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Citation for final published version:

Lasmar, Chaim J., Bishop, Tom R., Parr, Catherine L., Queiroz, Antônio C. M., Schmidt, Fernando A., Ribas, Carla R. and Economo, Evan 2021. Geographical variation in ant foraging activity and resource use is driven by climate and net primary productivity. *Journal of Biogeography* 48 (6) , pp. 1448-1459.
10.1111/jbi.14089 file

Publishers page: <http://dx.doi.org/10.1111/jbi.14089>
<<http://dx.doi.org/10.1111/jbi.14089>>

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

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

4

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21 **Acknowledgements**

22

23 This work was funded by the Rufford Foundation's Small Grants (Project number: 21757-1) and
24 Fundação de Amparo e Pesquisa de Minas Gerais (FAPEMIG, grant APQ-02551-16). We thank
25 the following agencies for conceding permission to sample in protected areas of the Brazilian
26 biomes: Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio licença de coleta
27 46564-1 and 19610), and Comissão Técnico-Científica, Instituto Florestal (COTEC-IF licença de
28 coleta 260108 – 008.767/2017). We are thankful for the staff of each of the six protected areas
29 where samples were carried out. We are also indebted to A.C. Souza, A.C. Reis, C. Rosa, C.V.
30 Oliveira, E.M.G.C. Silva, I.W.G. Carvalho, J.J.M. Aguiar, M.V. Mendes, M.A. Rabelo, M.A.
31 Angotti, M.M.G. Imata, R.C.R. Souza, R.G. Cuissi and S. Farsura for their important help in the
32 fieldwork. We are incredibly grateful to the staff at the Laboratório de Sistemática de Formigas of
33 Universidade Federal do Paraná for confirming ant identification, especially to R.M. Feitosa and
34 A. Casadei-Ferreira. We are also indebted to H.M. Griffiths for her help and advice on statistical
35 analyses and to C.A. Nunes, J. Barlow and E.J. Sayer for their helpful comments on an earlier draft
36 of the manuscript. This study was part of CJ Lasmar's Ph.D. thesis at UFLA that was supported by
37 Coordenação de Aperfeiçoamento Pessoal (CAPES, Finance code: 001).

38

39 **Conflict of Interest Statement:** Authors declare no conflict of interest.

40 **Abstract**

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

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

47 **Taxon:** Formicidae.

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

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

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

65

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

68

69 **1 INTRODUCTION**

70 Foraging is critical for animal fitness (Raubenheimer, Simpson, & Mayntz 2009; Smith 1978).
71 Through foraging for resources, animals are integrated into the diversity of ecological interactions
72 and nutrient cycles that make up functioning ecosystems (Folgarait, 1998; Tilman, Isbell, & Cowles
73 2014). Foraging activity varies substantially across space and time; for example, arthropod foraging
74 activity is generally higher in the tropics than in the temperate zone, higher at low elevations
75 compared with high elevations (Peters, Mayr, Röder, Sanders, & Steffan-Dewenter, 2014; Roslin
76 et al., 2017) and changes seasonally (Wolda 1978). Given that foraging behavior influences
77 numerous ecosystem processes (e.g. nutrient cycling, decomposition; Maisey, Haslem, Leonard, &
78 Bennett, 2020), identifying which drivers limit or promote foraging activity and resource use will
79 help us understand ecosystem functioning in a rapidly changing world.

80 Animal foraging activity is influenced by four main ecological drivers which are related to
81 ecosystem energy input and the prevailing climate. (1) Net primary productivity (NPP) is the fuel
82 for all animals and is often positively correlated with foraging activity (lizards: Buckley, Rodda, &
83 Jetz, 2008; birds: Meehan, Jetz, & Brown, 2004; and arthropods: Kaspari & de Beurs, 2019). (2)
84 Temperature has a substantial impact on biochemical reaction rates and animal metabolism
85 (Brown, 2014). Consequently, at higher temperatures, animals tend to be more active, move faster,
86 and are, up to a point, more likely to find resources while foraging (Stuble et al. 2013). (3) Overall
87 annual precipitation may lead to increased foraging activity due to reduced desiccation risk and
88 increased plant resource availability (Costa et al., 2018; Kaspari & Weiser 2000). Actual
89 precipitation events may, however, also reduce foraging activity (particularly for small
90 invertebrates) due to the difficulty of foraging in the rain (Poulsen, 2008). (4) Seasonality in both
91 temperature and rainfall can influence the availability of resources through time (Belchior,

