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Abiotic controls, but not species richness, shape niche overlap and breadth of ant assemblages along an elevational gradient in central Spain

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ABSTRACT

Niche overlap and breadth are fundamental characteristics of ecological niches that have been hypothesized to relate both to environmental conditions and to biotic interactions within a community. Abiotic factors and interspecific competition may have opposing effects on those niche characteristics by respectively filtering out species from the niche space and limiting among-species similarity. Here we set out to assess niche overlap and breadth of ant assemblages in Mediterranean grasslands along a 1668-m elevational gradient in the Guadarrama range (Central Spain). We carried out an outdoor cafeteria experiment considering two niche dimensions on resource acquisition: food type and period of aboveground activity. We compared metrics describing niche overlap and breadth to null models and related the metrics to elevation, temperature at ground level and a proxy of interspecific competition (species richness) with general linear models. Pianka's niche overlap indexes were higher than those calculated with random assemblages, but differences among observed and random assemblages were only significant at mid-elevations and were unrelated to the explanatory variables. Overlap along elevation seemed more due to overlap in period of activity. Niche breadth at the assemblage level was significantly smaller than null expectations and was related to elevation (negatively) and to species richness (positively). These were significantly larger than estimates for the species level. These results show that ant assemblages exploit a subset of available conditions, in a pattern only partially coincident with a scenario of abiotic control. Moreover, their constituent species share time of activity and, to a lesser extent, food resources, in spite of the interspecific competition structuring communities that is often assumed. Overall, the patterns we recorded suggest that other mechanisms should be acting to promote species coexistence, such as trade-offs among ecological functions.

Keywords: ant assemblages, Guadarrama range, mountains, niche breadth, niche overlap, Pianka's index.

1. Introduction

Niche overlap and breadth are fundamental characteristics of ecological niches that are most often assessed to evaluate community structure, to understand community assembly processes, and to address issues of biological conservation (e.g.: Hurlbert and Jetz 2010; Seoane et al. 2017; Pedrana et al. 2018). Overlap between close species in niche space is assumed to cause strong competition pressure, which leads to local population equilibriums where species partition the niche into smaller parts (niche packing) or segregate from each other (niche segregation, Colwell and Futuyma 1971; Hurlbert and Jetz 2010). Constraints to niche overlap between phylogenetically close species have been used to explain species distribution patterns along ecological gradients (Bastianelli et al., 2017) and co-occurrence and segregation patterns among geographical areas (Laiolo et al., 2017). These niche descriptors are somewhat labile, as individuals are known to modify them according to their ecological context, which translates to species consequently showing variable niche characteristics throughout their ranges (Shik et al., 2019). Thus, the analysis of niche metrics along ecological gradients may help to explain patterns of community assembly and the processes involved.

Niche overlap and breadth have been hypothesized to relate both to environmental conditions and to biotic interactions within a community (Scheele et al., 2017). The conditions may determine the range of species' behavioural and physiological responses suitable in a place, typically through the limiting effects of temperature and water availability or humidity, which make up

primary productivity. Thus, conditions may filter out from a site the species unable to use the available segments of condition-dependent niche dimensions. As a result, niches may aggregate, with species occurrence and possibly interspecific competition diminishing (Arnán et al. 2017; Cerdá et al. 1997; but see Hart and Marshall 2013). The interactions within a community clip the wider fundamental niches to narrower realized ones. This has been most often attributed to interspecific competition preventing sympatric species from sharing resources (the limiting similarity effect, Abrams 1983; Schwikl and Ackerly 2005). Thus, niche overlap and breadth in communities has been hypothesized to correlate with species richness, although the supporting evidence is not unequivocal (Mittelbach and McGill, 2019).

The studies on the characteristics of niches within communities have benefited most from the study of groups of taxa with large numbers of species intensely interacting with each other (e.g., insects: Retana et al. 2015; birds: Traba et al. 2015; mammals: Davis et al. 2018). Among invertebrates, ants have been frequently chosen to analyze niches because of their high prevalence and abundance, and relevance to ecological processes (Albrecht and Gotelli 2001, Arnán and Blüthgen 2015, Grevé et al. 2019). Ants are fierce competitors that divide up the niche in dimensions related to their use of food resources, their seasonal and daily periods of activity and to other behavioural and life-history traits that determine the way its populations grow and extend (Houadria et al., 2015; Retana et al., 2015; Segev and Ziv, 2012). Globally, ant species are numerous and include some well-known examples of super-specialists in behaviour (Ruano et al., 2013) or in food resource selection (Azcárate and Peco, 2003). Otherwise, local assemblages are often mostly composed of more generalist species with wider niches (Arnán et

al., 2017), which offers the opportunity to study their niche characteristics in relation to different environmental and competitive scenarios.

Ant species partition their niches most obviously according to their daily period of activity, and the food resources and habitats they exploit (Retana et al., 2015). Soil temperature and relative humidity change over the course of the day and directly determine ant activity (Cros et al. 1997). Thus, some species prefer cooler environments, and thus tend to show crepuscular activity and occupy shady habitats (such as forests), while others prefer warmer conditions found in open habitats at midday. Within species, the period of the day with peaks of activity have been reported to shift among seasons (e.g., *Messor barbarus* is partially nocturnal in the heat of the Mediterranean summer but diurnal in the cooler and wetter spring and autumn seasons, Azcárate et al. 2007), and to avoid interspecific competition (e.g., activity of *Cataglyphis* species peaks at midday in the Mediterranean, when the heat deters other species from foraging, Lenoir et al. 2009). Ants consume a wide range of food resources from grain (plant seeds) to floral resources (mainly nectar but also pollen) and animals (live prey and carcasses). They may be obligatory specialists in foraging, consuming just one of these food types, but often they are food generalists or facultative exploiters of several resource types, typically grain and another food type. There is some evidence that the preferred food resources are those that supply limiting micronutrients at a given site (Kaspari et al., 2008; Kay, 2004) and their selection may vary with the changing abiotic factors, such as those related to elevational gradients (Peters et al., 2014).

