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1 **Niche differentiation in rainforest ant communities across three**
2 **continents**

3 Short title: Niche differentiation in ant communities

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17

18 Author Contributions: FM conceived the study. MH and MG performed the field work. MG
19 and FM analysed the data. AA supervised the Australian field work and provided his expertise.
20 MG and FM wrote the manuscript. All authors helped to improve the manuscript.

21

22 **Abstract**

23 A central assumption of niche theory is that biotic communities are structured by niche
24 differentiation arising from competition. To date, there have been numerous studies of niche
25 differentiation in local ant communities, but, little attention has been given to the macroecology
26 of niche differentiation, including the extent to which particular biomes show distinctive
27 patterns of niche structure across their global ranges. We investigated patterns of niche
28 differentiation and competition in ant communities in tropical rainforests, using different baits
29 reflecting the natural food spectrum. We examined the extent of temporal and dietary niche
30 differentiation and spatial segregation of ant communities at five rainforest sites in the
31 neotropics, paleotropics, and tropical Australia. Despite high niche overlap, we found
32 significant dietary and temporal niche differentiation in every site. However, there was no
33 spatial segregation among foraging ants at the community level, despite strong competition for
34 preferred food resources. Although sucrose, melezitose, and dead insects attracted most ants,
35 some species preferentially foraged on seeds, living insects or bird feces. Moreover, most sites
36 harboured more diurnal than nocturnal species. Overall niche differentiation was strongest in
37 the least diverse site, possibly due to its lower number of rare species. Both temporal and dietary
38 differentiation thus had strong effects on the ant assemblages, but their relative importance
39 varied markedly among sites. Our analyses show that patterns of niche differentiation in ant
40 communities are highly idiosyncratic even within a biome, such that a mechanistic
41 understanding of the drivers of niche structure in ant communities remains elusive.

42

43 **Key words**

44 coexistence mechanism, community structure, Formicidae, interspecific competition, niche
45 partitioning

46

47 **Introduction**

48 The principle of limiting similarity is one of the central assumptions of niche-based community
49 ecology, stressing the importance of niche differentiation as the central mechanism of species
50 co-existence (Hutchinson 1959; Chase and Leibold 2003). According to niche theory, species
51 with identical niches cannot coexist in a stable equilibrium due to competitive exclusion
52 (MacArthur and Levins 1967; Lovette and Hochachka 2006; Sanders et al. 2007). Conversely,
53 interspecific competition is reduced if species occupy niches that differ in any dimension, such
54 as time (Albrecht and Gotelli 2001; Santini et al. 2007; Houadria et al. 2015), space (Tanaka et
55 al. 2010) or diet (McKane et al. 2002; Feldhaar et al. 2010). Niche differentiation also reduces
56 competition between species in non-equilibrial communities (Kingston et al. 2000; Leibold and
57 McPeck 2006), and can evolve in response to intraspecific competition (Maret and Collins
58 1997; Bolnick 2001). However, some studies also reported increased niche breadth in response
59 to competition (Bolnick et al. 2010).

60 Due to intense competition between species (Hölldobler and Wilson 1990), ants are an
61 ideal taxon to study how species partition their realised niches in the presence of competitors.
62 Many behaviourally dominant ant species displace others from high-quality resources and even
63 from their entire territories (Hölldobler 1983; Blüthgen and Fiedler 2004a; Parr and Gibb 2010).
64 Being highly diverse, and present in nearly all terrestrial ecosystems, ants encompass a major
65 proportion of terrestrial faunal biomass and play key roles in many ecosystem processes
66 (Folgarait 1998). Local ant species richness can be extremely high, especially in tropical
67 lowland forests, where several hundred species can occur within a few hectares (Floren and
68 Linsenmair 2005; Mezger and Pfeiffer 2011). Many of the functional roles played by ants relate
69 to food consumption (Houadria et al. 2016), which influences rates of nutrient cycling, the
70 dynamics of prey populations, defense of plants against herbivores and seed dispersal services
71 (Ness et al. 2010; Philpott et al. 2010).

72 Ants often show niche differentiation that separates foragers of different species in time
73 (Lynch et al. 1980; Devoto et al. 2011; Harvey et al. 2012; Stuble et al. 2013) or space (Brühl
74 et al. 1998; Philpott and Armbrrecht 2006; Baccaro et al. 2012). Ants often also show substantial
75 dietary niche differentiation (Santamaria et al. 2009; Menzel et al. 2012). Most ant species are
76 generalist scavengers and predators. Some are heavily reliant on carbohydrate-rich liquids
77 provided by plants or sap-feeding trophobionts (Davidson et al. 2004). However, many ant
78 species are specialized on a specific resource like termites (Mill 1984), seeds (Carroll and
79 Janzen 1973), or fungi (Quinlan and Cherrett 1979). In habitats where nitrogen is limited, some
80 species even feed on bird feces (Blüthgen & Feldhaar 2010). Dietary differentiation between
81 species is at least partly due to specialised foraging behaviours rather than differential
82 nutritional needs. For example, living insects contain largely similar nutrients to dead ones, but
83 morphological and behavioural specialisation on them can reduce competition with other
84 species.

85 Despite the ubiquity of niche differentiation in ant communities, and the many studies
86 addressing multiple niche dimensions (e.g. Chew 1977; Davidson 1977; Bernstein 1979; Lynch
87 *et al.* 1980; Torres 1984; Kaspari & Weiser 2000; Knaden & Wehner 2005; Andersen, Arnan
88 & Sparks 2013), the relative importance of the different niche dimensions remains largely
89 unknown. Moreover, the relative importance of niche differentiation as a driver of species
90 richness has been questioned (Andersen 2008), especially in highly diverse communities, where
91 niche differentiation does not appear sufficient to explain the co-existence of all species (Stuble
92 et al. 2013; Andersen et al. 2013; Houadria et al. 2015). Little attention has been given to the
93 macroecology of niche differentiation, addressing the extent to which the relative importance
94 of different niches dimensions can be predicted by climate and habitat structure. It is unknown,
95 for example, if ant communities within any particular habitat type show similar niche structure
96 across different biogeographic regions, due to similar patterns of resource availability.