92 Sendoya, & Del-Claro, 2016; Costa et al., 2018), and the physiology of living organisms – via the
93 effects described previously. Both usually make the warm, rainy season that parts of the Neotropics
94 experience, better for foraging (Baudier et al., 2018; Wolda, 1988). Thus, we may expect that high
95 seasonality affects foraging activity because, in highly seasonal environments, animals increase
96 activity in favorable seasonal periods to compensate for their inability to forage in harsh seasonal
97 periods (Kaspari, Alonso & O’Donnell., 2000). To date, there has not been an assessment of how
98 all four of these ecological drivers work in concert to influence geographical variation in foraging
99 activity.

100 Foraging activity may also change depending on the resource being foraged for, with resource
101 demand or resource shortfall interacting with climate and NPP to drive resource use (Raubenheimer
102 et al., 2009). Resource demand can be seen, for example, when the climate drives the demand for
103 particular energy or nutrient sources. At higher temperatures, animals expend more effort collecting
104 specific resources in order to compensate for the accelerated metabolic (e.g. sugar and sodium),
105 excretion (e.g. sodium) and growth rates (e.g. amino acids) (Kutz, Sgrò, & Mirth, 2019; Prather,
106 Roeder, Sanders, & Kaspari, 2018). At low temperatures, on the other hand, there may be high
107 levels of lipid consumption because of its thermal insulating properties (Heinze, Foitzik, Fischer,
108 Wanke, & Kipyatkov, 2003; Peters et al., 2014). In cases of resource shortfall, animals will dedicate
109 a disproportionately high foraging effort to collect resources that are in deficit in the environment
110 (Kaspari, Yanoviak, & Dudley, 2008; Kaspari, 2020). For example, at low levels of NPP, animals
111 bias their foraging effort toward collecting high-energy sugar (Kaspari, Welte & Beurs, 2020).
112 Similarly, as precipitation events are positively linked to plant resource availability (Costa et al.,
113 2018), we may also expect greater foraging effort for high-energy resources in drier regions. In
114 environments with high climatic seasonality, there may be significant foraging effort put in toward

115 collecting lipids, as they are easier to store for use in harsh periods (Heinze et al., 2003). In sum,
116 resource use can vary geographically according to shortfall and demand, which may in turn be
117 influenced by climate and NPP (Kaspari et al., 2020).

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

125 Ants are an excellent model taxon for studying the variation in foraging activity and resource use
126 because they are some of the most abundant living animals. Through their foraging activities, ants
127 are essential components of terrestrial ecosystems as seed dispersers, granivores, scavengers,
128 predators, and for cycling of nutrients (Folgarait, 1998; Blüthgen & Feldhaar, 2010, Griffiths et al.
129 2018). Ants require a range of different macro and micronutrients for their development, and they
130 must interact in different ways with plants, other animals and with the environment to obtain
131 resources (Blüthgen & Feldhaar, 2010). Sugar and lipids are the main sources of energy for the
132 entire colony, while lipids and amino acids are important for colony growth and development of
133 larvae (Csata & Dussutour, 2019). Sodium is important for several physiological and metabolic
134 processes (Csata & Dussutour, 2019). Hence, the foraging behavior of ants provides a model
135 system to investigate how climate and NPP interact to influence geographical variation in foraging
136 activity and resource use.

