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Title: Geographical variation in ant foraging activity and resource use is driven by climate and net primary productivity

Short running title: Geography of ant foraging activity and resource use

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Abstract

Aim: Foraging activity is critical for animal survival. Comprehending how ecological drivers influence foraging behavior would benefit our understanding of the link between animals and ecological processes. Here, we evaluated the influence of ecological drivers on ant foraging activity and relative resource use.

Location: Six Brazilian biomes: Amazon, Atlantic rainforest, Caatinga, Cerrado, Pampa and Pantanal.

Taxon: Formicidae.

Methods: We assessed ant foraging activity and resource use by sampling across 60 sites. We placed baited tubes that contained one of five liquid resources (sugar, lipids, amino acid, sodium and distilled water). We used model selection to assess the influence of ecological drivers (temperature, precipitation, temperature seasonality and net primary productivity) on ant foraging activity and relative resource use.

Results: Foraging activity was higher in wetter, more productive and less thermally seasonal environments. The relative use of amino acids increased at higher temperatures while the relative use of lipids decreased. The relative use of sugar increased in drier and less productive environments with high temperature seasonality while the relative use of amino acid and sodium decreased in those environments. The relative use of lipids was complex: increasing with increasing temperature seasonality and decreasing with increasing precipitation. Further, the relative use of sodium was greater where the foraging activity was high.

Main conclusions: We demonstrate how ecological drivers are correlated to ant foraging activity and resource use in the field across large spatial scales. The search for resources encompasses different interactions involving ants with abiotic and biotic components in the ecosystem. Thus, we suggest that changes in climate and NPP, which influence the intensity and the way that ants search for resources, will result in changes in ant-mediated ecological processes.

Keywords: Ants, Biogeography, Climate effects, Feeding activity, Foraging behaviour, Macroecology, Neotropics, Nutritional Ecology.

1 INTRODUCTION

Foraging is critical for animal fitness (Raubenheimer, Simpson, & Mayntz 2009; Smith 1978). Through foraging for resources, animals are integrated into the diversity of ecological interactions and nutrient cycles that make up functioning ecosystems (Folgarait, 1998; Tilman, Isbell, & Cowles 2014). Foraging activity varies substantially across space and time; for example, arthropod foraging activity is generally higher in the tropics than in the temperate zone, higher at low elevations compared with high elevations (Peters, Mayr, Röder, Sanders, & Steffan-Dewenter, 2014; Roslin et al., 2017) and changes seasonally (Wolda 1978). Given that foraging behavior influences numerous ecosystem processes (e.g. nutrient cycling, decomposition; Maisey, Haslem, Leonard, & Bennett, 2020), identifying which drivers limit or promote foraging activity and resource use will help us understand ecosystem functioning in a rapidly changing world.

Animal foraging activity is influenced by four main ecological drivers which are related to ecosystem energy input and the prevailing climate. (1) Net primary productivity (NPP) is the fuel for all animals and is often positively correlated with foraging activity (lizards: Buckley, Rodda, & Jetz, 2008; birds: Meehan, Jetz, & Brown, 2004; and arthropods: Kaspari & de Beurs, 2019). (2) Temperature has a substantial impact on biochemical reaction rates and animal metabolism (Brown, 2014). Consequently, at higher temperatures, animals tend to be more active, move faster, and are, up to a point, more likely to find resources while foraging (Stuble et al. 2013). (3) Overall annual precipitation may lead to increased foraging activity due to reduced desiccation risk and increased plant resource availability (Costa et al., 2018; Kaspari & Weiser 2000). Actual precipitation events may, however, also reduce foraging activity (particularly for small invertebrates) due to the difficulty of foraging in the rain (Poulsen, 2008). (4) Seasonality in both temperature and rainfall can influence the availability of resources through time (Belchior, Sendoya, & Del-Claro, 2016; Costa et al., 2018), and the physiology of living organisms – via the effects described previously. Both usually make the warm, rainy season that parts of the Neotropics experience, better for foraging (Baudier et al., 2018; Wolda, 1988). Thus, we may expect that high seasonality affects foraging activity because, in highly seasonal environments, animals increase activity in favorable seasonal periods to compensate for their inability to forage in harsh seasonal periods (Kaspari, Alonso & O'Donnell., 2000). To date, there has not been an assessment of how all four of these ecological drivers work in concert to influence geographical variation in foraging activity.

Foraging activity may also change depending on the resource being foraged for, with resource demand or resource shortfall interacting with climate and NPP to drive resource use (Raubenheimer et al., 2009). Resource demand can be seen, for example, when the climate drives the demand for particular energy or nutrient sources. At higher temperatures, animals expend more effort collecting specific resources in order to compensate for the accelerated metabolic (e.g. sugar and sodium), excretion (e.g. sodium) and growth rates (e.g. amino acids) (Kutz, Sgrò, & Mirth, 2019; Prather, Roeder, Sanders, & Kaspari, 2018). At low temperatures, on the other hand, there may be high levels of lipid consumption because of its thermal insulating properties (Heinze, Foitzik, Fischer, Wanke, & Kipyatkov, 2003; Peters et al., 2014). In cases of resource shortfall, animals will dedicate a disproportionately high foraging effort to collect resources that are in deficit in the environment (Kaspari, Yanoviak, & Dudley, 2008; Kaspari, 2020). For example, at low levels of NPP, animals bias their foraging effort toward collecting high-energy sugar (Kaspari, Welti & Beurs, 2020). Similarly, as precipitation events are positively linked to plant resource availability (Costa et al., 2018), we may also expect greater foraging effort for high-energy resources in drier regions. In environments with high climatic seasonality, there may be significant foraging effort put in toward collecting lipids, as they are easier to store for use in harsh periods (Heinze et al., 2003). In sum, resource use can vary geographically according to shortfall and demand, which may in turn be influenced by climate and NPP (Kaspari et al., 2020).