97 Here we analyse the niche structure of tropical-rainforest ant communities across five
98 sites on three continents, focussing on the two key niche dimensions of diet and foraging time.
99 Using a standardized sampling design with high spatial replication, we document the degree of
100 dietary and temporal specialisation of each species. Our aims were, firstly, to elucidate the
101 relative importance of dietary and temporal niche differentiation for ant species composition.
102 To this end, we conducted comprehensive analyses of overall dietary and temporal niche
103 structure within communities. In addition, we studied dietary and temporal specialisation for
104 each species separately to test whether sites differ in number or proportion of specialised
105 species. Our second aim was to use species co-occurrence in pitfalls and at baits to detect
106 patterns of competition for food. These results were compared between sites on different
107 continents, including primary and secondary forests, to determine if the observed patterns are
108 consistent across different biogeographic regions with independently evolved ant communities
109 and subject to different levels of disturbance.

110

111 **Material and methods**

112 **Study sites**

113 We sampled five rainforest sites on three continents, comprising:

- 114 • Two Neotropical forests in French Guiana - a primary forest in Les Nouragues Natural
115 Reserve (Neotropical Primary Forest - NPF), and a secondary forest fragment in
116 Campus Agronomique, Kourou (Neotropical Secondary Forest - NSF)
- 117 • Two Paleotropical forests in Sabah, Malaysian Borneo - a primary forest in the Danum
118 Valley Conservation Area (Paleotropical Primary Forest - PPF), and a secondary forest
119 in the Malua forest reserve (Paleotropical Secondary Forest - PSF)
- 120 • An Australian monsoonal forest (AMF) (Holmes Jungle nature reserve, Darwin,
121 secondary rainforest fragment)

122 Further site information is provided in Appendix S1.

123 **Sampling**

124 The study was based on sampling ants recruiting to seven food resources during the day and
125 night, along with catches in pitfall traps. The sampling was performed with 64 spatial replicates
126 per site. The food resources reflected those naturally available to tropical ants (Houadria et al.
127 2015): dead, crushed insects (scavenging); large prey (living grasshoppers or mealworms;
128 predation); small prey (living termites; predation); sucrose solution (for sugars from floral or
129 extrafloral or fruits); melezitose solution (a common trisaccharide in the honeydew of aphids
130 and other ant-tended trophobionts; Völkl, Woodring & Fischer (1999) (both sugar solutions
131 were 20 vol. %; 3 mL soaked on paper tissue); bird feces (coprophagy); seeds (mixture of
132 ground corn and sunflower, barley, soya, millet, lin, dari, *Phalaris* and grass seeds; granivory).
133 Being holometabolous, ants need amino acids or proteins largely for larval growth, while the
134 adult metabolism largely requires carbohydrates (Nation 2002; Blüthgen and Feldhaar 2010).
135 Thus, our baits reflected resources largely required for raising brood as well as resources mostly

136 important for adult metabolism. Although novelty or rarity can bias the attractiveness of a
137 resource (Kay 2004), we believe the resources offered were common and known to the ants
138 enough such that these effects should play a minor role.

139 Baiting was conducted at 64 points arranged in 4 x 4 grids with 10 m spacing, with four such
140 grids at each site. The four grids were separated by 50 – 300 m. To reduce habitat variation
141 between grid points, we took care to avoid forest gaps, i.e. all points were under a closed canopy
142 and on flat terrain. Each food resource was presented at each point for 90 mins, once at night
143 and once during the day. All food resources were presented in circular plastic boxes with paper
144 tissue at the base and slit-shaped openings (1 cm height and 8 cm length) on opposite sides to
145 allow access to ants. Only one resource was presented at a grid point at any given time to avoid
146 any interference between different baits. After the 90-min period, all ants occurring at the
147 resource were collected. Pitfall traps were operated for three 10-hr periods between 20h00 to
148 6h00 (nocturnal traps) or 7h00 to 17h00 (diurnal traps) over three consecutive days when no
149 food resources were presented, such that we obtained a total of 30h of pitfall sampling per grid
150 point and per time of day. Pitfall data were used to assess temporal niches, co-occurrence, and
151 background ant diversity. Sampling was conducted between February 2012 and December 2014
152 (Appendix S1).

153 **Statistical analyses**

154 For statistical analysis, we used two types of data: frequency (total number of occurrences at
155 baits) and incidence (number of grid points out of 64 per site where an ant species was found).

156 **The relative extent of temporal and dietary niche differentiation**

157 We quantified daily time of activity and diet as two factors structuring ant communities. Spatial
158 effects, i.e. turnover between grid points, will also influence species richness and composition.

159 We analysed which of these factors had the strongest effect on the community structure and
160 compared the effect sizes between the sites.