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

147

148 **2 MATERIAL AND METHODS**

149 **2.1 Study area**

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

153

154 **2.2 Sampling of foraging ants**

155 In each of the six biomes, we installed 10 transects as sampling units (60 transects in total)
156 separated by at least 1 km, except for two in the Amazon biome and two in the Pampa biome where
157 they were separated by 800 m due to spatial constraints. Each transect was 750 m long with 25
158 sampling points separated by 30 m. At each sampling point, we provided one of five liquid food

159 resources in the epigeic strata. The food resources were placed in 50-mL Fisher Scientific
160 polypropylene centrifuge tubes with a 5 cm cotton ball containing 10 ml of the following solutions
161 in distilled water: 1% sodium (NaCl), 20% sugar (CHO, made with sucrose), 20% amino acids
162 (AA, made with unflavored whey protein isolate), lipids (100% extra virgin olive oil, without
163 water), and distilled water as a control. Similar liquid resources have successfully been used in
164 previous studies (e.g., Fowler, Lessard, and Sanders 2014; Peters et al. 2014; Tiede et al. 2017).
165 We placed the baited tubes horizontally on the ground. Hence, along each transect, each liquid food
166 resource was repeated five times in the same sequence along each transect (following the order:
167 control, carbohydrates, lipids, amino acid and sodium). Consequently, there were five
168 pseudoreplicates of each of the five resource types per transect (5 pseudoreplicates × 5 resource
169 types = 25 sampling points per transect), giving a total of 250 sampling points per biome (25
170 sampling points × 10 transects) and 1500 sampling points across the study (250 × 6 biomes).

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

178 In the laboratory, we counted all ant workers and identified them to genera following Baccaro et
179 al. (2015) and where possible, to species level or morphospecies by matching them with the ant
180 reference collection of Laboratório de Ecologia de Formigas of the Universidade Federal de Lavras
181 (UFLA). After that, we confirmed the identification at Laboratório de Sistemática de Formigas of

182 the Universidade Federal do Paraná (UFPR). Voucher specimens were deposited in the reference
183 collection of Laboratório de Ecologia de Formigas at UFLA and the Entomological Collection
184 Padre Jesus Santiago Moure of UFPR (DZUP).

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

193

194 **2.3 Ecological drivers**

195 Data for climate and NPP were obtained for 60 1-km² grid cells, which each contained one sampled
196 transect. We obtained data for temperature, precipitation and climate seasonality from the
197 WorldClim 2 database (Fick & Hijmans, 2017), which represents average climate between 1970
198 and 2000. For each transect, we extracted the WorldClim variables mean annual temperature (C°),
199 annual precipitation (mm), temperature seasonality (standard deviation of annual mean
200 temperature), and precipitation seasonality (coefficient of variation of annual precipitation). For
201 the months in which we sampled ants in each biome, we also extracted the data for monthly mean
202 temperature (°C), and monthly precipitation (mm; Table 1). We obtained net primary productivity
203 (NPP) from MODIS, using annual NPP from 2000-2015 (MOD17) from the NASA Earth
204 Observation System repository at the University of Montana (www.ntsug.umt.edu/), which has been

205 improved by correcting for cloud-contaminated pixels and uses a model that considers the
206 difference between gross primary productivity and autotrophic respiration (Zhao and Running,
207 2010).

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

217

218 **2.4 Data analyses**

219 Before analysing the data, we checked for collinearity between our climate and productivity drivers
220 ('Psych' package (Revelle, 2011) in R version 3.4.1 (R Development Core Team 2017). We found
221 strong associations (correlation $R > 0.65$) between annual mean and monthly mean temperatures,
222 annual and monthly precipitation, as well as between temperature seasonality and precipitation
223 seasonality (see Fig. S1.3 in Appendix S1). Consequently, we performed all subsequent analyses
224 with monthly mean temperature, monthly precipitation, temperature seasonality and NPP to
225 represent the ecological drivers of temperature, precipitation, seasonality and NPP. As temperature
226 and precipitation may vary substantially across the year, using mean monthly values is a more
227 accurate way to represent the climate in our sampling periods. In addition, we chose temperature

228 seasonality instead of precipitation seasonality because ant metabolism is expected to be directly
229 affected by temperature (Gillooly, Brown, West, Savage, & Charnov, 2001). Proportional foraging
230 activity and relative resource use data were logit-transformed to meet Gaussian assumptions
231 (Warton & Hui, 2011).