Despite the potential influence of NPP and climate drivers on foraging behavior, most studies of foraging activity patterns and resource use have focused mainly on the effects of temperature and net primary productivity (e.g. Kaspari & de Beurs, 2019). Furthermore, most have not directly assessed foraging activity but have instead used indirect measurements such as counting the number of individuals in a trap and bite marks in artificial plasticine animals (e.g. Gibb, Grossman, Dickman, Decker & Wardle, 2019; Kaspari & de Beurs, 2019, but see Kaspari et al. 2020; Sheard et al. 2020).

Ants are an excellent model taxon for studying the variation in foraging activity and resource use because they are some of the most abundant living animals. Through their foraging activities, ants are essential components of terrestrial ecosystems as seed dispersers, granivores, scavengers, predators, and for cycling of nutrients (Folgarait, 1998; Blüthgen & Feldhaar, 2010, Griffiths et al. 2018). Ants require a range of different macro and micronutrients for their development, and they must interact in different ways with plants, other animals and with the environment to obtain resources (Blüthgen & Feldhaar, 2010). Sugar and lipids are the main sources of energy for the entire colony, while lipids and amino acids are important for colony growth and development of larvae (Csata & Dussutour, 2019). Sodium is important for several physiological and metabolic processes (Csata & Dussutour, 2019). Hence, the foraging behavior of ants provides a model system to investigate how climate and NPP interact to influence geographical variation in foraging activity and resource use.

Given that ants play an important role in numerous ecosystem processes, understanding the influence of ecological drivers that potentially drive their foraging activity and their differential resource use will allow us to assess how changes in climate and NPP could affect future ant-mediated ecosystem function. Here, we assessed ant foraging activity and relative resource use across six biomes in Brazil which vary in their climate and NPP. Specifically, we predict that: (i) ant foraging activity will respond positively to temperature, precipitation, NPP and climate seasonality; (ii) temperature will positively affect the relative use of sugar, amino acid and sodium, and negatively affect the relative lipid use; (iii) low precipitation and NPP will increase the relative use of high-energy resources (sugar and lipids); (iv) climatic seasonality will increase the relative use of lipids.

2 MATERIAL AND METHODS

2.1 Study area

We sampled in protected areas across six different biomes in Brazil which have different climates and vegetation types (Fig. 1; Table 1). We carried out sampling in the rainy season of each biome (i.e. usually when foraging activity is highest), between November 2016 and March 2018.

2.2 Sampling of foraging ants

In each of the six biomes, we installed 10 transects as sampling units (60 transects in total) separated by at least 1 km, except for two in the Amazon biome and two in the Pampa biome where they were separated by 800 m due to spatial constraints. Each transect was 750 m long with 25 sampling points separated by 30 m. At each sampling point, we provided one of five liquid food resources in the epigaeic strata. The food resources were placed in 50-mL Fisher Scientific polypropylene centrifuge tubes with a 5 cm cotton ball containing 10 ml of the following solutions in distilled water: 1% sodium (NaCl), 20% sugar (CHO, made with sucrose), 20% amino acids (AA, made with unflavored whey protein isolate), lipids (100% extra virgin olive oil, without water), and distilled water as a control. Similar liquid resources have successfully been used in previous studies (e.g., Fowler, Lessard, and Sanders 2014; Peters et al. 2014; Tiede et al. 2017). We placed the baited tubes horizontally on the ground. Hence, along each transect, each liquid food resource was repeated five times in the same sequence along each transect (following the order: control, carbohydrates, lipids, amino acid and sodium). Consequently, there were five pseudoreplicates of each of the five resource types per transect (5 pseudoreplicates × 5 resource types = 25 sampling points per transect), giving a total of 250 sampling points per biome (25 sampling points x 10 transects) and 1500 sampling points across the study (250 x 6 biomes).

For all biomes, baiting was restricted to sunny periods, and never in rain or on totally cloudy days. We began placement of the baited tubes at 7:00 am at each site for all biomes except in the sites of Caatinga biome, where we delayed placement until 1:00 pm because light rainfall during the morning may have reduced ant activity in this period. By restricting the sampling to one period (mornings or afternoon) in each study area, we avoided large variation in temperature. We left all tubes open for three hours, after which we capped the tubes to collect the ants inside. A tube was classed as visited when there was at least one ant individual inside.

In the laboratory, we counted all ant workers and identified them to genera following Baccaro et al. (2015) and where possible, to species level or morphospecies by matching them with the ant reference collection of Laboratório de Ecologia de Formigas of the Universidade Federal de Lavras (UFLA). After that, we confirmed the identification at Laboratório de Sistemática de Formigas of the Universidade Federal do Paraná (UFPR). Voucher specimens were deposited in the reference collection of Laboratório de Ecologia de Formigas at UFLA and the Entomological Collection Padre Jesus Santiago Moure of UFPR (DZUP).

We considered the proportional occurrence of foraging ants (the overall proportion of visited tubes per transect across all ants, irrespective of species identity) as a proxy of ant foraging activity. Relative resource use was then calculated as the number of visited tubes of a given resource, divided by the total number of visited tubes (including control tubes) per transect. Consequently, relative resource use indicates the use of a given resource type in relation to all others and is not dependent on the different occurrences of foraging ants in transects, whereby a relative use of 1 indicates that all foraging was focused on a given resource, whereas a relative use of 0 means than no foraging took place on that resource.

2.3 Ecological drivers

Data for climate and NPP were obtained for 60 1-km^2 grid cells, which each contained one sampled transect. We obtained data for temperature, precipitation and climate seasonality from the WorldClim 2 database (Fick & Hijmans, 2017), which represents average climate between 1970 and 2000. For each transect, we extracted the WorldClim variables mean annual temperature (C°), annual precipitation (mm), temperature seasonality (standard deviation of annual mean temperature), and precipitation seasonality (coefficient of variation of annual precipitation). For the months in which we sampled ants in each biome, we also extracted the data for monthly mean temperature (°C), and monthly precipitation (mm; Table 1). We obtained net primary productivity (NPP) from MODIS, using annual NPP from 2000-2015 (MOD17) from the NASA Earth Observation System repository at the University of Montana (www.ntsg.umt.edu/), which has been improved by correcting for cloud-contaminated pixels and uses a model that considers the difference between gross primary productivity and autotrophic respiration (Zhao and Running, 2010).