161 To this end, we performed a PERMANOVA which allows to simultaneously assess the
162 importance of diet, time and spatial variation. Furthermore, it allows to test whether there are
163 interactions between the two niche dimensions – e.g. whether dietary differentiation differs
164 between day and night. Since each bait was presented at each time of day at each grid point, we
165 could account for potential spatial heterogeneity using this approach by incorporating grid point
166 identity in the analysis. At the same time, we could use grid point information to estimate the
167 effect of spatial heterogeneity compared to effects of different food sources or times of day.
168 Due to the standardized experimental setup, we could exclude that any differences between
169 sites or niche dimensions were due to differences in statistical power. We analysed niche
170 differentiation, separately for each site with a PERMANOVA (software PRIMER 6.1.14 and
171 PERMANOVA+, Primer-E Ltd.) for which we used frequency data for each ant species,
172 separately for all food resources, grid points, and times of day. The PERMANOVA with 999
173 permutations had the fixed factors ‘food source type’ and ‘time of day’ and the random factor
174 ‘grid point’. The percentage of explained variance (sum of the squared deviation per factor
175 divided by the total sum of squares) was used to compare effect sizes between the two niche
176 dimensions and between the sites. The strength of this approach is that the relative roles of diet,
177 time, spatial variation and their interactions can be easily compared within a single
178 comprehensive analysis. Community composition was visualized using non-metric
179 multidimensional scaling (NMDS), based on species frequency data.

180 **Dietary and temporal niche overlap**

181 We analysed whether species were more similar in their preferences than would be expected
182 from random by analysing niche overlap (as suggested in Fowler et al. 2014) using null model
183 analyses (EcoSim version 7.0, Gotelli & Entsminger (2004), Fowler et al. (2014)). We created
184 two matrices per site in which each row represented a different species and each column
185 represented a different food resource x time combination. The matrices contained the number

186 of times each species was found on the given food resources or time of day. We analysed niche
187 overlap using Pianka's index (Pianka 1973), which quantifies niche overlap ranging from 0
188 (indicating no overlap) and 1 (complete overlap) for each species pair. We simulated 1000
189 matrices using RA3. This randomization algorithm retains niche breadth but randomizes which
190 particular resource states are utilized. We chose this algorithm since we offered all food
191 resources at day and night and thus, at all grid points, there was equal access to all resources.
192 Using this model, we tested whether the observed mean niche overlap significantly differed
193 from random (mean of simulated indices).

194 To compare the effect sizes of niche overlap and co-occurrences (see next section) between
195 sites, we used the simulations to compute the standardized effect size (SES) of niche overlap
196 and co-occurrences as $SES = (I_{obs} - I_{sim})/s_{sim}$ with I_{obs} as the observed index (niche overlap or
197 C-score), I_{sim} as the mean simulated index and s_{sim} as the standard deviation of the simulations,
198 following Gotelli & Ellison (2002). SES values larger than 1.96 or lower than -1.96 indicate
199 significant effects. To compare the effect sizes between the sites, we plotted the SES of niche
200 overlap and co-occurrences, irrespective of whether SES values were significant or not.

201 **Species-specific food specialization**

202 We analysed dietary and temporal specialisation for each species separately and calculated
203 absolute and relative preferences using a 'hotlink' analysis (see below). The relative extent of
204 temporal and dietary niche differentiation was compared between sites based on effect sizes
205 and numbers of specialized species.

206 Food specialization was calculated for each species with an incidence ≥ 5 (i.e. number of
207 different grid points where the species was found; total number of species = 109; ranging from
208 11 - 31 per site). For each of the n species, its food specialisation index (fS_n) was calculated as
209 $fS_n = \sum p_{i,n}^2$, with $p_{i,n}$ being its frequency on a food resource i divided by its total frequency
210 (analogous to the Simpson index). We calculated fS_n 1000 times based on 5 randomly drawn

211 occurrences, to avoid a bias caused by differences in overall frequency of common and rare
212 species. f_{S_n} ranges from 0 (for a generalist) to 1 (for a dietary specialist). We compared f_{S_n}
213 values across sites (as independent variable) using a linear model (LM), assuming normal
214 distribution.

215 While f_{S_n} describes the degree of food specialization of a species, it does not provide
216 information about the type of food resource that a species prefers. This was evaluated by
217 calculating absolute and relative food preferences of each species with a total incidence ≥ 5 .
218 The 'absolute preference' of a species indicates whether a certain resource is more attractive to
219 this species than other resources. In contrast, its 'relative preference' indicates whether a certain
220 resource is more attractive to this species compared to the other species. The latter is especially
221 relevant given that many ant species were attracted to the same resources.

222 For the *absolute* food preferences, for each species we calculated a null model based on the
223 incidence per food resource (pooled for day and night). In 1000 permutations, we randomly
224 assigned all occurrences to the seven food resources and compared it with the real incidences
225 per food resource. If the species occurred more often on a food source than expected by random
226 ($\alpha = 0.025$), the resource was defined as significantly preferred.

227 *Relative* food preferences were calculated based on the 'hot link/ cold link'- analyses from
228 Junker et al. (2010). In contrast to the absolute preferences, we constructed a bipartite network
229 with species incidences vs. the seven resources. The 'hot link/ cold link' analysis compared the
230 number of occurrences of a species on a resource relative to the occurrences of the whole
231 community on this resource. It revealed whether a species occurred more often on a resource
232 than other species, even if it was an unattractive resource seldom visited by most species. Thus,
233 relative preferences give a clearer picture about (realised) niche differentiation that is unbiased
234 by overall resource attractiveness. Here, a null model was created which randomly shuffled
235 species occurrences among the resources, but with total species-wise incidences kept constant

236 and equal to the real data (Junker et al. 2010). Based on 1000 randomizations, the realized
237 number of occurrences of a species on each food source was compared with the whole number
238 of occurrences of all species on each food source. If a species were more common on a food
239 source than expected, it was defined as a relative preference ($\alpha = 0.025$). Note that all the
240 preferences reflect ‘realised’ rather than ‘fundamental’ preferences since they are based on data
241 in the presence of competitors. We use the term ‘preference’ to distinguish this data (on the
242 identity of a preferred resource type) from ‘specialisation’, which is a single value ranging from
243 generalisation to specialisation.