232 All analyses were carried out using proportional values per transect of ant foraging activity and
233 relative resource use as response variables ($n = 60$). To assess the influence of ecological drivers
234 on the ant foraging activity, we constructed generalized linear mixed models (GLMM) with logit-
235 transformed proportional occurrence of foraging ants as the response variable and temperature,
236 precipitation, temperature seasonality and NPP as explanatory variables (fixed effects). Biome was
237 assigned as the random effect to account for the possibly spatial autocorrelation between transects
238 in the same biome. We used the *dredge* function ('MuMIn' package version 1.10.5; Barton 2014)
239 to run all possible models, ranking them based on the Akaike information criterion corrected
240 (AICc), and considering only the models with $\Delta\text{AICc} < 2$ (Burnham & Anderson, 2002). We ran
241 the modelling process with and without the data for control tubes. Because results from the two
242 sets of modelling procedures did not differ, there was no evidence that control tubes affected the
243 foraging patterns found (Appendix S2; Table S2.2). Therefore, we only report results without
244 control tubes. We searched for potential "uninformative parameters" within the models where
245 $\Delta\text{AICc} < 2$ by following the approach proposed by Leroux (2019). Leroux's (2019) approach
246 involves two steps. First, we compared the log-likelihoods of the top model and those models
247 within $\Delta\text{AICc} < 2$ that had additional parameters not in the top model. If the log likelihoods were
248 different, we considered the additional parameters as informative. If the log likelihoods were
249 similar, we checked to see if the 95% confidence intervals of the additional parameters overlapped

250 zero. If the confidence intervals overlapped zero, we considered the parameters to be
251 uninformative, if they did not overlap zero, we considered them to be informative.

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

258 To assess how ecological drivers influence relative resource use, we performed the same model
259 selection of GLMMs using the *dredge* function, modelling each relative resource use (control,
260 sugar, lipids, amino acids and sodium) as the response variable and including temperature,
261 precipitation, temperature seasonality and NPP as explanatory variables (fixed effects) and, the
262 biome as random effect. We also looked for uninformative parameters in the models with $\Delta AICc$
263 < 2 as proposed by Leroux (2019). Furthermore, as the availability of water in the sugar, amino
264 acids and sodium solutions could influence their use as resources, we performed another model
265 selection that included the relative use of the control tubes (distilled water) as an extra explanatory
266 variable. We expected that, if ants visited those resources because they were attracted to the water,
267 then the relative use of the controls alone would explain most of the variation in resource use.

268

269 **3 RESULTS**

270 **3.1 How do ecological drivers influence ant foraging activity?**

271 We sampled 16,065 ant workers belonging to 188 ant species and 30 genera across all transects
272 (Table S2.4 in Appendix S2). The best models ($\Delta\text{AICc} < 2$) explaining ant foraging activity
273 included precipitation, temperature seasonality, and NPP (Table 2). Thus, foraging activity
274 increased with increasing precipitation and NPP, and decreased with temperature seasonality (Fig.
275 2).

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

285

286 **3.2 How do ecological drivers influence relative resource use of foraging ants?**

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

290 Almost all the best models ($\Delta AICc < 2$) for each resource type included temperature, precipitation,
291 temperature seasonality and NPP (Table 2). However, the influence of the climatic drivers and NPP
292 on foraging differed strongly among resource types (Fig. 3 and Fig. S1.5-S1.8 in Appendix S1).
293 Our results show that with increasing temperature, there was an increase in the relative use of amino
294 acids, whereas the relative use of lipids decreased, but there was no influence of temperature on
295 the relative use of sugar and sodium (Fig. 3a). With increasing precipitation, there was an increase
296 in the relative use of sodium and a decrease in the relative use of sugar and lipids. Amino acids
297 remained unaffected by precipitation (Fig. 3b). With greater temperature seasonality the relative
298 use of sugar increased, while the relative use of lipids, amino acids and sodium decreased (Fig. 3c).
299 The influence of NPP on resource use also varied markedly among resource types: relative sugar
300 use declined with increasing NPP, whereas the relative use of amino acids and sodium increased
301 (Fig. 3d). We identified possible uninformative parameters for the best models for relative use of
302 sugar and sodium. We did not consider the effect of temperature on the relative use of sugar because
303 temperature was present in the second-best model and did not considerably improve the log
304 likelihood in relation to the top model (log likelihood difference = 0.45; Table 2) and its estimate
305 overlapped zero (CI 95% = -0.031, 0.090). We also did not consider the temperature effect on the
306 relative use of sodium because temperature was present in the third-best model, did not
307 considerably improve the log likelihood in relation to the top model (log likelihood difference =
308 0.57; Table 2) and its estimate overlapped zero (CI 95% = -0.036, 0.121).