We compared the WordClim estimates of climate to nearest climatic station (NCS) weather data from 1970 to the present (See Appendix 1). We did this to check whether (1) our sampling periods experienced extreme weather compared to the historical average and, (2) to assess whether WorldClim reliably predicted NCS estimates of local conditions. The NCS data showed that the time periods in which we sampled we not extreme relative to the historical record (Fig. S1.1 in Appendix 1), and that the WorldClim data closely matched the estimates of temperature and rainfall for all sites (Fig S1.2 in Appendix 1). Consequently, we opt to use WorldClim data in our analyses as a good representation of both local weather during sampling and long term climatic trends and because WorldClim provides better spatial cover of the sampling sites.

2.4 Data analyses

Before analysing the data, we checked for collinearity between our climate and productivity drivers (‘Psych’ package (Revelle, 2011) in R version 3.4.1 (R Development Core Team 2017). We found strong associations (correlation $R > 0.65$) between annual mean and monthly mean temperatures, annual and monthly precipitation, as well as between temperature seasonality and precipitation seasonality (see Fig. S1.3 in Appendix S1). Consequently, we performed all subsequent analyses with monthly mean temperature, monthly precipitation, temperature seasonality and NPP to represent the ecological drivers of temperature, precipitation, seasonality and NPP. As temperature and precipitation may vary substantially across the year, using mean monthly values is a more accurate way to represent the climate in our sampling periods. In addition, we chose temperature seasonality instead of precipitation seasonality because ant metabolism is expected to be directly affected by temperature (Gillooly, Brown, West, Savage, & Charnov, 2001). Proportional foraging activity and relative resource use data were logit-transformed to meet Gaussian assumptions (Warton & Hui, 2011).

All analyses were carried out using proportional values per transect of ant foraging activity and relative resource use as response variables (n = 60). To assess the influence of ecological drivers on the ant foraging activity, we constructed generalized linear mixed models (GLMM) with logit-transformed proportional occurrence of foraging ants as the response variable and temperature, precipitation, temperature seasonality and NPP as explanatory variables (fixed effects). Biome was assigned as the random effect to account for the possibly spatial autocorrelation between transects in the same biome. We used the *dredge* function ('MuMIn' package version 1.10.5; Barton 2014) to run all possible models, ranking them based on the Akaike information criterion corrected (AICc), and considering only the models with ΔAICc < 2 (Burnham & Anderson, 2002). We ran the modelling process with and without the data for control tubes. Because results from the two sets of modelling procedures did not differ, there was no evidence that control tubes affected the foraging patterns found (Appendix S2; Table S2.2). Therefore, we only report results without control tubes. We searched for potential "uninformative parameters" within the models where ΔAICc < 2 by following the approach proposed by Leroux (2019). Leroux's (2019) approach involves two steps. First, 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, we considered the additional parameters as informative. If the log likelihoods were similar, we checked to see if the 95% confidence intervals of the additional parameters overlapped zero. If the confidence intervals overlapped zero, we considered the parameters to be uninformative, if they did not overlap zero, we considered them to be informative.

Since foraging activity can be related to species richness and abundance (Gibb et al., 2019; Kaspari et al., 2000), we also ran a GLM to assess whether the foraging activity was correlated with the number of ant workers or species richness for each transect. Where a significant correlation was detected, we extracted the model residuals (as the response variable) and performed another model selection using the *dredge* function to determine how the foraging activity was influenced by ecological drivers, while controlling for these correlations.

To assess how ecological drivers influence relative resource use, we performed the same model selection of GLMMs using the *dredge* function, modelling each relative resource use (control, sugar, lipids, amino acids and sodium) as the response variable and including temperature, precipitation, temperature seasonality and NPP as explanatory variables (fixed effects) and, the biome as random effect. We also looked for uninformative parameters in the models with ΔAICc < 2 as proposed by Leroux (2019). Furthermore, as the availability of water in the sugar, amino acids and sodium solutions could influence their use as resources, we performed another model selection that included the relative use of the control tubes (distilled water) as an extra explanatory variable. We expected that, if ants visited those resources because they were attracted to the water, then the relative use of the controls alone would explain most of the variation in resource use.

3 RESULTS

3.1 How do ecological drivers influence ant foraging activity?

We sampled 16,065 ant workers belonging to 188 ant species and 30 genera across all transects (Table S2.4 in Appendix S2). The best models (ΔAICc < 2) explaining ant foraging activity included precipitation, temperature seasonality, and NPP (Table 2). Thus, foraging activity increased with increasing precipitation and NPP, and decreased with temperature seasonality (Fig. 2).

The proportion of visited tubes increased with both ant species richness and the number of ant workers ($R^2 = 0.84$; Fig. S1.4 in Appendix 1). However, the model selection procedure using the residuals of the relationship between foraging activity and the number of ant workers retained the same explanatory variables as the original modelling plus temperature (Table 2). The model selection procedure using the residuals of the relationship between foraging activity and species richness did not retain any ecological drivers as explanatory variables (Table 2). This indicates that despite the fact that ant foraging activity is correlated with ant species richness and the number of ant workers, the influence of ecological drivers on foraging activity seems to be strongly linked to ant species richness but not with the number of ant workers.

3.2 How do ecological drivers influence relative resource use of foraging ants?

The most visited resource types were sugar and lipids, each with 34% of visited tubes over the whole study, followed by sodium with 17%, amino acids with 12% and distilled water with 3% (see full details in Table S2.3 in Appendix S2).