We set out to study niche characteristics of ants, at the assemblage and species level, along an elevational gradient in a Mediterranean mountain range to explore the drivers of niche structure. Specifically, we aim to (a) estimate niche overlap and breadth considering food type and period

of aboveground activity, and compare them to null expectations, and (b) regress those estimates to elevation and species richness, as proxies, respectively, of abiotic and biotic controls for the assemblage of communities. We hypothesize that there should be a relationship of niche overlap and breadth with elevation if the main control of niche characteristics is environmental. This is because conditions change gradually with elevation, mainly due to a decrease in temperature but also a decrease in summer drought. If these conditions play a main role in filtering out species from communities, we would expect a larger mean niche overlap, averaged from the local species pool, in areas with harsher conditions because some parts or combinations of their niche dimensions would be forbidden. The relationship to elevation would be either monotonic if low temperatures at high elevations are particularly limiting (with higher areas having larger overlap and narrower breadths), or quadratic (with larger overlaps at both extremes of the elevational gradient) if high temperatures and low relative humidity at low elevations also impose limiting conditions (Flores et al., 2018). Alternatively, we hypothesize that metrics of niche overlap and breadth should correlate more strongly with species richness if niche structure is mainly controlled by biotic interactions. If so, the constituent species of richer communities should show narrower niches with less overlap and, consequently, average niche breadth and overlap of communities should be small.

2. Material and methods

2.1. Study area

The study was conducted on the southern slope of the Guadarrama range (Madrid, Central Spain). The area has a continental Mediterranean climate, with mean annual temperatures ranging from ca. 15°C at the foothills (500m elevation) to ca. 4°C in the summits (2428m), and a mean annual

rainfall of 550mm to 1500mm (Ninyerola et al., 2005). The landscape of the study area is dominated by forests of holm oak (*Quercus ilex* subsp. *ballota*), Pyrenean oak (*Quercus pyrenaica*) and Scots pine (*Pinus sylvestris*). Natural and semi-natural grasslands are also abundant as a consequence of extensive traditional livestock grazing (by cows and sheep) and wild herbivory (by wild boar, mountain goats, rabbits and roe deer).

2.2. Data collection

We selected a subset of six 100 x 100 m sampling sites from a larger survey (Flores et al., 2018; Silvestre et al., 2019) that covered an elevational gradient of 1668 m (range: 684 – 2352; Table 1; figure 1). All sampling sites were Mediterranean south-facing dry grasslands growing on siliceous substrate with gentle slopes (<10%).

Site	Coordinates	Elevation (m a.s.l.)	Species richness
Valdeloshielos (PS1)	30T 437745 4494344	684	7
Soto del Real (PS3)	30T 431575 4513574	1044	14
La Barranca (PD4)	30T 416166 4511164	1331	16
Puerto de Cotos (PD6)	30T 419717 4519643	1786	4
Laguna Chica (PS8)	30T 419276 4520625	2026	5
Pico Peñalara (PD9)	30T 419192 4522196	2352	4

Table 1. Location, elevation and species richness (number of species registered at baits) of sampling sites. Coordinates are UTM in datum WGS84. Elevation and species richness are used to explain niche metrics.

We aimed to describe the niche of the species considering two main dimensions on resource acquisition: food type and period of aboveground activity. We assessed ants' preferences in both niche dimensions (food type and period of aboveground activity) with an outdoor cafeteria experiment. Available data on the study area (Flores et al. 2018; Silvestre et al. 2019) show that the regional species pool is dominated by generalists and liquid-food feeders, with the presence of some granivorous, predator and scavenger species, similarly to observations in other Mediterranean localities (Arnan et al. 2019). To encompass a wide as possible range of food resource types but limiting their number to a manageable quantity, we set the following four levels: sugar water, live crickets, dry worms and seeds (a mixture of commercial seeds of different weights, from clovers to lentils; Table 2). We presumed sugar water would be favoured for species that forage on aphid drops and nectar, while dry worms were aimed at scavenger species and seeds at

165 specialist or facultative granivorous species. Live crickets were offered as baits by tying the
166 crickets with thread to nails attached to Petri dishes. It was assumed that these would be most
167 attractive to predator species (raw data publicly available at DOI
168 10.6084/m9.figshare.13246619).

169

Species	Family	Weight (mg)
<i>Lens culinaris</i>	Fabaceae	80
<i>Phalaris canariensis</i>	Poaceae	35
<i>Lactuca sativa</i>	Asteraceae	1.8
<i>Nasturtium officinale</i>	Brassicaceae	1.5
<i>Cynodon dactylon</i>	Poaceae	0.8
<i>Trifolium repens</i>	Fabaceae	0.5

Table 2. Family and mean weight of the commercial seeds offered in petri dishes to describe the niche resource of ant assemblages