244 We compared the numbers of species with and without absolute or relative food preferences
245 across sites using χ^2 tests. Since less common species are predicted to have a low impact on
246 their community and for a higher clarity of the results, we show only the analysis for the most
247 common species that comprised 80 % of all occurrences (see Table S1 for an analysis of species
248 with incidence ≥ 5). As a site-level measure of overall niche differentiation, we divided the total
249 number of significant absolute or relative preferences by the number of species.

250 **Species-specific temporal specialization**

251 For each species n with a frequency ≥ 5 ($N = 155$), we calculated its temporal niche tn_n as

252
$$tn_n = 2 * \frac{freq.day_n}{freq.day_n + freq.night_n} - 1$$
, with $freq.day_n$ as the total number of occurrences of

253 species during day and $freq.night_n$ during the night (Houadria et al. 2015) on food resources
254 and in pitfall traps. tn_n ranges from -1 for purely nocturnal to +1 for purely diurnal species. A
255 species was considered specialized if its day and night frequency significantly differed from
256 random according to a χ^2 test. We compared the temporal niches (tn) across the sites with a LM
257 (with tn as dependent and site as independent variable). In contrast to the temporal niche,
258 temporal specialization ts was calculated as its absolute value ($ts_n = |tn_n|$), being 0 for
259 unspecialized and 1 for maximally specialized species. We compared species-specific temporal
260 specialization across sites using two approaches. Firstly, ts was calculated for the same set of

261 species and compared across sites using a LM (with *ts* as dependent and site as independent
262 variable). Secondly, we compared the proportion of temporally specialized species per site with
263 a χ^2 test.

264 Finally, we determined whether a species was relatively more frequent during day or night
265 compared to the whole community, by conducting the 'hot link'-analysis for temporal niche
266 differentiation. This was necessary to reveal deviations from the community average, since e.g.
267 more ant species tend to be active during the day than at night (Houadria et al. 2016).

268 **Overall co-occurrences and co-occurrences per resource type and time of day**

269 We performed co-occurrence analyses to find patterns of spatial segregation (pitfalls) and
270 resource monopolization (food resources) within a community. The standardized effect sizes
271 for niche overlap in diet and time were then compared to overall spatial co-occurrence. Co-
272 occurrence was assessed based on two datasets, each time using a species x grid point matrix
273 with presence/absence data (day and night pooled) for all species. Firstly, we calculated co-
274 occurrences based on pitfall data, i.e. unaffected by competition for food resources. Secondly,
275 we calculated co-occurrence based on baiting data only, separately for each food resource type
276 and time of day, i.e. conducted 14 analyses per site (total n = 70). This approach allowed a
277 comparison of spatial segregation at food sources (i.e. bait monopolisation) between resource
278 types and times of day. Note that the goal of these bait-based analyses was not to quantify
279 whether species would co-occur in the same territory or foraging range, but rather to assess
280 whether ants would tend to monopolise baits and displace others from the same bait. Ants
281 frequently compete for highly attractive resources but may show less competitive displacement
282 on less attractive resources (Blüthgen and Fiedler 2004a). Hence, by estimating monopolisation
283 rates for each food resource (via co-occurrence analysis), we could estimate how the degree of
284 competition for different resources. We obtained standardized effect sizes (SES) that were then
285 compared between sites and food source using a LM.

286 For all these analyses, co-occurrence was quantified using the C-score as implemented in
287 EcoSim. We simulated 5000 random communities, where the occurrences of each species were
288 randomly assigned to the grid points, such that the total number of occurrences per species
289 equalled those in the original matrix. Each grid point had the same probability of being assigned
290 an ant occurrence (fixed-equiprobable algorithm (Gotelli and Ellison 2002)). This algorithm
291 was chosen since all grid points were in a rather homogeneous habitat without clearly noticeable
292 differences in habitat structure. Furthermore, all baits were presented at all grid points, such
293 that any spatial heterogeneity would equally affect all resource types and both times of day.
294 Hence, any heterogeneity in species numbers at baits could have been biologically meaningful;
295 using the fixed-fixed algorithm would therefore rather correct for, and thus conceal potentially
296 important biological patterns.

297 All LMs and the hotlink analysis were conducted in R version 3.1.2 (R Development Core
298 Team 2016). LMs were tested using ANOVA (command *Anova*, package *car*).

299

300 **Results**

301 **Overview**

302 The five ant communities differed strongly in sampled species richness, with totals summed for
303 food resources and pitfalls ranging from 27 (AMF) to 107 (NPF). Species richness varied
304 markedly among the different food resources, from 10-26 species per site for sucrose to 8-16
305 species for bird feces (Table 1). Numerical dominance varied between sites (see incidence and
306 frequency data provided in Table 3): the most common species in the Australian monsoonal
307 forest AMF (*Pheidole* sp. A) occurred on all grid points, at PSF *Lophomyrmex bedoti* occurred
308 on 97% of all grid points, whereas in the NSF the most common species (*Pheidole subarmata*)
309 occurred on only 67% of all grid points.

310 **Effects of diet, time and space on ant communities**

311 Ant assemblages were strongly affected by both food resource and time in all sites. Food
312 resource (mean of 39.4%) and time (37.6%) explained a similar amount of variation overall in
313 ant species composition, but their relative importance varied markedly among sites (Table 2).
314 For example, in PSF food resource explained 66% of variation (pseudo- $F_6 = 22.26$) and time
315 only 11% (pseudo- $F_1 = 3.05$), whereas in NSF time explained 55% (pseudo- $F_1 = 25.63$) and
316 food resource only 22% (pseudo- $F_1 = 9.04$). Variation among sites in the relative importance of
317 food resource and time as niche dimensions is illustrated by variation in ant species composition
318 for each food resource x time combination. This can be seen in Fig.1 where ant assemblages on
319 melezitose, sucrose and crushed insects are highly similar to each other (both for day and night),
320 and cluster together closer than in the other sites. In both neotropical sites, time explained more
321 variance than diet, while in the paleotropical sites (especially PSF), diet had a stronger
322 influence. Notably, the highest percentage of explained variance by diet plus time (including
323 the interaction) was in the less species-rich AMF. Spatial variation in ant assemblage
324 composition accounted for only 5-14% of the total variation (Table 2).