Almost all the best models (ΔAICc < 2) for each resource type included temperature, precipitation, temperature seasonality and NPP (Table 2). However, the influence of the climatic drivers and NPP on foraging differed strongly among resource types (Fig. 3 and Fig. S1.5-S1.8 in Appendix S1). Our results show that with increasing temperature, there was an increase in the relative use of amino acids, whereas the relative use of lipids decreased, but there was no influence of temperature on the relative use of sugar and sodium (Fig. 3a). With increasing precipitation, there was an increase in the relative use of sodium and a decrease in the relative use of sugar and lipids. Amino acids remained unaffected by precipitation (Fig. 3b). With greater temperature seasonality the relative use of sugar increased, while the relative use of lipids, amino acids and sodium decreased (Fig. 3c). The influence of NPP on resource use also varied markedly among resource types: relative sugar use declined with increasing NPP, whereas the relative use of amino acids and sodium increased (Fig. 3d). We identified possible uninformative parameters for the best models for relative use of sugar and sodium. We did not consider the effect of temperature on the relative use of sugar because temperature was present in the second-best model and did not considerably improve the log likelihood in relation to the top model (log likelihood difference = 0.45; Table 2) and its estimate overlapped zero (CI 95% = -0.031, 0.090). We also did not consider the temperature effect on the relative use of sodium because temperature was present in the third-best model, did not considerably improve the log likelihood in relation to the top model (log likelihood difference = 0.57; Table 2) and its estimate overlapped zero (CI 95% = -0.036, 0.121).

No changes to the patterns of relative resource use were detected when the models were rerun including the relative use of controls as an explanatory variable (Table S2.2 in Appendix S2), indicating that ants visited the tubes containing sugar, amino acids and sodium solutions to forage for the resource, rather than for the water in the solutions.

4 DISCUSSION

Our study highlights the importance of ecological drivers for explaining geographical variation in ant foraging activity and resource use. Precipitation, temperature seasonality and NPP are related to the variation in ant foraging activity. This result, however, may partly be due to differences in species richness. Overall, ants preferred sugar and lipids across the six Brazilian biomes. This is consistent with previous studies in North America and Africa (e.g. Fowler et al., 2014; Peters et al., 2014) and indicates that high-energy resources are the most sought after by ants. This may explain the high dominance behavior of ants in protecting and monopolizing high-energy resources in the wild (Grover, Kay, Monson, Marsh, & Holway, 2007) such as plant exudates and hemipteran honeydew. However, the novelty of our study is that geographical variation in four types of resources can be linked to climate and NPP.

4.1 How do ecological drivers influence ant foraging activity?

Ant foraging activity was higher in wetter and more productive environments with low temperature seasonality (Fig. 2). However, the lack of relationship between temperature and foraging activity in this study could be because considerable changes in temperature were not experimented by ants during our study – although temperature positively influenced foraging activity when controlling for the number of ant workers (Table 1). We interpret the ecological drivers as influencing ant foraging activity in two different ways. First, the majority of Neotropical ants originated in hot and humid tropical forests and diversified following forest expansion (Moreau & Bell 2013; Price et al., 2014, Vasconcelos et al., 2018). Consequently, the greater ant foraging activity in wetter environments could represent a niche characteristic that has been conserved through evolutionary time. The positive and direct influence of precipitation (through moisture) could improve foraging performance by reducing desiccation stress while ants forage (Gibb et al., 2019). Second, temperature seasonality and NPP effects may also be linked with ant abundance in addition to acting on foraging performance. Previous studies have shown that ant abundance is higher in less seasonal and more productive environments (e.g. Kaspari et al., 2000; Kaspari & de Beurs, 2019). This may be because ants are able to harvest more energy due to their foraging for longer periods throughout the year in more climatically stable environments (Kaspari et al., 2000). In addition, there is greater energy and carbon availability for individuals in more productive environments, which also increases abundance (Kaspari & de Beurs, 2019). Thus, higher ant abundances may also be correlated with greater foraging activity in productive environments with low temperature seasonality. In this sense, we propose that precipitation, temperature seasonality and NPP directly influence ant foraging activity, however, the influence of temperature seasonality and NPP can also operate indirectly through their effects on ant abundance.

The influence of climate and NPP on foraging activity, however, appears to be linked to species richness. When we controlled for differences in ant species richness, we found no influence of any ecological driver. Previous long-term studies have found that ant species richness is positively influenced by ant foraging activity (e.g., Gibb et al., 2019). This might indicate that the foraging activity of ants is intrinsically linked to their diversity patterns. Nevertheless, our observational study cannot determine whether foraging activity regulates species richness or vice versa, or whether ecological drivers independently influence both.

4.2 How do ecological drivers influence relative resource use of foraging ants?

We interpret the influences of precipitation, temperature seasonality and NPP on our relative resource use largely as a trade-off between sugar on the one hand, and amino acids and sodium on the other. In drier and less productive environments with high temperature seasonality, the relative use of sugar increased, while the relative use of sodium and amino acids decreased (Fig. 3b, c and d). Previous studies have demonstrated that low NPP, low precipitation and high climatic seasonality can limit how much energy ants can capture (Costa et al., 2018; Kaspari et al., 2020). This may explain the increase of the relative use of sugar in these environments (e.g. Caatinga and Pampa biomes, Table S2.3 in Appendix S2). Thus, we think that first ants try to address energy deficits by foraging more for sugar where the available energy is low. Then, when and where ants have sufficient levels of energy resources (e.g. in wetter and productive environments with low temperature seasonality) or where they are able to forage for longer periods throughout the year (e.g. environments with low temperature seasonality), ants increase the demand for amino acids that improve colony size (Asano & Cassill, 2012) and for sodium that support the high costs of foraging activity (Prather et al., 2018; Fig. 3b, c, d). A similar trade-off between sugar and protein has also been observed in studies at small spatial scales, where the resource preference of ants depends on availability of nectar from plants (e.g. Vidal, Silva, & Sendoya, 2019). Yet, our findings are novel because the influence of precipitation, temperature seasonality and NPP on this trade-off occurs at large spatial scales and this trade-off not only involves the relationship between sugar and amino acids, but also between sugar and sodium.