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

313

314 **4 DISCUSSION**

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

325 **4.1 How do ecological drivers influence ant foraging activity?**

326 Ant foraging activity was higher in wetter and more productive environments with low temperature
327 seasonality (Fig. 2). However, the lack of relationship between temperature and foraging activity
328 in this study could be because considerable changes in temperature were not experimented by ants
329 during our study – although temperature positively influenced foraging activity when controlling
330 for the number of ant workers (Table 1). We interpret the ecological drivers as influencing ant
331 foraging activity in two different ways. First, the majority of Neotropical ants originated in hot and
332 humid tropical forests and diversified following forest expansion (Moreau & Bell 2013; Price et
333 al., 2014, Vasconcelos et al., 2018). Consequently, the greater ant foraging activity in wetter
334 environments could represent a niche characteristic that has been conserved through evolutionary
335 time. The positive and direct influence of precipitation (through moisture) could improve foraging

336 performance by reducing desiccation stress while ants forage (Gibb et al., 2019). Second,
337 temperature seasonality and NPP effects may also be linked with ant abundance in addition to
338 acting on foraging performance. Previous studies have shown that ant abundance is higher in less
339 seasonal and more productive environments (e.g. Kaspari et al., 2000; Kaspari & de Beurs, 2019).
340 This may be because ants are able to harvest more energy due to their foraging for longer periods
341 throughout the year in more climatically stable environments (Kaspari et al., 2000). In addition,
342 there is greater energy and carbon availability for individuals in more productive environments,
343 which also increases abundance (Kaspari & de Beurs, 2019). Thus, higher ant abundances may
344 also be correlated with greater foraging activity in productive environments with low temperature
345 seasonality. In this sense, we propose that precipitation, temperature seasonality and NPP directly
346 influence ant foraging activity, however, the influence of temperature seasonality and NPP can also
347 operate indirectly through their effects on ant abundance.

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

355 **4.2 How do ecological drivers influence relative resource use of foraging ants?**

356 We interpret the influences of precipitation, temperature seasonality and NPP on our relative
357 resource use largely as a trade-off between sugar on the one hand, and amino acids and sodium on
358 the other. In drier and less productive environments with high temperature seasonality, the relative

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

375 Precipitation, temperature seasonality also affected the relative use of lipids. However, we should
376 interpret these results with caution. Lipids supply the energy demand for larval growth, while sugar
377 supplies are needed for adult ants (Blüthgen & Feldhaar, 2010). As plant resource availability is
378 influenced by precipitation (Costa et al., 2018), it is likely lipid resources are lower in drier
379 environments. This may explain the same pattern for the relative use of sugar and lipids as they
380 both increased in drier environments (Fig. 3b). Besides supplying resources for larval growth, ants
381 also access components in lipids that are important for egg production and ovary development, all

382 related to the colony growth (Blüthgen & Feldhaar, 2010). Thus, following the same pattern as
383 amino acids, it is possible that ants forage more for lipids in environments with low temperature
384 seasonality (Fig. 3c) to facilitate colony growth since energy demand has already been achieved.
385 Considering that little is known about the diet requirements in ants of lipids (Csata & Dussutour,
386 2019), the influence of ecological drivers on the relative use of lipids appears complex. We should
387 not assume the role of lipids for ants is only to meet energy demands, but also for colony growth.

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

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

405 limiting resource for ant foraging activity, as it is for ecological interactions, decomposition, and
406 carbon cycle processes in tropical forests (Kaspari, 2020).