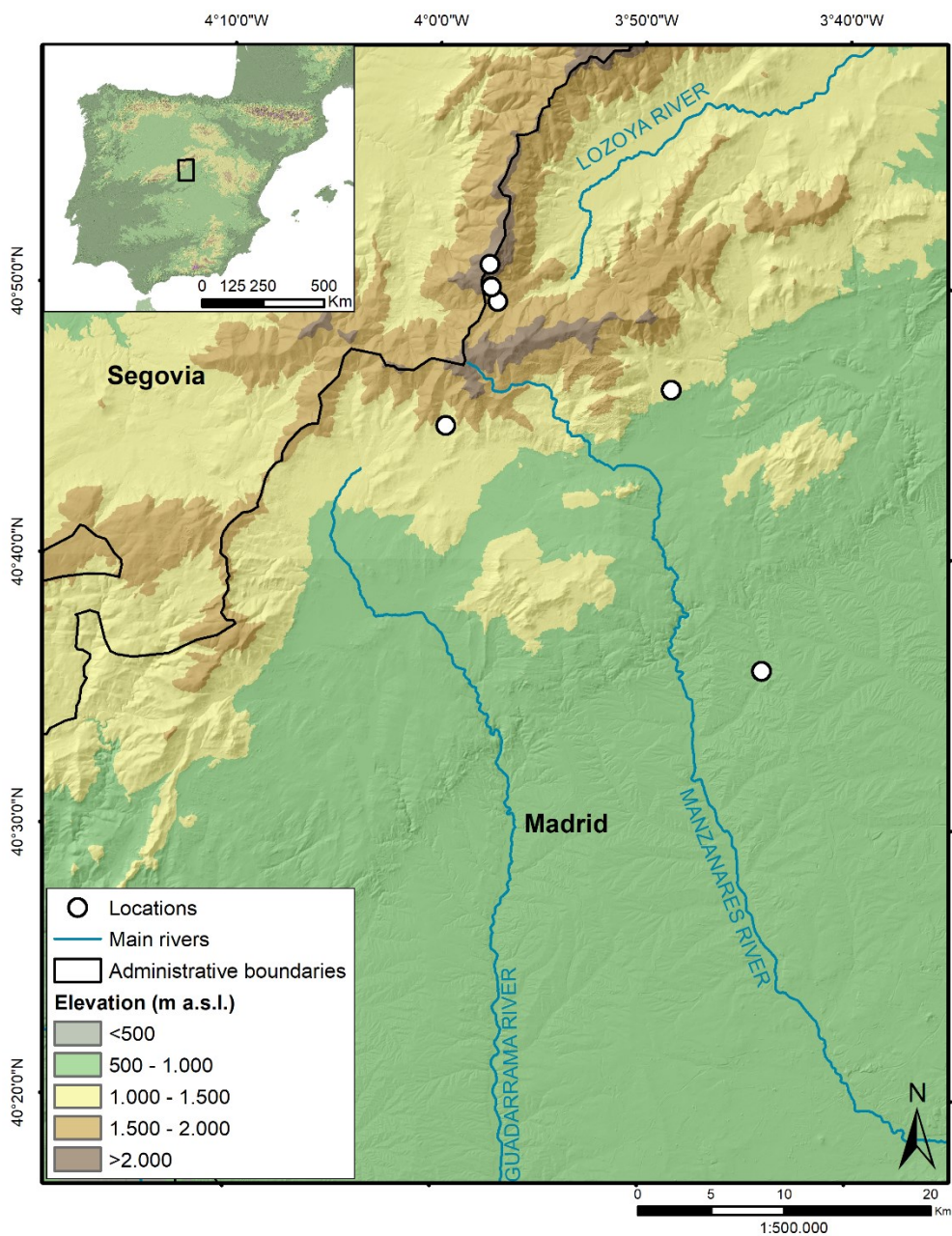


Figure 1. Geographic locations used in the study area.

To define the period of activity, we divided up the 24h cycle of a day into the following four 6-hour periods: morning (6 am to 12 am), afternoon (12 am to 6 pm), evening (6 pm to 12 pm) and night (12 pm to 6 am). We expected to find a low number of species and individuals during the afternoon period, due to limiting high temperatures (although some species are known to forage mainly during this period: e.g., *Cataglyphis iberica* (Cerdá et al. 1998; Lenoir et al. 2009). We estimated the use of each food resource by offering baits. The four food resources were offered in plastic Petri dishes (5.5cm diameter x 0.7cm depth) with two 1.5cm openings to facilitate food collection by ants (Figure 2).



Figure 2. Bait types offered during field sampling. (A) Seed mix, (B) dry worms, (C) live cricket and (D) sugar water. In A, C and D, cages were removed to take the photo.

191
192 The dishes were placed on the ground at 5-m intervals along a zig-zag transect, following a
193 systematic order to maximize distance of baits belonging to the same food resource. We placed
194 5 replicates per resource type. Plastic dishes were covered with a plastic green cage (14 x 14 x 6
195 cm, mesh size 1x1 cm) to prevent the removal of resources by mammals or birds. Subsequently,
196 we walked the line of dishes to systematically assess them, recording species occurrence,
197 capturing individuals for further identification and replacing the bait if needed. We replicated this
198 survey in each time period on five non-consecutive days, using at least 3 h around the middle of
199 the period (i.e., we sampled symmetrically around 9 am, 3 pm, 9 pm and 3 am). Thus, there were
200 5 replicates for each combination of food resource and time period (n = 16 combinations, 80 Petri
201 dishes), called resource category hereafter for simplicity (Figure 3). The surveys were conducted
202 on days with sunny and warm conditions during summer (between 22 July and 9 August 2015),
203 a period with intense ant activity at all elevations, including the higher altitudes in which cold
204 temperatures constraint ant activity for most of the year (Silvestre et al. 2019). During this period,
205 we monitored ambient temperature at the surface by placing two digital thermometers (HOBO
206 pendant 0.1°C resolution) per site, buried at ground level. Temperature was recorded at 30-minute
207 intervals.

