Ant functional responses along environmental gradients

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<tr>
<td>Key-words:</td>
<td>biomes, climate, Formicidae, foraging strategy, functional composition, functional traits, productivity, worker size</td>
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Ant functional responses to the environment

Ant functional responses along environmental gradients

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ABSTRACT

- Understanding species distributions and diversity gradients is a central challenge in ecology and requires prior knowledge of the functional traits mediating species’ survival under particular environmental conditions. While the functional ecology of plants has been reasonably well explored, much less is known about that of animals. Ants are among the most diverse, abundant, and ecologically significant organisms on earth, and they perform a great variety of ecological functions.

- In this study, we analyze how the functional species traits present in ant communities vary along broad gradients in climate, productivity, and vegetation type in the southwestern Mediterranean.

- To this end, we compiled one of the largest animal databases to date: it contains information on 211 local ant communities (including eight climate variables, productivity, and vegetation type) and 124 ant species, for which 10 functional traits are described. We calculated two complementary functional trait community indices (‘trait average’ and ‘trait dissimilarity’) for each trait, and we analyzed how they varied along the three different gradients using generalized least squares (GLS) models that accounted for spatial autocorrelation.

- Our results show that productivity, vegetation type, and, to a lesser extent, each climate variable per se might play an important role in shaping the occurrence of functional species traits in ant communities. Among the climate variables, temperature and precipitation seasonality had a much higher influence on functional responses than their mean values, whose effects were almost lacking.
Our results suggest that strong relationships might exist between the abiotic environment and the distribution of functional traits among southwestern Mediterranean ant communities. This finding indicates that functional traits may modulate the responses of ant species to the environment. Since these traits act as the link between species distributions and the environment, they could potentially be used to predict community changes under future global change scenarios.

Keywords: biomes, climate, diet, Formicidae, foraging strategy, functional composition, functional traits, productivity, worker size
INTRODUCTION

Understanding the processes responsible for variation in species richness and community composition along gradients is a central challenge in ecology. Many studies suggest that the environment is a key factor driving such variation (e.g. Pausas & Austin 2001; Werner et al. 2007; Dunn et al. 2009). Although the link between the environment and species distributions or community composition has largely been addressed from a taxonomic or phylogenetic standpoint, the importance of using a functional approach has recently been underscored (McGill et al. 2006). This approach argues that by examining an organism’s functional traits and the way in which they relate to the environment (environmental filtering), a mechanistic and predictive framework for the study of species distribution patterns and coexistence can be constructed (McGill et al. 2006; Swenson & Weiser 2010). Thus, quantifying how functional traits relate to different environmental factors provides insight into the mechanisms governing species distributions; it is also a necessary step in assessing how ongoing environmental changes such as climate change may alter biological communities and ecosystem processes that are coupled with diversity (McGill et al. 2006; Pollock, Morris & Vesk 2012).

Most studies addressing the functional composition of communities have been carried out on plants (e.g. Díaz et al. 2007; Swenson & Weiser 2010; Pollock et al. 2012). In animals, these types of studies are scarce, probably due to the inherent difficulty of obtaining information on the functional traits of mobile organisms. Furthermore, of the few studies that have been published that link functional traits and species distributions in animals, most have been conducted on small scales and have considered a limited number of environmental variables and/or functional traits. There is therefore a need to analyze patterns of animal functional diversity along wide, variable
environmental gradients to provide insights into the trait-filtering that occurs along particular

gradients.

Ants are among the most diverse, abundant, and ecologically significant organisms on earth (Hölldobler & Wilson 1990). They can modify the abiotic and biotic properties of their environment by performing a variety of ecological functions (Hölldobler & Wilson 1990; Wardle et al. 2010; Zelikova, Sanders & Dunn 2011). Consequently, ants are considered to be crucial components of most terrestrial ecosystems (Hölldobler & Wilson 1990; Lach, Parr & Abbott 2010). As ant communities commonly vary in composition along environmental gradients (e.g. Sanders et al. 2007; Dunn et al. 2009; Arnan, Cerdá & Retana 2012), relationships between functional diversity and the environment are expected in most of the world’s principal terrestrial ecosystems.

In this study, we analyze how the functional traits found in ant communities vary along environmental gradients in climate, productivity, and vegetation type in the southwestern Mediterranean. The aim is to predict the distribution of ant communities on the basis of functional traits and their relationship with the abiotic environment. We used data from 211 ant communities that include a total of 124 ant species, and we generated a data set of 10 functional traits that are important in ant autecology and/or relate to ecosystem functioning. We believe that, to date, this database is the largest compiled for animals (or at least for insects) that includes a large number of species-specific functional traits from different communities across broad environmental gradients. We specifically ask: how do the functional traits of ant species respond to gradients of climate, productivity, and vegetation type?
MATERIAL AND METHODS

Ant community composition data

We assembled data from our own studies and most of the scientific articles and Ph.D. theses examining southwestern Mediterranean ant communities; only studies that contained species abundance or presence-absence data from single locations were used. We discarded highly disturbed and urbanized sites. Overall, the dataset consisted of 217 sites, of which 211 were included in the analyses (see Appendix S1); they spanned a latitudinal gradient running from approximately 36.74º to 43.66º N and from -7.12º to 4.98º W. These communities comprised a total of 133 ant species, of which 124 were considered in the analyses (see Appendix S1). We determined the latitude and longitude coordinates of all the sites, either directly when they were stated or indirectly based on the maps and information provided in the articles. We focused our analyses on presence-absence data because they are more comparable among sites than abundance data, which were measured in different ways (i.e. number of nests, individuals at baits, or individuals in pitfall traps) in different studies and were thus difficult to compare.