407 **4.3 Uncertainties and remaining knowledge gaps**

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

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

428 future studies should address if precipitation can actually reduce sodium availability in plants and
429 soil and thus influence sodium use (Kaspari, 2020).

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

434 **5 CONCLUSION**

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

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

447

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 <i>strictu sensu</i>	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

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

Question 1: How do ecological drivers influence ant foraging activity?								
Model	d.f.	AICc	$\Delta AICc$	ω	Log Likelihood	Marginal R ²	Conditional R ²	
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	$\Delta AICc$	ω	Log Likelihood	Marginal R ²	Conditional R ²	
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	$\Delta AICc$	ω	Log Likelihood	Marginal R ²	Conditional R ²	
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	$\Delta AICc$	ω	Log Likelihood	Marginal R ²	Conditional R ²	
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	$\Delta AICc$	ω	Log Likelihood	Marginal R ²	Conditional R ²	
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	$\Delta AICc$	ω	Log Likelihood	Marginal R ²	Conditional R ²	
MMTemp + TSeas + NPP	6	173.6	0.00	0.39	-79.98	0.32	0.32	

NaCl							
Model	d.f.	AICc	Δ AICc	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

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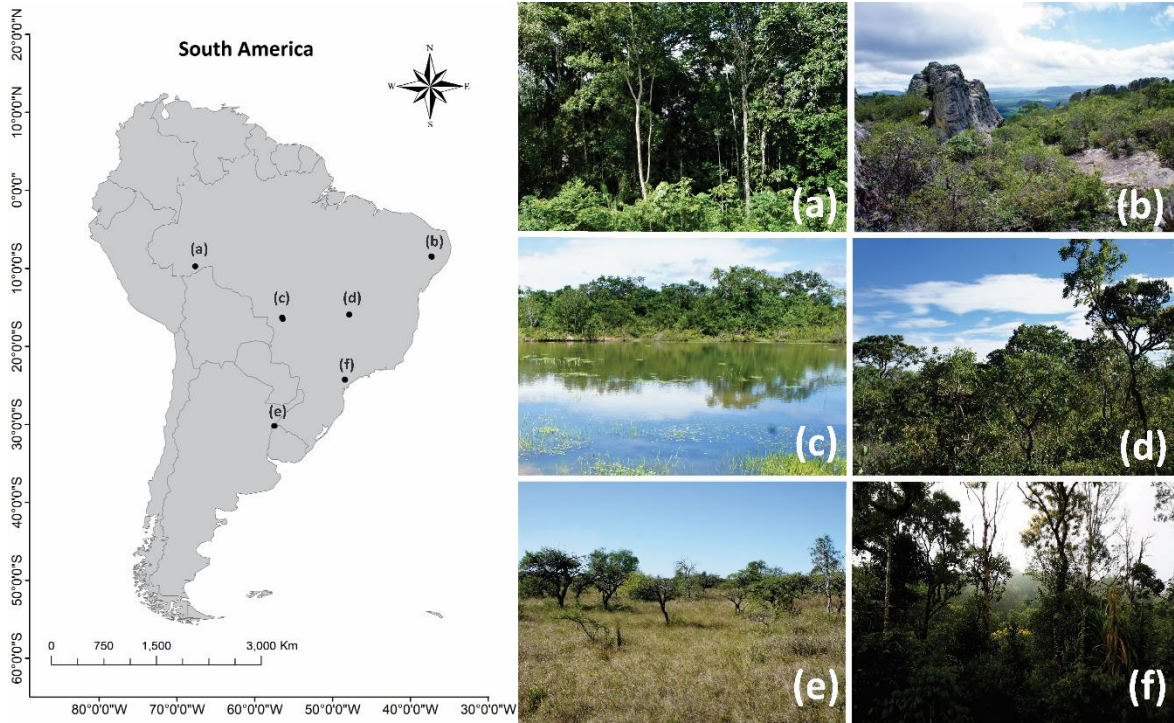
464 **List of figures legends**