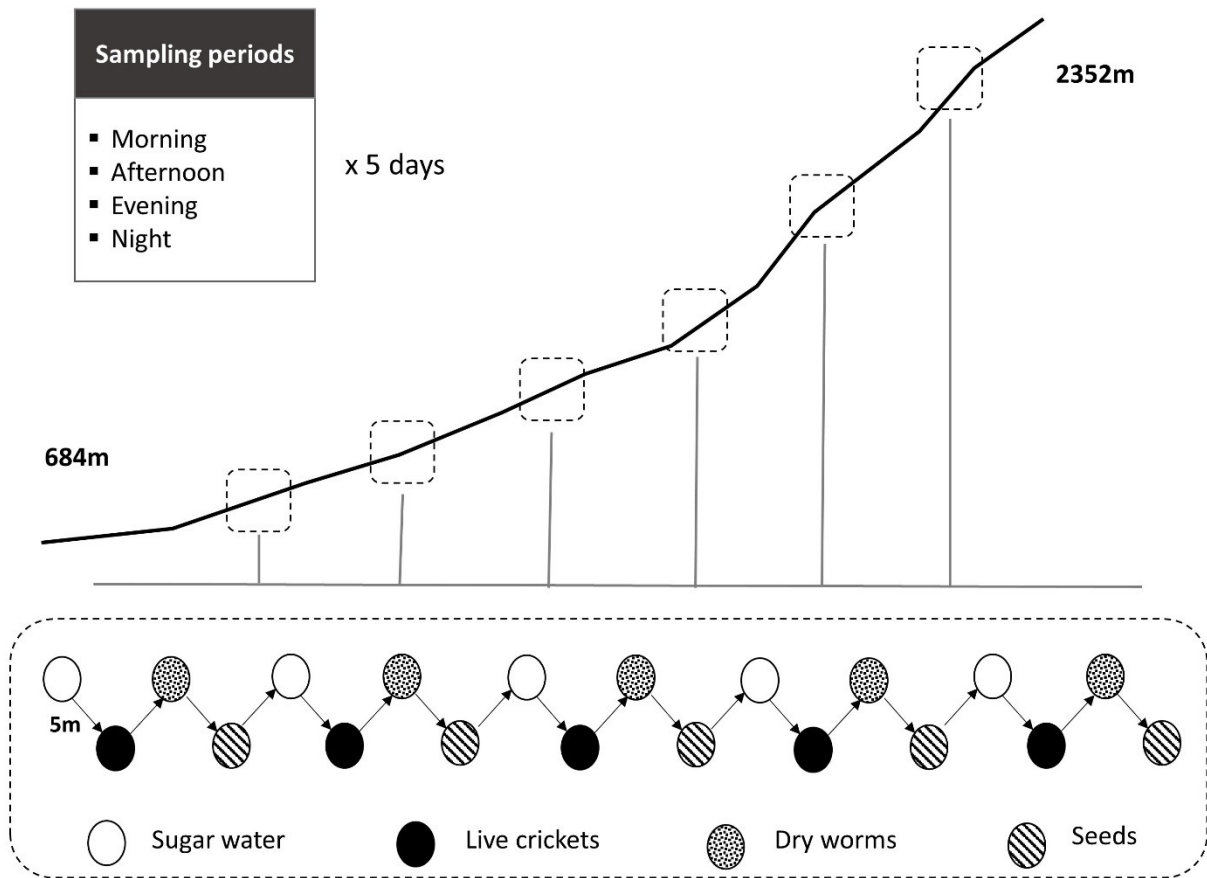


Figure 3. Schematic representation of the sampling design.

2.3. Data analysis

We focussed on two main characteristics of ecological niches to assess community structure and community assembly processes: niche overlap and breadth. First, we built a matrix with species (in rows) by resource category (in columns) for each site separately. The species were those captured in baits, thus the number of rows differed among sites. The columns give the combinations of food type and time period (sixteen columns for every site). The cells are the sum of occurrences of each species in each resource category: values ranged from 0 for species present

in the local species pool but not recorded in that niche category, to 5 for species occurring in every one of the 5 replicates of a resource category.

We calculated Pianka's niche overlap index (Pianka, 1974) for each site and compared them to null expectations (Gotelli et al., 2015). This index averages niche overlap among pairs of species within a community and ranges from 0 (no overlap) to 1 (complete overlap).. The overlap was estimated both for the two-dimensional description of niche and for each niche axis separately. Overlap indexes were compared with null models based on randomisation, which simulate the overlap expected if species used resource categories independently of each other. The randomisation algorithm reshuffled row values (one thousand times) preserving species' niche breadth.

We then estimated niche breadth considering the two-dimensional description of niches ($n = 16$ resource categories). To do so, we followed the framework of De Cáceres and Legendre (2009) to describe niche breadths at the assemblage level (De Cáceres and Legendre's populations) and at the species level within assemblages (De Cáceres and Legendre's average estimates for individuals within populations). Differences among sites were tested by a Kruskal-Wallis rank sum test. Observed niche breadths were compared with null models based on one thousand reshufflings of rows and columns of resource x species matrices for each site separately.

We fitted linear regressions of the indexes to describe the patterns of niche overlap and breadth along two alternative ecological gradients: the one defined by the abiotic environment (summarised by elevation) and the one defined by the biotic interactions (summarised by species richness, which was estimated as the total number of species recorded in the set of baits placed in each site). We built alternative regressions with linear or, alternatively, second-order polynomial terms for elevation and species richness as predictor variables for the indexes

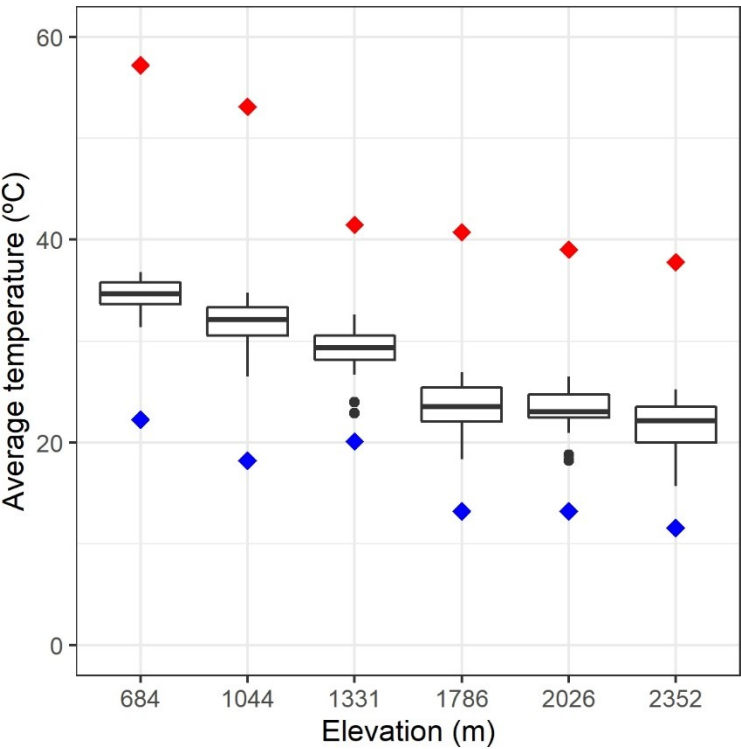
242 calculated on the six assemblages. Finally, we compared the position of the assemblages in each
243 niche axis with χ^2 tests and inspected residuals to assess whether particular food types or time
244 periods were favoured in any assemblage.