325 **Niche specialization and overlap**

326 There was no variation among sites in the extent of species-specific dietary specialization (*fs*)
327 (LM: $F_4 = 0.72$; $p = 0.58$). The same was true for the proportion of species with absolute food
328 preferences, although this ranged from 19% to 55% (χ^2 test: $\chi^2_4 = 8.58$; $p = 0.07$; Table S3).
329 Similarly, neither temporal specialisation (*ts*) (LM: $F_4 = 1.92$; $p = 0.11$) nor temporal niche (*tn*)
330 (LM: $F_4 = 0.81$, $p = 0.52$) varied among sites. However, the proportion of absolute temporal
331 specialists differed among sites (χ^2 test: $\chi^2_4 = 6.39$; $p = 0.011$), ranging from 20 % in PPF to 44
332 % in NPF (Fig. 3). Notably, all sites except PSF harboured more diurnal than nocturnal species
333 (Fig. 3). This was true also for relative temporal preferences that accounted for overall
334 community preferences (Table 3).

335 Dietary niche overlap between species was higher than expected by chance in all five sites (p_{obs}
336 $> p_{\text{exp}}$; $p < 0.025$; Table S2a, Fig. 2). In contrast, only the NPF community showed significant
337 temporal niche overlap (Table S2a, Fig. 2). Standardized effect sizes for time were significantly
338 smaller than those for diet (paired t test: $t_4 = 5.03$, $p = 0.0073$).

339 **Food preferences**

340 Overall, crushed insects, sucrose, and melezitose were most attractive as measured by their
341 frequencies (Fig. 4a). This attractiveness was reflected in the species-wise preferences: absolute
342 preferences in any species mostly concerned these three resources (green cells in Table 3; Fig.
343 4b). Few absolute preferences were detected for other resources, with examples including large
344 prey (*Odontomachus haematodus* in NSF), seeds (*Carebara* sp. in PSF) or bird feces
345 (*Camponotus femoratus* in NPF, Table 3). However, when we accounted for overall
346 attractiveness by analysing relative preferences, we detected relative specialisation on a broader
347 spectrum of resources. Many species showed relative preferences (red cells in Table 3) for non-
348 attractive resources, which resulted in a more even distribution of preferences across resource
349 types (Table 3, Fig. 4b) (Shannon evenness for all absolute preferences across the seven
350 resource types: 0.65; per site: 0.57 ± 0.03 ; Shannon evenness for all relative preferences: 0.93;
351 per site: 0.61 ± 0.15).

352 Using this approach, we found strong patterns of dietary niche differentiation among the most
353 common species of each site (Table 3). AMF showed the strongest of niche differentiation,
354 measured by the number of absolute and relative preferences per species (Fig. 4c). Here, the
355 most common species (*Pheidole* sp. A) foraged more on seeds and termites compared to the
356 other two species most common species, although in absolute terms, it foraged most on crushed
357 insects and sucrose. The second-most common species, *Nylanderia* sp.1, similarly foraged most
358 on crushed insects, sucrose and melezitose, but relative to the other two species foraged more
359 on melezitose and sucrose. The third common species, *Oecophylla smaragdina*, fed on large

360 prey more than the other species. Thus, AMF showed a relatively high level of niche
361 partitioning, which we quantified via the number of significant preferences compared to the
362 number of analysed species. In PPF, PSF and NPF, dominant species (like *Carebara* sp.1,
363 *Pheidole* cf. *nitella*, *Camponotus femoratus*) frequently foraged more on less attractive
364 resources like seeds or bird feces. Only in NSF, the three most common species showed no
365 discernible bait differentiation.

366 **Co-occurrence on food resources and in pitfalls**

367 We measured spatial segregation on food resources as an indicator for the monopolisation of a
368 resource type. There was significant variation among sites in spatial segregation (LM: $F_4 = 7.34$
369 $p < 0.0001$; Fig. 5a). Paleotropical primary forest (PPF) had the highest level of segregation,
370 which we interpret as strongest degree of competitive exclusion at food sources. The
371 numerically dominant species of PSF and PPF showed not only high frequencies, but also high
372 mean abundances (number of workers) per occurrence and food resource (e.g. *L. bedoti*: 100.6
373 in PSF, 94.8 in PPF; *Carebara* sp.1: 247.36 in PPF), indicating that they were well able to
374 exclude other species from a food resource. In general, over all sites, segregation was highest
375 on the three highly attractive resources (effect of resource type: LM: $F_6 = 12.1$; $p < 0.0001$; Fig.
376 5b). Time of day did not affect segregation (LM: $F_1 = 1.91$; $p = 0.17$).

377 In contrast to segregation at baits, segregation at pitfalls was much lower. Here, standardized
378 effect sizes per site ranged from 0.66 (AMF) to -2.11 (NPF). Thus, co-occurrence in pitfalls
379 was different from random only at NPF (Table S2b, Fig. 2).

380

381 **Discussion**

382 In this study, we address the extent to which ant communities in tropical rainforest across
383 different biogeographic regions show consistent patterns of dietary and temporal niche
384 differentiation, and of species co-occurrence. To our knowledge, this is the first

385 macroecological study of niche differentiation in ant communities, using a consistent sampling
386 methodology to examine the extent to which the relative importance of different niches
387 dimensions can be predicted by climate and habitat structure.