465 **Figure 1.** Location of the sampling sites across six Brazilian biomes: (a) Amazon, (b) Caatinga,
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468 occurrence of foraging ants) and (a) mean monthly temperature; (b) monthly precipitation;
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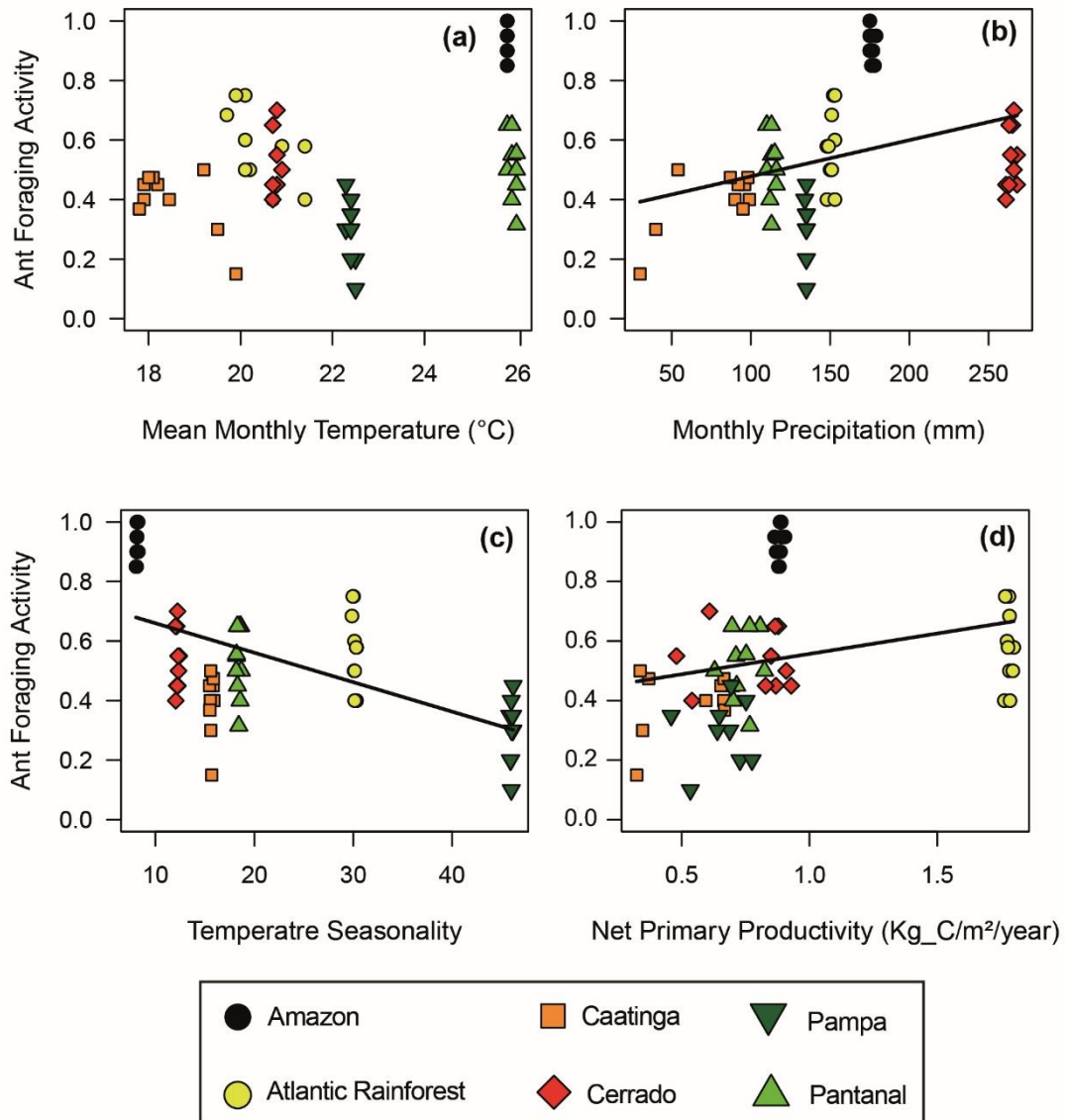