245 The analyses were done in R 3.5.1, with specialised packages (indicpecies: De Cáceres and
246 Legendre 2009; EcoSimR 0.1.0: Gotelli et al. 2015) and our own code.

247

248 **3. Results**

249 Mean temperature at ground level during the 19-day sampling period varied from 34.5°C at the
250 lowest site to 21.5°C at the highest site (Figure 4). Average daily temperature oscillations were
251 around 30°C at all sites, with absolute oscillations being higher than 40°C at several sites (raw
252 data publicly available at DOI 10.6084/m9.figshare.13248752).



253
254 **Figure 4** Boxplots of ground level temperature range (in °C) at sampling sites in
255 Guadarrama range (central Spain) during the study period (22 July – 9 August 2015).
256 Maximum temperatures are depicted with diamonds (red for absolute maximum and
257 blue for absolute minimum).
258

259 *3.1. Niche overlap*

260 Pianka's niche overlap indexes ranged from 0.142 (se = 0.115) at the highest elevation (site PD9:
261 2352 m a.s.l.), to 0.657 (se = 0.061) at intermediate elevations (site PD6: 1786 m a.s.l.).

Most observed overlap indexes were higher than those calculated with random assemblages, but the differences were only significant at mid-elevations (sites PD4 and PD6, Table 3, Figure 5A).

Site	Overlap	Breadth _(assemblage)	Breadth _(species)
PS1	0.38(0.080)	0.46(0.000)	0.35(0.000)
PS3	0.34(0.393)	0.46(0.000)	0.35(0.114)
PD4	0.38(0.000)	0.46(0.000)	0.33(0.157)
PD6	0.66(0.001)	0.45(0.000)	0.42(0.002)
PS8	0.30(0.208)	0.45(0.000)	0.30(0.281)
PD9	0.14(0.718)	0.44(0.235)	0.28(0.004)

Table 3. Niche overlap and niche breadth statistics for six ant assemblages along the elevational gradient of Sierra de Guadarrama range (central Spain). For each assemblage (Site), ordered by increasing elevation, the mean overlap of all possible species pairs according to the Pianka index (Overlap mean) is shown, along with the estimates of niche breadth estimated for the whole assemblage (Breadth_(assemblage)) or as individual species' averages (Breadth_(species)). P values from comparisons to null models based on 1000 random reshufflings of species x sites matrices are shown in parentheses.

Neither the linear nor the quadratic polynomial regressions of mean Pianka's overlap index on elevation were significant (respectively, $F_{1,4} = 0.37$, $p = 0.58$ and $F_{2,3} = 1.32$, $p = 0.39$; Figure 5A). Likewise, linear and quadratic polynomial regressions of mean Pianka's overlap index on local species richness were not significant (respectively, $F_{1,4} = 0.006$, $p\text{-value} = 0.98$ and $F_{2,3} = 0.01$, $p = 0.98$; Figure 5D). When calculated separately for each niche dimension, the indexes of overlap that considered only the period of activity (Figures 5C, 5F) were smaller than the indexes

that considered only food resource (Figures 5B, 5E), although differences were not significant (paired Wilcoxon rank-sum test: $V = 20$, $p = 0.063$). Unidimensional indexes based on the period of activity were more similar to the indexes built with both niche dimensions ($r_s = 0.94$ and $p = 0.017$, compare Figures 5C with 5A and 5F with 5D) than were those based on only food resource ($r_s = 0.60$, $p = 0.241$, compare Figures 5B with 5A and 5E with 5D), which suggests that the patterns of niche overlap with elevation were due more to overlap in period of activity.