Precipitation, temperature seasonality also affected the relative use of lipids. However, we should interpret these results with caution. Lipids supply the energy demand for larval growth, while sugar supplies are needed for adult ants (Blüthgen & Feldhaar, 2010). As plant resource availability is influenced by precipitation (Costa et al., 2018), it is likely lipid resources are lower in drier environments. This may explain the same pattern for the relative use of sugar and lipids as they both increased in drier environments (Fig. 3b). Besides supplying resources for larval growth, ants also access components in lipids that are important for egg production and ovary development, all related to the colony growth (Blüthgen & Feldhaar, 2010). Thus, following the same pattern as amino acids, it is possible that ants forage more for lipids in environments with low temperature seasonality (Fig. 3c) to facilitate colony growth since energy demand has already been achieved. Considering that little is known about the diet requirements in ants of lipids (Csata & Dussutour, 2019), the influence of ecological drivers on the relative use of lipids appears complex. We should not assume the role of lipids for ants is only to meet energy demands, but also for colony growth.

Temperature likely influences relative resource use by acting on the physiology of ants. At small spatial scales, ants forage more for sugar and sodium to supply accelerated metabolic rates caused by temperature (Prather et al., 2018). However, we found no support for this since the influence of temperature on relative use of sugar and sodium in our study seemed to be an uninformative parameter in our models (sensu Leroux, 2019). On the other hand, at high temperatures the relative use of amino acids increased, probably to support accelerated colony growth, as suggested by theoretical studies (e.g. Asano & Cassill 2012). By contrast, at low temperatures, ants increased the relative use of lipids probably because they are important components for thermal insulation (Heinze et al., 2003). Similar patterns have been found across elevational gradients (e.g. Peters et al., 2014). This probably indicates that the thermal insulation properties of lipids could be more important for the fitness of ant colonies in cold places.

Interestingly, another general pattern we found is that all drivers present in the best models of ant foraging activity were also present in the best models of relative use of sodium (Table 2). The influences of ecological drivers on both foraging activity and relative sodium use were also in the same direction (Fig. 2 and 3b, c, and d). Thus, we propose that the demand for sodium could be greater where foraging activity is higher since greater activity demands high levels of sodium for metabolic functioning (Prather et al., 2018; Kaspari, 2020). Therefore, sodium could be a critical limiting resource for ant foraging activity, as it is for ecological interactions, decomposition, and carbon cycle processes in tropical forests (Kaspari, 2020).

4.3 Uncertainties and remaining knowledge gaps

Our work shows that ecological drivers explain the geographical variation in foraging activity and resource use by ants. However, we must account for some methodological caveats and for remaining knowledge gaps about foraging behavior. First, as we were unable to disentangle the direct influence of ecological drivers on foraging activity from the influence of ant species richness, future experimental work is needed to assess the causality of the positive relationship between foraging and species richness. Second, there were low visits to amino acids baits in Caatinga and Pampa biomes (Table S2.3 in Appendix S2), which contrasts with the apparent attractiveness of other protein baits (e.g. canned sardine or tuna baits; Yanoviak & Kaspari, 2000). A possible explanation for this different use of bait type is that sardine/tuna baits present other nutrients such as lipids and sodium, which could supply more than only amino acids requirements and, therefore, attract more ants.

Third, although we propose that all ecological drivers studied here increase foraging activity, which in its turn increases sodium demand, we should also account for the fact that foraging for sodium can also be high in environments where it is in shortfall (Kaspari et al., 2008). Considering the drivers in this study we think that only precipitation could directly affect sodium availability in the environment. As sodium is water soluble, high precipitation could easily leach it from the environment (Clay, Donoso, & Kaspari, 2015; Kaspari, 2020). Furthermore, increased plant growth due to higher precipitation may dilute sodium concentrations in plant tissue, which are a sodium source for ants (Kaspari, 2020; Kaspari et al., 2020). Thus, sodium may also be in shortfall in wetter environments, also explaining the increased relative use of sodium with precipitation. In this sense, future studies should address if precipitation can actually reduce sodium availability in plants and soil and thus influence sodium use (Kaspari, 2020).

Finally, our study is based on ants foraging at only one habitat stratum. As there may be differences in foraging activity and resource use across different habitat strata (Yanoviak & Kaspari, 2000; Law & Parr, 2020), it would be useful for future studies to address such question to fully understand the foraging behavior of ants at large spatial scales.

5 CONCLUSION

Overall, our study shows that differences in climate and NPP are correlated with ant foraging activity and resource use across large spatial scales. Given that ant foraging activity and resource use involves numerous biotic and abiotic interactions, it is conceivable that global climate change and changes in NPP may shift these patterns in foraging behavior. In turn, changes to foraging could result in changes in ant-mediated ecosystem functions. Considering the influence of ecological drivers on the variation of foraging activity and the resource use for other taxa (e.g. fishes, Barneche et al., 2009: birds, Barnagaud et al., 2019; primates, Coleman & Hill, 2014; arthropods, Kaspari & de Beurs, 2019; Mayr et al., 2020), future studies would benefit from our findings to investigate the links between ecological drivers, resource requirements and foraging activity.

Table 1. Sampling sites characterization. Vegetation types of the sampled areas across six Brazilian biomes. Climate data were obtained from WorldClim Version 2 (Fick and Hijmans, 2017) just from one geographical point to represent each biome.