388 **The importance of diet and time varies among sites**

389 Both, resource type and time of day significantly influenced the composition of ant assemblages
390 at each site. However, their relative importance differed (Table 2). In NSF and NPF, time of
391 day played a larger role than dietary differentiation, while the reverse was true in PSF. Both
392 factors were approximately equally important in the Australian forest (AMF). Thus, the effect
393 of single niche dimensions on community composition seems to be highly idiosyncratic and
394 specific to the site studied.

395 Variation among sites in the importance of diet and time is reflected by variation in niche
396 preferences of dominant species. For example, the three most abundant species in NPF all
397 showed absolute temporal specialisation, whereas none of the three most abundant species in
398 PSF did so (green cells in Table 3). This is consistent with the high impact of time in NPF, but
399 low in PSF. Similarly, the high impact of diet on community structure in PSF and PPF reflects
400 the extremely high abundance of *Lophomyrmex bedoti*, which mostly monopolised attractive
401 resources and thereby caused community differences between attractive and non-attractive
402 resources. Thus, temporal and dietary specialisation of dominant species can directly affect
403 overall community patterns, especially given that bait monopolisation and competitive
404 exclusion are largely driven by them (Blüthgen and Fiedler 2004a; Parr and Gibb 2010; Arnan
405 et al. 2011; Ellwood et al. 2016). Moreover, their numerical abundance and tendency to
406 monopolise can strongly influence both community structure and the level of spatial
407 segregation. Our findings at PSF and PPF demonstrate that a single dominant species can
408 greatly affect community-wide patterns of niche partitioning. These effects are idiosyncratic
409 and hard to predict based on community composition alone (Houadria and Menzel 2017).

410 Next to diet and time, spatial variation also significantly contributed to community
411 composition, but only accounted for 5-14% of the variation. Note that, due to the balanced
412 experimental design of our study, the spatial variation could not affect our results concerning
413 relative impacts of the two niche dimensions, niche overlap, preferences, and specialisation.

414 **Specialisation per species**

415 Despite the different effect sizes for dietary and temporal differentiation, average specialisation
416 per species (f_s and t_s) did not differ across sites. However, species-specific values ignore the
417 numerical importance of each species and do not consider specialisation relative to the
418 remaining community: rare species with little effect on community structure had the same
419 weight as common species. Thus, average specialisation of a community does not necessarily
420 yield information on the actual importance of a certain niche dimension for community
421 structure. To thoroughly assess the role of a niche dimension, one should take into account each
422 species' ecological importance, and measure 'relative specialisation', i.e. how different each
423 species is from the remaining community, rather than absolute specialisation (Houadria and
424 Menzel 2017).

425 **High overall niche overlap**

426 Across the entire communities, dietary niche overlap was always higher than expected from
427 random. This is due to three resources (sucrose, melezitose, and crushed insects) that were
428 widely preferred. Nevertheless, these seemingly generalistic species showed signs of niche
429 differentiation as revealed by the hotlink analyses: some species preferentially foraged on
430 otherwise less attractive resources compared to the remaining community. Note however, that
431 other food specialists might be entirely missing from our study – it is likely that specialised
432 predators, leaf-cutters or fungivores may not have been attracted to the baits at all. By missing
433 these specialists, we have underestimated overall potential food partitioning.

434 Besides the dietary niche, one of the sites (NPF) also showed a higher temporal niche overlap
435 than expected. This is probably because, especially in NPF, there are more diurnal than
436 nocturnal species. Compared to NSF, PPF, and PSF, the difference in species richness between
437 day and night was highest for NPF (Table S2 in Houadria *et al.* 2016).

438 **Niche differentiation despite strong niche overlap**

439 Dietary niche partitioning became more apparent using relative preferences (hot links), which
440 analyse species-specific preferences relative to the remaining community. They revealed that
441 some of the numerically dominant species preferred less attractive resources like termites
442 (*Pheidole* A in AMF), seeds (*Pheidole* A in AMF, *Carebara* sp.1 in PPF, *Pheidole* cf. *nitella*
443 and *Pheidole* sp.6 in NPF) and large prey (*Oecophylla* in AMF). Moreover, certain species were
444 more active at night compared to the remaining community even if they did not show absolute
445 temporal specialisation (Table 3). Many previous studies also found niche differentiation in ant
446 communities in dimensions such as seasonal or daily activity pattern (Albrecht and Gotelli
447 2001), diet (Blüthgen *et al.* 2003) or daily activity (Santini *et al.* 2007; Stuble *et al.* 2013). Thus,
448 niche partitioning can be detected even in rather generalised communities if overall resource
449 preferences are accounted for.

450 **Spatial segregation at baits and pitfalls**

451 Spatial segregation at baits of the same type indicates resource monopolisation in this study,
452 and hence reflects current competition for this resource type. Our data showed strong spatial
453 segregation at attractive baits, but less so at non-attractive baits. This indicates that resource
454 competition depends on the quality of the resource (Blüthgen and Fiedler 2004b), for example,
455 if extrafloral sugar concentration is lower at night (Anjos *et al.* 2017). In pitfalls, spatial
456 segregation was not higher than expected, indicating that segregation at baits was not due to
457 spatial heterogeneity or territoriality. The aggregation found in pitfalls of NPF was probably

458 due to the two mutualistic species *Crematogaster levior* and *Camponotus femoratus*, which
459 were among the most common species in this site and always occurred together.

460 It should be noted that interspecific competition for food may not reflect competition for other
461 resources, such as nest sites (Tanaka et al. 2010; Ellwood et al. 2016). Other mechanisms to
462 reduce competition may be differences in foraging behaviour, e.g. species particularly good in
463 discovering food sources vs in defending or monopolising them. Such trade-offs, however, are
464 likely to differ between sites and may not be present in many habitats (Parr and Gibb 2012).
465 Due to the high number of baits (total n = 4480), we could not perform behavioural observations
466 or time series (to observe species turnover) for each bait.