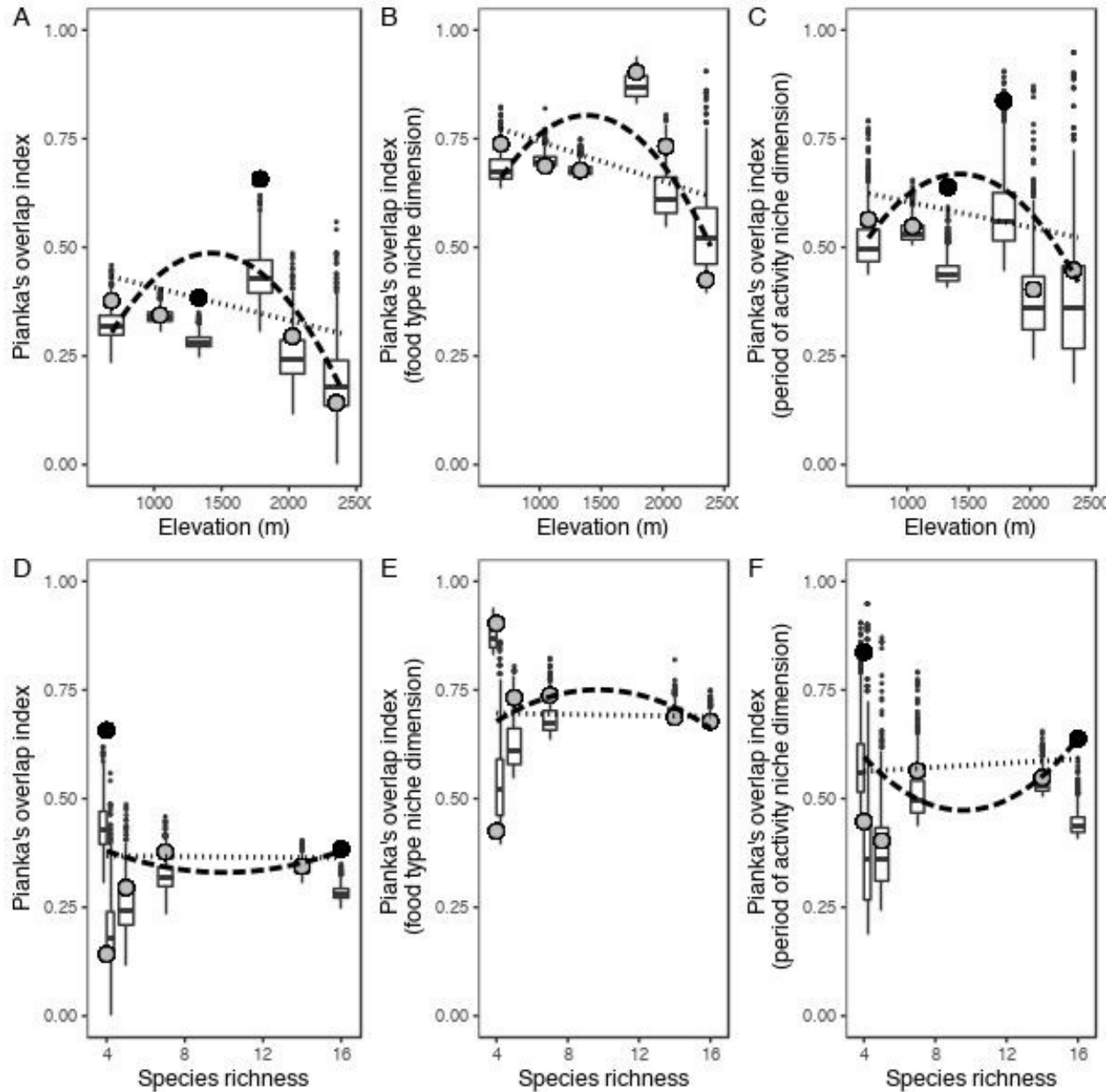


Figure 5. Pianka's niche overlap indexes for ant assemblages against elevation (top row) and species richness (bottom row) along the elevational gradient in Guadarrama range (central Spain). Ecological niches were described by two axes of food type (four categories: sugar water, live crickets, dry worms and seeds) and time of activity (four 6h daily periods). A and D show relationships for the summary of niche according to those two axes. Relationships for unidimensional summaries of niches are shown in B and E (for food type) and C and F (for time period). Circles indicate the observed value of indexes. Black circles indicate indexes significantly different from null expectations. Grey circles do not differ from null expected values.. Null expectations were calculated with 1000 random communities and summarised with box-plots. The

lines show the linear (dotted) or second-order polynomial regressions (dashed) fitted to observed indexes ($p > 0.05$ in all cases).

3.2. *Niche breadth*

Niche breadth at the assemblage level varied slightly from 0.44 at the highest site to 0.46 at mid-elevation. These estimates were significantly smaller than null expectations except for the highest site, whose null distribution nevertheless showed considerable variability (Table 1, Figure 6A, 6B). Niche breadth at the species level (that is, the average of species' niche breadths estimates at each site) ranged from 0.28 (sd = 0.19) to 0.42 (sd = 0.04), but the differences among sites were not significant (Kruskal-Wallis rank sum test, $K = 4.31$, $df = 5$, $p\text{-value} = 0.506$; Figures 6C, 6D). Relationships of whole assemblage breadths against elevation and richness (Figures 6A, 6B) suggest that high elevation limits niche breadth ($p = 0.008$, $R^2 = 0.86$, $AICc = -34.4$ and $p = 0.012$, $R^2 = 0.95$, $AICc = -10.5$ for linear and quadratic polynomial regressions against elevation, respectively) and that the larger the size of the local species pool the larger the niche breadth ($p = 0.054$, $R^2 = 0.65$, $AICc = -29.0$ and $p = 0.049$, $R^2 = 0.87$, $AICc = -4.79$ for linear and quadratic regressions against richness, respectively). In contrast, relationships between assemblage niche breadths estimated as individual species' averages were not clearly related to either elevation or richness (Figures 6C, 6D). These estimates of niche breadths were narrower than those calculated on permuted data, although differences were significant only for some sites. Breadth estimates for the assemblage level were significantly larger than estimates for the species level (Mann-Whitney test, $U = 0$, $p = 0.002$).