Biome and location	Vegetation type	Annual mean temperature (°C)	Annual minimum mean temperature (°C)	Annual maximum mean temperature (°C)	Annual precipitation (mm)	Precipitation of the driest month (mm)	Precipitation of the wettest month (mm)	Altitude (average) (m.a.s.l)	Sampling period
Amazon Reserva Florestal de Humaitá (9°46'13"S, 67°37'7"W).	Open rainforest with palm trees and bamboo	25.2	17.8	31.5	1,720	46	233	185	Nov/2016
Atlantic rainforest Parque Estadual Intervales (24°17'13"S, 48°26'41"W).	Montane dense rainforest	17.7	8.5	26.6	1,419	50	207	800	Mar/2018
Caatinga Parque Nacional do Catimbau (8°30'19"S, 37°18'37.86"W).	Shrublands	20.5	13.9	29	721	17	128	970	Jul/2017
Cerrado Reserva Ecológica do IBGE and Jardim Botânico de Brasília (15°55'33"S, 47°52'59"W).	Brazilian savannah; Cerrado *strictu senso*	20.1	11.5	27.5	1,519	8	263	1,100	Dec/2017
Pampa Parque Estadual do Espinilho (30°11'25"S, 57°29'51"W).	Humid steppe savannah	19.8	7.7	31.2	1,474	67	165	51	Nov/2017
Pantanal Sesc Pantanal (16°31'22.59"S, 56°24'6.41"W).	Mixed vegetation: from grasslands and natural forest remnants, also natural floods	25.2	14.9	34.9	1,317	19	215	123	Apr/2017

Table 2. Model selection using the *dredge* function (Barton, 2015) based on the Akaike information criterion corrected (AICc) ranking of ecological drivers influence on ant foraging activity and resource use (n = 60) across six Brazilian biomes. The generalized linear mixed models were constructed for question 1 and 2 with the explanatory variables: temperature (monthly mean temperature, MMTemp), precipitation (monthly precipitation, MPrec), temperature seasonality (TSeas), net primary productivity (NPP). Biome was the random variable. In question 1, we also performed the same model selection using the residuals from the correlation between ant foraging activity and ant species richness and using the residuals from the correlation between ant foraging activity and number of ant workers. In question 2, Models were run separately for four resource types represented as a solution of: 20% sugar (CHO, made with sucrose), lipids (extra virgin olive oil), 20% amino acids (AA, made with unflavored whey protein isolate), and 1% sodium (NaCl) and. We only considered and pointed out models equal or lower than ΔAICc = 2. Degrees of freedom of the model (d.f.), differences in AICc-values (ΔAICc) and Akaike weight (ω) are shown. Marginal R² is the coefficient of determination of fixed effects (ecological drivers) and Conditional R² is the coefficient of determination of fixed effects plus random effects (biomes).

Question 1: How do ecological drivers influence ant foraging activity?

Model	d.f.	AICc	ΔAICc	ω	Log Likelihood	Marginal R²	Conditional R²
MPrec	4	121.3	0.00	0.16	-56.31	0.19	0.82
MPrec + TSeas	5	121.8	0.43	0.13	-55.32	0.38	0.82
TSeas	4	121.8	0.50	0.11	-56.55	0.32	0.79
TSeas + NPP	5	122.5	1.15	0.10	-55.69	0.32	0.79
Null Model	3	122.6	1.24	0.08	-58.08	-	-

Question 1: using the residuals from the correlation between ant foraging activity and ant species richness.

Model	d.f.	AICc	ΔAICc	ω	Log Likelihood	Marginal R²	Conditional R²
Null model	3	126.0	0.00	0.30	-59.80	-	-

Question 1: using the residuals from the correlation between ant foraging activity and the number of ant workers.

Model	d.f.	AICc	ΔAICc	ω	Log Likelihood	Marginal R²	Conditional R²
MPrec + TSeas + NPP	6	110.5	0.00	0.31	-48.45	0.39	0.39
TSeas + NPP	4	110.8	0.30	0.27	-49.83	0.36	0.36
MMTemp + MPrec + TSeas + NPP	7	111.6	1.14	0.18	-47.73	0.41	0.41
MMTemp + TSeas + NPP	6	111.8	1.37	0.16	-49.13	0.38	0.38

Question 2: How do ecological drivers influence relative resource use of foraging ants?

CHO

Model	d.f.	AICc	ΔAICc	ω	Log Likelihood	Marginal R²	Conditional R²
MPrec + TSeas + NPP	6	132.7	0.00	0.54	-59.57	0.46	0.46
MMTemp + MPrec + TSeas + NPP	7	134.4	1.67	0.23	-59.12	0.47	0.47

Lipids

Model	d.f.	AICc	ΔAICc	ω	Log Likelihood	Marginal R²	Conditional R²
MMTemp + TSeas	5	127.4	0.00	0.19	-58.12	0.13	0.23
MMTemp	4	127.4	0.05	0.18	-59.34	0.13	0.26
MMTemp + MPrec + TSeas	6	128.4	1.03	0.11	-57.40	0.21	0.22
Null Model	3	128.6	1.27	0.09	-61.09	-	-

AA

Model	d.f.	AICc	ΔAICc	ω	Log Likelihood	Marginal R²	Conditional R²
MMTemp + TSeas + NPP	6	173.6	0.00	0.39	-79.98	0.32	0.32