467 **Highest niche differentiation in the least diverse site**

468 The Australian forest (AMF) was the species-poorest site, and at the same time showed the
469 strongest niche differentiation, both measured as percent explained variance and as the number
470 of significant preferences per species (Fig. 4c). Two non-exclusive explanations for this
471 coincidence are plausible: either the strong patterns are a result of the lower number of rare
472 species compared to the other sites, which are less specialised and dilute overall patterns, or
473 differentiation is really stronger in species-poor communities. Firstly, niche differentiation is
474 harder to detect for rare species – their lower abundances lower the statistical power. Thus,
475 higher niche differentiation in a species-poor community may be a statistical artefact. Secondly,
476 competition is usually highest between dominant and subdominant species, but lower between
477 dominant and subordinate species (Arnan et al. 2011). Hence, rare species, which are typically
478 subordinate, may experience less pressure to partition their niches among each other. Andersen
479 (2008) proposed that ant communities are to a significant extent a ‘lottery’ system where colony
480 establishment strongly depends on chance. Once a colony is established, it is very persistent
481 and competition will not lead to nest mortality but will rather reduce performance (Gordon and
482 Kulig 1996; Gordon and Wagner 1997; Andersen 2008). Furthermore, rare species exert less

483 pressure on each other since they occur at lower densities. In order to coexist, a rare species
484 primarily has to differ from the dominant species, not from other rare ones. At high levels of
485 competitive exclusion, a rare species' chance to establish may be highly random, which further
486 reduces the role of co-occurring competitors and the need for niche partitioning. This idea is
487 consistent with the highly competitive exclusion in PPF, which coincides with the lowest level
488 of dietary and temporal differentiation (measures as percent explained variance).

489 **Conclusion**

490 All our rainforest ant communities showed substantial niche differentiation despite high niche
491 overlap. In particular, each community contained species that foraged on less attractive food
492 resources, indicating that relatively unattractive and low-quality resources can be important for
493 competitively inferior species. However, the relative importance of dietary and temporal niche
494 differentiation varied markedly among our sites, despite their similar climate and vegetation
495 structure. A mechanistic understanding of the global drivers of niche structure in ant
496 communities therefore remains elusive. However, site-specific idiosyncrasies appear to depend
497 on traits of the locally dominant species, and so a fruitful avenue for future studies is to
498 determine how ecological traits of dominant species affect niche structure and spatial
499 segregation, and to understand the drivers of dominant species with different ecological traits.

500

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513

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680

681 **Figure legends**

682 Figure 1. NMDS ordinations (based on presence/absence data) of the ant assemblages attracted
683 to the seven food resources and the two time periods for each of the five sites. Cru – crushed
684 insects; See – seeds; Suc – sucrose; Mel – melezitose; Pre – large prey (live
685 grasshoppers/mealworms); Ter – live termites; Chi – bird feces. Full circles represent nocturnal
686 and empty circles diurnal communities. In addition, the level of stress for each NMDS
687 ordination is stated.

688

689 Figure 2. Niche overlap plotted against spatial co-occurrence. The points represent standard
690 effect sizes (SES) per site for dietary and temporal niche overlap (y axis) and for spatial co-
691 occurrence at pitfalls (x axis). Sites with SES values greater than 1.96 (dashed lines) indicate
692 significant species segregation (x axis) or higher niche overlap than expected from random (y
693 axis), respectively. SES values less than -1.96 indicate significant species aggregation (x axis)
694 or niche partitioning (y axis).

695

696 Figure 3. Percentage and number of temporally specialized species on each site (out of a total
697 *N* of 155).

698

699 Figure 4. a) Total frequency per species (mean \pm standard error) per resource type at the five
700 sites. Plots with the same letters are not significantly different based on Tukey's HSD.

701 b) Number of significant absolute (abs.) and relative (rel.) preferences for attractive (attr.)
702 (crushed insects, sucrose, melezitose) and non-attractive (non-attr.) (bird feces, seeds, living
703 termites, living large prey) food sources per site. A 'preference' is defined here as a species that
704 occurred more frequently on a given resource type than expected. Note that a single species can
705 have significant preferences for multiple resources.

706 c) Number of significant absolute and relative preferences per species and site, summed for all
707 resources.

708

709 Figure 5. Species co-occurrence on food resources, shown as standardized effect sizes. Co-
710 occurrence was calculated separately for each food source and time of day. a) Co-occurrence
711 on different sites (n = 14 per site [7 baits, 2 times of day]). b) Co-occurrence per food source (n
712 = 10 per food resource [2 times of day, 5 sites]). Values greater than 1.96 (dashed lines) indicate
713 significant species segregation; values less than -1.96 indicate significant species aggregation.
714 Plots with the same letters are not significantly different based on Tukey's HSD comparisons.
715 See Fig. 2 for co-occurrence in pitfalls.

716

Table 1. Overview of variation in ant species richness among sites, sampling methods, resources and time of day. The table gives the total species richness (baits and pitfalls pooled), species richness on food resources and in pitfalls. Furthermore, the table shows the number of species with incidence ≥ 5 and, in brackets, the total number of species per food source (food resources only), as well as the number of species with frequency ≥ 5 and, in brackets, total number of species, per time of day (food resources and pitfalls).