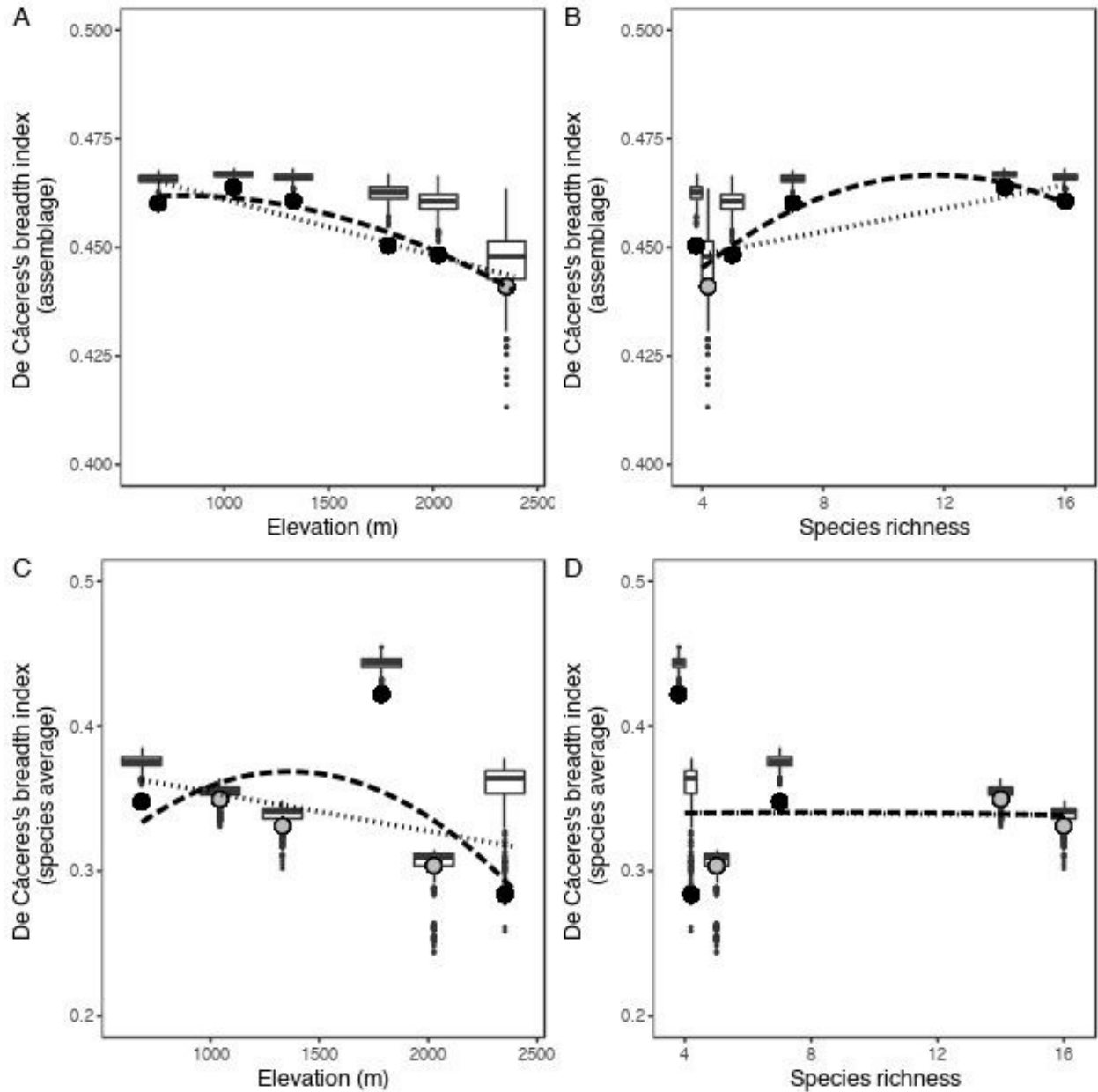


Figure 6. Niche breadths against elevation (A and C) and species richness (B and D) in 6 grassland ant assemblages in Guadarrama range, central Spain. Indexes of breadth estimated for the whole assemblage (A and B) and as individual species averages (C and D) after De Cáceres et al 2011. Boxplots show the distribution of pseudo-values obtained from 1000 random permutations of original resources-by-species matrices, to be compared with observed niche breadth values (circles, black colour for significant differences from random expectations). The lines show the fit for linear (dotted) or second-order polynomial regressions (dashed). These were significant in 6A (respectively, $p = 0.008$ and $p = 0.012$), marginally significant in 6B (respectively, $p = 0.054$ and

0.049) and non-significant in 6C and 6D. Note ordinate scales are different between the top row (with larger values) and the bottom row.

3.3. Resource use

The use of food resources did not differ significantly among sites ($\chi^2 = 12.209$, $p = 0.6747$, p -value computed for a Monte Carlo test with 2000 replicates, Table 4a), while there were significant differences in time periods of activity ($\chi^2 = 51.305$, $p = 0.0005$, Table 4b). Larger χ^2 residuals ($> |2|$) were recorded during night (negative residuals implying avoidance for the highest sites and positive residuals implying preference for the second lowest). The highest site (PD9) recorded the largest positive χ^2 residual during afternoon.

(a)

site	cricket	seed	sugar	worm
PS1	35(1.2)	20(-1.3)	35(0.0)	31(0.1)
PS3	44(-0.6)	47(0.4)	59(0.0)	53(0.2)
PD4	41(-0.8)	50(1.1)	56(-0.1)	49(-0.1)
PD6	17(0.1)	16(0.2)	24(0.8)	13(-1.1)
PS8	15(0.6)	10(-0.6)	17(0.2)	13(-0.2)
PD9	6(0.1)	4(-0.6)	4(-1.1)	10(1.6)

(b)

site	morning	afternoon	evening	night
PS1	41(-1.0)	10(-0.8)	44(1.4)	26(0.2)
PS3	65(-1.7)	20(-0.4)	57(-0.3)	61(3.0)
PD4	83(0.7)	21(0.0)	55(-0.3)	37(-0.5)
PD6	35(1.4)	5(-0.9)	20(-0.1)	10(-1.2)
PS8	31(2.0)	7(0.4)	13(-0.8)	4(-2.2)
PD9	8(-0.5)	9(4.0)	7(0.0)	0(-2.2)

Table 4. Contingency tables for ant use of (a) food resources and (b) time periods along an elevational gradient in central Spain. Figures in each sub-table show the number of occurrences of any species in a given niche dimension and, in parentheses, the standardised residual for the χ^2 test of independence. The sampling was designed with five replicates within each niche dimension and site. Sites are ordered by increasing elevation. The maximum possible value of occurrence is 100 (5 days x 5 replicates x 4 levels of niche dimension).

4. Discussion

Overall, our results show that ant species apportion the niche space in Mediterranean grasslands but provide limited evidence of effects on niche structure associated with the elevational gradient. Ant assemblages exploit a subset of available conditions, as suggested by their niche breadths being narrower than random expectations. Their constituent species share time of activity and, to a lesser extent, food resources, as suggested by their largely overlapping niches. However, niche metrics did not change unequivocally with elevation or richness and did not support either of our two initial hypotheses. While niche breadth showed narrower niches at high elevations, niche overlap peaked at intermediate elevations, the opposite of predictions based on a scenario of control mediated by environmental conditions. We found no evidence in favour of biotic control of ant assemblages, since ant communities presented narrower niches but more overlap in species-richer localities.

Temperature and humidity strongly limit ant activity (Azcarate et al., 2007; Fotso Kuate et al., 2008; Muser et al., 2005; Talbot, 1946), and determine which species occur and co-occur within local communities (Cavender-Bares et al., 2009; Weiher and Keddy, 2001). In Mediterranean elevational gradients, hydric deficit at low elevations and cold temperatures at high elevations are the two major stress sources (Schöb et al., 2013), which sustain the prediction of narrower usable niche segments and wider niche overlaps in the extremes of the gradient. However, our data reveal higher niche overlaps at intermediate elevations (1.331 and 1786 m a.s.l.), where we assumed environmental constraints are less stringent. Our data also show that niche breadth and overlap are, respectively, narrower and wider than expected in most of the gradient, suggesting that environmental pressures determine ant activity at all elevations (Bishop et al., 2014; Villalta et al., 2020). This is consistent with the facts that niche overlap was mostly caused by

coincidences in the period of activity, and with the dependence on elevation of the preferred time periods, e.g. with avoidance of night (and therefore colder) activity periods at high elevations. Our finding of a generalised overlap of niche contrasts with other studies in less varied environments, like temperate forests (Wittman et al., 2010) and tropical areas (Grevé et al., 2019; Houadria et al., 2015), but also in Mediterranean systems (Cros et al., 1997; Retana and Cerdá, 2000). However, these latter studies were carried out under a more benign variant of Mediterranean climate, closer to the coast and presumably less affected by the marked daily temperature and humidity variation routinely observed in our study area (around 40°C temperature amplitude at ground level).