NaCl

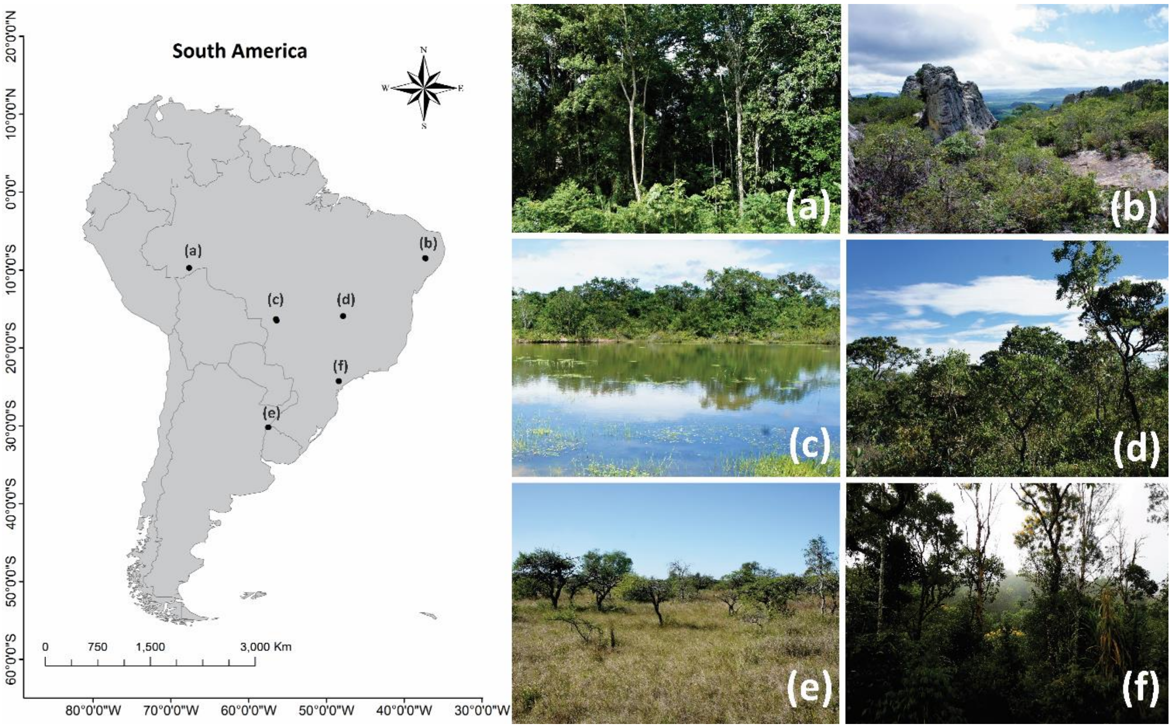
Model	d.f.	AICc	ΔAICc	ω	Log Likelihood	Marginal R^2	Conditional R^2
MPrec + TSeas + NPP	6	164.2	0.00	0.40	-75.29	0.51	0.51
MPrec + TSeas	5	165.3	1.12	0.23	-77.09	0.48	0.50
MMTemp + MPrec + TSeas + NPP	7	165.6	1.43	0.20	-74.72	0.52	0.52

List of figures legends

Figure 1. Location of the sampling sites across six Brazilian biomes: (a) Amazon, (b) Caatinga, (c) Pantanal, (d) Cerrado, (e) Pampa and (f) Atlantic rainforest.

Figure 2. Relationship between ant foraging activity (measured by the proportional occurrence of foraging ants) and (a) mean monthly temperature; (b) monthly precipitation; (c) temperature seasonality and (d) net primary productivity (NPP) across 60 transects in six biomes in Brazil (n = 60). Points show the proportions of visited tubes per transect in each biome discriminated by specific symbols and colors and black lines represent significant relationships with ecological drivers. Lines are model predictions back transformed into the original variable scale based only in the fixed effects for best visualization.

Figure 3. Relationship between relative use of sugar (CHO; Blue triangle), lipid (Orange circle), amino acid (AA; Red rhombus) and sodium (NaCl; Green upside-down triangle) and (a) mean monthly temperature; (b) monthly precipitation; (c) temperature seasonality and (d) net primary productivity (NPP) across 60 transects in six biomes in Brazil (n = 60). Points show the relative use of each resource in the respectively symbols and colors as well as lines and the respectively colors represent significant relationships with ecological drivers. Lines are model predictions back transformed into the original variable scale based only in the fixed effects for best visualization.



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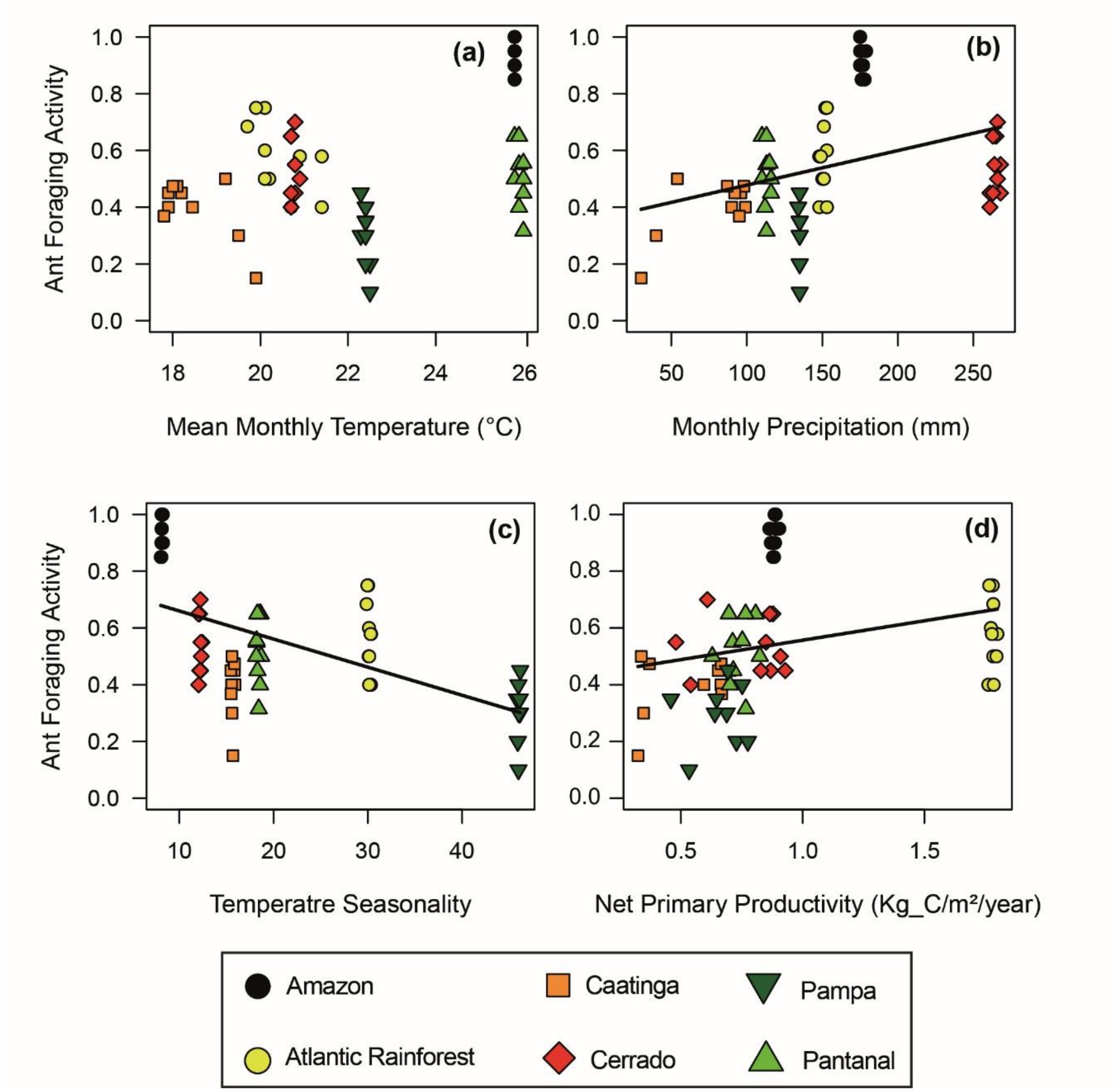