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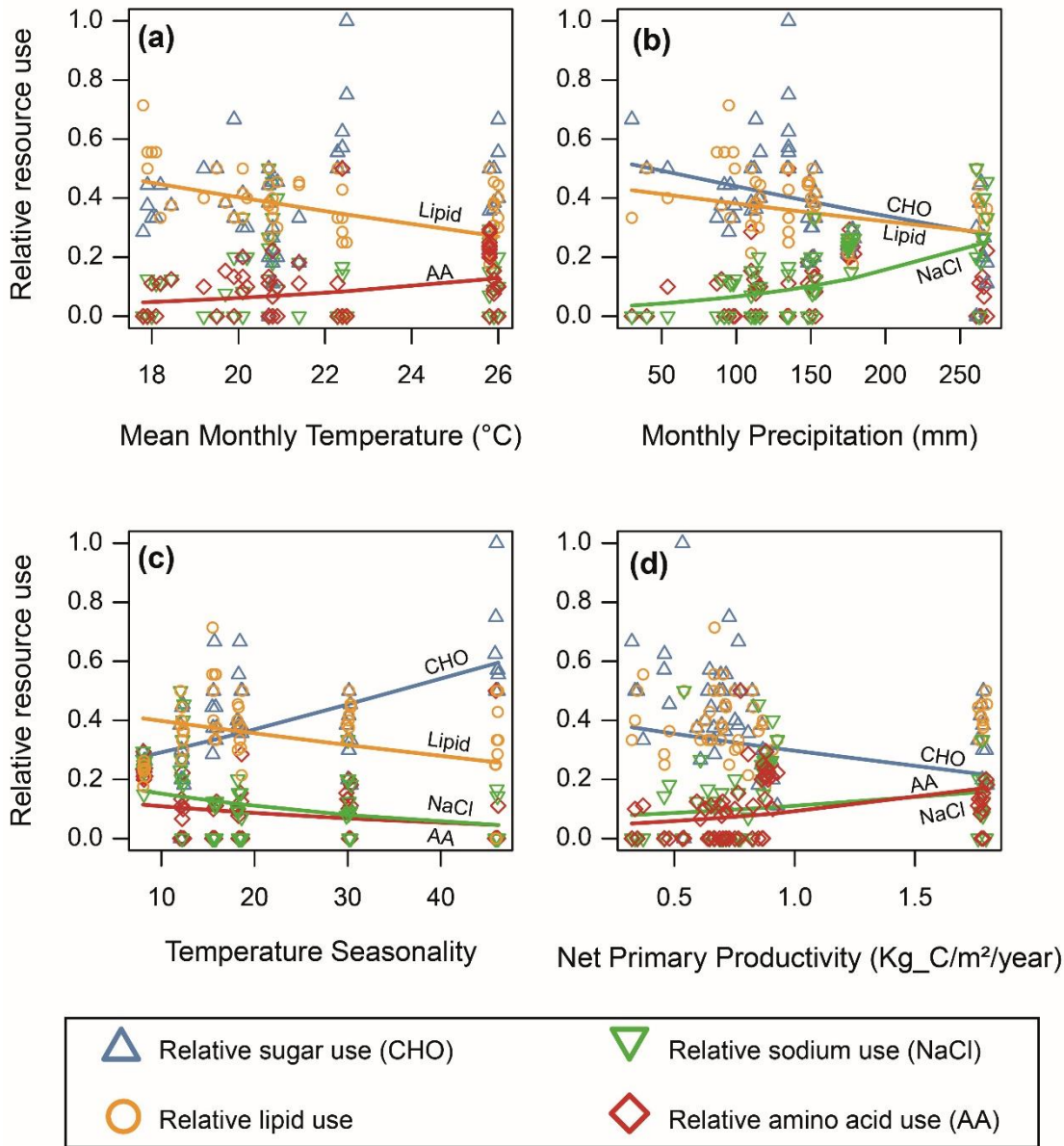
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505

506 **Data availability statement:** All data have been uploaded to Dryad
507 (<https://doi.org/10.5061/dryad.6wwpzgmx>).

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