748-9326/ac8f5c

Trew, B.T. & Maclean, I.M. (2021) Vulnerability of global biodiversity hotspots to climate change. *Global Ecology and Biogeography*, 30(4), 768–783. Available from: https://doi.org/10.1111/geb.13272

Urrutia-Escobar, M.X. & Armbrecht, I. (2013) Effect of two agroecological management strategies on ant (Hymenoptera: Formicidae) diversity on coffee plantations in southwestern Colombia. *Environmental Entomology*, 42(2), 194–203. Available from: https://doi.org/10.1603/EN11084

Venables, W.N. & Ripley, B.D. (2002) *Modern applied statistics with S-PLUS*. New York: Springer Science & Business Media.

Warton, D.I. & Hui, F.K. (2011) The arcsine is asinine: the analysis of proportions in ecology. *Ecology*, 92(1), 3–10. Available from: https://doi.org/10.1890/10-0340.1

Watkins, J.F. (1976) *The identification and distribution of New World army ants (Dorylinae: Formicidae)*. Waco, Texas: Baylor University Press.

Wickham, H. (2016) *ggplot2: elegant graphics for data analysis*. Switzerland: Springer-Verlag New York.

Wild, A.L. (2007) *Taxonomic revision of the ant genus Linepithema (Hymenoptera: Formicidae)*. California: University of California Publications in Entomology.

Wilder, S.M., Barnes, C.L. & Hawlena, D. (2019) Predicting predator nutrient intake from prey body contents. *Frontiers in Ecology and Evolution*, 7, 42. Available from: https://doi.org/10.3389/fevo.2019.00042

Wilder, S.M. & Eubanks, M.D. (2010) Extrafloral nectar content alters foraging preferences of a predatory ant. *Biology Letters*, 6(2), 177–179. Available from: https://doi.org/10.1098/rsbl.2009.0736

Wilder, S.M., Norris, M., Lee, R.W., Raubenheimer, D. & Simpson, S.J. (2013) Arthropod food webs become increasingly lipid-limited at higher trophic levels. *Ecology Letters*, 16(7), 895–902. Available from: https://doi.org/10.1111/ele.12116

Wilker, I., Lasmar, C.J., Schmidt, F.A., da Costa, M.M.S., Almeida, D.D.F., Dutra, D.B.D.S. et al. (2023) Land-use change in the Amazon decreases ant diversity but increases ant-mediated predation. *Insect Conservation and Diversity*, 16(3), 379–392. Available from: https://doi.org/10.1111/icad.12632

Wilker, I., Bishop, T.R., Lasmar, C.J., Alves, D.A., Souza, L.G., Queiroz, A.C.M., et al (2024a) Effects of land use and microclimate changes on ant foraging in two Neotropical biomes. figshare. Dataset. Available from: https://doi.org/10.6084/m9.figshare.27089392.v1

Wilker, I., Queiroz, A.C.M., Ribas, C.R., Morini, M.S.C., Lasmar, C.J., Schmidt, F.A. et al. (2024b) A systematic review of the land use change effects on ant diversity in neotropics. *Biological Conservation*, 299, 110778. Available from: https://doi.org/10.1016/j.biocon.2024.110778

Williams, J.J. & Newbold, T. (2020) Local climatic changes affect biodiversity responses to land use: a review. *Diversity and Distributions*, 26(1), 76–92. Available from: https://doi.org/10.1111/ddi.12999

Wilson, E.O. (2003) *Pheidole in the New World. A dominant, hyperdiverse ant genus*. Cambridge: Harvard University Press.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Data S1. Supporting Information.

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