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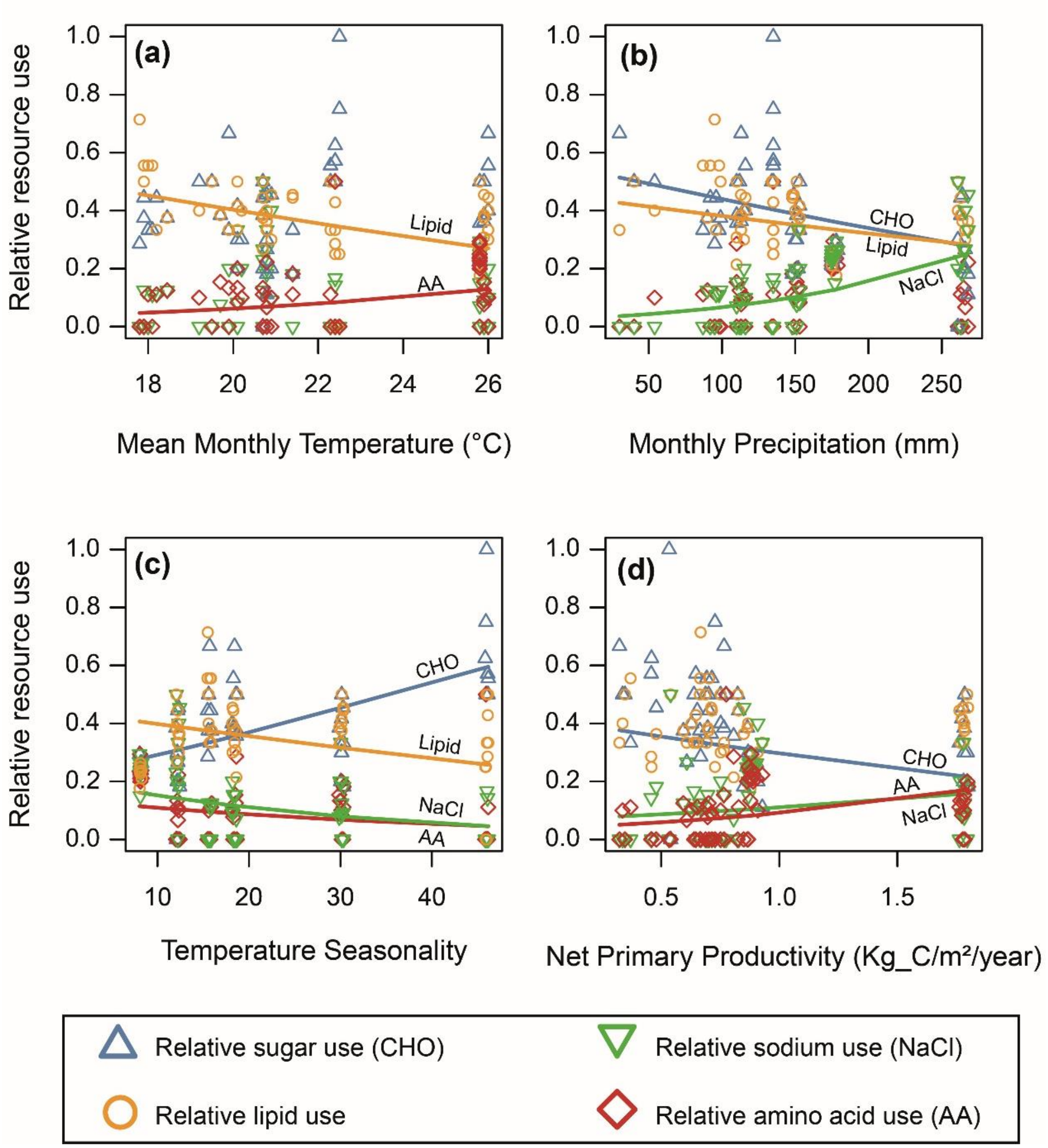

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Data availability statement: All data have been uploaded to Dryad (https://doi.org/10.5061/dryad.6wwpzgmxc).

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