Site	Total	Food		Sucrose	Melezitose	Crushed insects	Small prey	Seeds	Large prey	Bird feces	Day		Night	
		resources	Pitfalls											
AMF	27	16	21	10 (11)	10 (11)	12 (14)	9 (9)	9 (11)	7 (7)	8 (8)	12 (19)	11 (19)		
PPF	92	53	76	26 (33)	20 (26)	22 (29)	23 (28)	19 (24)	16 (21)	19 (26)	41 (82)	41 (76)		
PSF	85	59	54	15 (29)	15 (28)	14 (24)	10 (19)	10 (20)	14 (15)	11 (20)	21 (61)	23 (60)		
NPF	107	52	86	26 (34)	24 (34)	23 (32)	24 (30)	18 (19)	19 (23)	13 (16)	48 (83)	46 (78)		
NSF	52	34	47	19 (21)	19 (20)	21 (25)	18 (19)	20 (21)	17 (19)	16 (17)	28 (47)	28 (34)		

Table 2. Factors explaining community composition in the five sites. The table shows results of a PERMANOVA that was based on the incidence of each species at each of the seven food sources. It included the fixed factors ‘food resource’ and ‘time of day’ their interaction, and ‘grid point’ as a random factor. The pseudo-F values indicate the effect size of each factor on the ant communities. Also shown are percentages of variance explained by diet, time, space (i.e. grid point) as well as the total variance explained by the factors: diet+time+the diet:time-interaction. Significant *p* values are given in bold.

Site	Food resource (df = 6)			Time (df = 1)			Grid point (df = 63)			Diet : Time interaction (df = 6)		Total variance explained by diet * time
	Pseudo-F	<i>p</i>	Explained variance	Pseudo-F	<i>p</i>	Explained variance	Pseudo-F	<i>p</i>	Explained variance	Pseudo-F	<i>p</i>	
AMF	23.86	0.001	45%	15.89	0.001	41%	3.2	0.001	5%	2.33	0.004	89%
PPF	7.86	0.001	35%	6.74	0.001	33%	3.58	0.001	14%	1.19	0.193	73%
PSF	22.26	0.001	66%	3.05	0.009	11%	3.27	0.001	9%	1.75	0.015	82%
NPF	8.47	0.001	29%	12.72	0.001	48%	2.57	0.001	7%	2.05	0.001	83%
NSF	9.04	0.001	22%	25.63	0.001	55%	4.95	0.001	11%	2.58	0.001	83%

Table 3. Absolute (green) and relative (red) preferences for food and time of day, shown for the most common species (together accounting for 80% of all occurrences on food sources) per site. Incidence (number of grid points) and frequency (on food sources) per species are given additionally. The food resources are sorted by its attractiveness in declining order (see Fig 4a). Based on null model randomizations a food resource was defined as absolutely preferred (green) if a species foraged on it significantly more often than on other food resources, and as relatively preferred (red) if a species foraged significantly more often on it than the other species within its community. On the right, absolute and relative temporal preferences are shown, based on total frequencies (food sources and pitfalls combined, not shown) per species. At the bottom, the total number of absolute and relative preferences is shown.

AMF	Incidence	Frequency									
			Sucrose	Melezitose	Crushed insects	Small prey	Seeds	Large prey	Bird feces	Day	Night
<i>Pheidole</i> sp.A	64	417	■			■	■				■
<i>Nylanderia</i> sp.1	51	137	■	■	■						■
<i>Oecophylla smaragdina</i>	44	118			■			■		■	
PPF											
<i>Lophomyrmex bedoti</i>	56	252	■		■	■				■	■
<i>Carebara</i> sp.1	50	98					■				■
<i>Lophomyrmex longicornis</i>	27	55							■		■
<i>Nylanderia</i> sp.4	27	41	■	■							
<i>Tapinoma</i> sp.1	13	36									
<i>Pheidole</i> sp.6	20	34		■							
<i>Pheidole</i> sp.5	12	33									
<i>Euprenolepis</i> sp.1	15	25	■								
<i>Recurvidris</i> sp.2	17	24							■	■	
<i>Pheidole</i> sp.40	8	22									
<i>Dinomyrmex gigas</i>	18	21						■			
<i>Carebara</i> sp.8	15	16									
PSF											
<i>Lophomyrmex bedoti</i>	62	364	■	■	■						
<i>Carebara</i> sp.1	35	49				■	■				■
<i>Technomyrmex</i> sp.2	20	34	■	■							
<i>Myrmecaria</i> sp.1	10	25							■	■	
<i>Lophomyrmex longicornis</i>	9	22							■	■	
<i>Recurvidris</i> sp.2	11	18							■		
NPF											
<i>Pheidole</i> cf. <i>nitella</i>	52	137	■				■				■
<i>Crematogaster levior</i>	42	96			■				■		
<i>Camponotus femoratus</i>	30	74			■	■		■	■		
<i>Crematogaster limata</i>	31	61			■				■	■	
<i>Pheidole</i> sp.6	27	42					■				
<i>Solenopsis</i> sp.15	24	34	■	■							
<i>Pheidole</i> sp.8	16	29	■	■							
<i>Pheidole</i> sp.28	15	24		■	■						
<i>Nylanderia</i> sp.2	16	22									
<i>Ectatomma</i> sp.4	13	21		■	■						
<i>Pheidole</i> sp.19	12	20	■	■					■	■	
<i>Solenopsis</i> sp. 9	13	19									
NSF											
<i>Pheidole subarmata</i>	43	175	■								
<i>Pheidole pugnax</i>	40	138	■	■					■		
<i>Camponotus</i> sp.2	51	110	■								■
<i>Solenopsis</i> sp. D2	25	50									
<i>Solenopsis</i> sp. D1	29	43									
<i>Nylanderia</i> sp.1	16	33	■	■	■						
<i>Solenopsis</i> sp.1	18	44									
<i>Pheidole zeteki</i>	23	35	■				■		■	■	
<i>Odontomachus haematodus</i>	19	30						■	■		
<i>Pheidole</i> sp.5	12	31							■	■	
<i>Crematogaster limata</i>	13	27			■	■			■	■	
<i>Pheidole</i> sp.1	13	24							■	■	
Total number of absolute preferences			15	9	9	0	1	1	1	16	3
Total number of relative preferences			3	4	3	2	6	2	3	11	6