We think that the average milder conditions at intermediate elevations likely lead to higher productivity, and presumably to higher resource availability for ants, which can help explain the increase in species richness observed in this elevational belt (see Flores et al. 2018; Silvestre et al. 2019 in the same area). In this belt, ant communities show narrow niches, forage at the same time periods, and do not segregate food resources, which should increase the likelihood of encountering potential competitors (Wittman et al., 2010), and thus raises the question of how ant species manage to coexist. Food preference has been observed to contribute directly to niche partitioning in ant communities (Arnán et al., 2019; Blüthgen and Feldhaar, 2010), although in other studies local assemblages have been found to be mostly composed of generalist species with wider niches (Arnán et al., 2017), which would explain the lack of niche segregation patterns. However, the narrow niches detected here go against the view that our species use generalist strategies, and at the same time the lack of segregation in trophic niche does not support a strategy mainly based on differences in food preferences (but see Arnán et al., 2019). Our results could be explained by the facilitation of ant species co-occurrence by constraints other than

resource availability. It is known that competitive outcomes are highly conditioned by environmental variation (Andersen, 2008; Chesson, 1994), and at the same time, limited activity periods could keep population sizes below the critical values above which biotic interactions play a major role. Moreover, top-down processes such as predation (by vertebrates and invertebrates) and parasitism could also decrease ant forager abundance and nest density (Cerdá et al., 2013; Lebrun and Feener, 2007), which facilitates temporally synchronous species co-occurrence due to a decrease in ant species interactions. Last, we cannot rule out the possibility that niche overlap might be higher when resources are more abundant due to a reduced interspecific competence.

According to the principle of limiting similarity (Macarthur and Levins, 1967), species with similar traits are not expected to coexist, at least when communities are mainly driven by competitive interactions. Indeed, several studies about ant communities have found that limiting similarity acts as a mechanism precluding the local coexistence of species with similar traits (Ellwood et al., 2016; Nipperess and Beattie, 2004). In fact, Silvestre et al. (own data unpublished) detected this pattern in the same study area among sampling plots, where ant communities presented strong functional divergence. However, our results suggest that competitive interactions are not the main drivers of the studied communities, given the non-segregation and overlap patterns observed along most of the gradient. In fact, if environmental conditions strongly filter community composition, positive associations of species with similar traits are expected across sites (Jackson et al., 1992).

Thus, if we are to understand how the set of study species coexist sharing niches without temporal or resource segregation, we need to consider the ways these species exploit the ecosystem's resources. Tradeoffs among ecological functions are common mechanisms allowing species

coexistence in communities (Kneitel and Chase, 2004) by promoting partitioning of resource exploitation (Tilman, 1994; Yurewicz, 2004). Two main types of tradeoffs have been described for ant assemblages: the dominance–discovery tradeoff (Fellers, 1987) and the dominance–thermal tolerance tradeoff (Cerdá et al. 1997, 1998; Bestelmeyer 2000; Lessard et al. 2009). The dominance–discovery tradeoff is based on the compromise between the degree of species behavioural dominance and the time needed to obtain the resource. Species capable of finding resources more quickly tend to be subordinate (low aggressiveness), while species that find resources slowly tend to be more aggressive, dominating and even monopolising a food resource. Thus, subordinate species may coexist with dominants by discovering and exploiting resources early until dominants displace them. The dominance–thermal tolerance tradeoff proposes that behaviourally dominant ant species can forage in a relatively narrow range of temperatures, while behaviourally subordinate species need to forage in a wider range of temperatures to avoid interactions with dominant ant species (Cerdá et al. 1998). Subordinate species may coexist with dominants by exploiting resources when conditions are beyond the critical temperature maximum for dominants. Last, we should note that ant species sometimes co-occurred in the same baits at the same time, where they tended to either segregate by accessing them from different sides of the Petri dishes, or to capture part of the bait and remove it. These behavioral responses promote local segregation and may partly explain the different exploitation of ecosystem resources (Grevé et al., 2019). Overall, we believe that future research in Mediterranean systems should combine the analysis of niche partitioning considering tradeoffs as possible mechanisms allowing coexistence among ant species, especially when overlapping or non-segregating niches are detected (Stuble et al. 2013, 2017).

5. Conclusions

In summary, we found no evidence of a major role for elevational gradients driving the ways in which Mediterranean ant communities apportion their niche. However, our study extends our understanding of the niche structure of ant assemblages, observing a general trend towards narrow, highly overlapping niches, particularly marked and intriguing at intermediate elevations. Although these results suggest a predominance of abiotic control in most of the gradient, they are not entirely conclusive regarding the role of biotic interactions. Thus, it is necessary to further explore the possible existence of mechanisms such as behavioural tradeoffs that allow the coexistence of species assemblages that coincide in their foraging periods without a clear segregation of trophic resources.

Author contributions

Declaration of authorship: JS and FMA conceived and designed the experiments. RA, MS and VH performed the experiments. MS and FMA curated the taxonomic database. JS, analyzed the data. JS, FMA and MS wrote the manuscript; other authors provided editorial advice.

Declaration of competing interest

None.

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Appendix A. Supplementary data

R code for main analyses:

CompetenciaNicho_hormigas-2019-07-19-AppendixR-v2.[html](#)

The raw data are publicly available at figshare:

- ant occurrences on baits: DOI 10.6084/m9.figshare.13246619-
- soil temperatures: DOI 10.6084/m9.figshare.13248752

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