Ant trait data

We described each of the 124 species used in our analyses in terms of functional traits that have been recognized as being important in ant autecology and/or relating to ecosystem functioning (e.g. Hölldobler & Wilson 1990; Bihn, Gebauer & Brandl 2010; Lach et al. 2010; Arnan et al. 2012, 2013). Functional traits are defined as any morphological, physiological, or phenological features measurable at the individual level that affect individual performance (McGill et al. 2006; Violle et al. 2007). Ants are a unique group of organisms because they live in complex societies composed of a dozen to a million individuals. A colony is comparable to a superorganism since its
reproductive and somatic functions are performed by queens and workers, respectively (Wheeler 1913; Hölldobler & Wilson 2009). Although the superorganism metaphor has its limitations, it underscores that natural selection can occur at both the individual and the colony level (Keller 1995). Therefore, ant functional traits may be quantified at both the level of the individual worker and that of the colony. Classical studies of ant functional traits have focused on the morphological or physiological performance of individuals or colonies. In our study, in contrast, we examined a wider variety of individual- and colony-level functional traits, mainly life-history traits but also morphological and behavioral traits. Overall, we studied 10 functional traits, whose descriptions and functional significance are provided in Table 1. We used these traits because they are frequently examined in the literature and they are good proxy measures for ant species ecology. As in other functional diversity studies (e.g. Swenson & Weiser 2010; Arnan et al. 2012, 2013), functional traits were assumed to be species-specific and not demonstrate intersite variability. If such variation exists, then its omission from analyses would likely result in a bias towards weaker trait-climate relationships. Future work will be needed to explore variability in traits among sites and/or model its potential importance.

First, we gathered functional trait data from our own research records and via personal communication with different colleagues (Anna Alsina, Jordi Bosch, Raphaël Boulay, Soledad Carpintero, Valentín Cavia, Sebastià Cros, Xavier Espadaler, Paqui Ruano, and Alberto Tinaut). This initial database was then expanded by conducting an exhaustive search of public databases and the scientific literature. Overall, our literature review involved more than 1000 articles and 1300 search hours. A full list of the data sources utilized in this study is provided in Appendix S2. For details on how we completed gaps in the species-trait database, see Appendix S1.
Environmental gradient data

Climate

Climate data for the 211 sites included in our analyses came from the WorldClim database (http://www.worldclim.org/bioclim); we used rasters with the highest available resolution (30 arc-seconds). We obtained site-specific values for eight climate variables: mean annual temperature, maximum temperature, minimum temperature, temperature seasonality (standard deviation of monthly mean temperature), annual precipitation, precipitation in the wettest month, precipitation in the driest month, and precipitation seasonality (coefficient of variation of the monthly precipitation level). We also noted the altitude of each site. Since we found that several of these variables were highly correlated (Spearman’s r>0.7; Table S1), we retained only four: mean annual temperature, temperature seasonality, annual precipitation, and precipitation seasonality. In our correlational analyses, we took into account spatial autocorrelation within the data using the “Dutilleul” method in SAM (Rangel, Diniz-Filho & Bini 2006); this software program calculates the appropriate degrees of freedom given the observed level of non-independence in the data.

Productivity

We estimated productivity at each site using the remotely sensed normalized difference vegetation index (NDVI), which is commonly used by ecologists as a proxy for vegetation productivity (e.g. Petitorelli et al. 2005). First, we obtained monthly NDVI values from April to September from 2001 to 2009 (the only years for which data were available) from the USGS website (https://lpdaac.usgs.gov/products/modis_products_table/mod13q1). Although it would have been preferable to use NDVI data from the years during which the studies were carried out, these data were not available for most of the ant communities sampled; it is for this reason that we decided to use the average for the 2001-2009 time period for all the sites. We focused on the time period from
April to September because a) it limits large contrasts between sites with and without deciduous vegetation and b) it corresponds to the season when ants are active and thus reflects conditions outside the nest that might affect them. We computed mean NDVI values from April to June (NDVI\textsubscript{spring}) and from April to September (NDVI\textsubscript{spring+summer}) by averaging values across all years. Because the correlation between NDVI\textsubscript{spring} and NDVI\textsubscript{spring+summer} was very high (Pearson r=0.99, p<0.001), we included only the latter variable in our analyses. This variable was not highly correlated (i.e. Spearman’s r<0.7; Table S2) with any of the other climate variables, which underscores their independence.

**Vegetation type**

To evaluate whether vegetation type influences the distribution of functional traits on a large geographical scale, we assigned each plot to one of the six most common vegetation types found in the study region: grasslands, shrublands, open (=dehesa-like) woodland, sclerophyllous forests, conifer forests, and broadleaf forests. We conducted spatial generalized least squares (GLS) models (see below) to investigate how climate and productivity varied among the different vegetation types. We found that only temperature seasonality differed significantly (ANOVA table from GLS model: F=433.7, p<0.0001, df=5): open woodlands demonstrated higher temperature seasonality than did the other vegetation types, which did not differ from each other. Neither productivity (F=1.25, p=0.287, df=5) nor the other climate variables (annual mean temperature: F=0.3, p=0.904; annual precipitation: F=0.1, p=0.997; and precipitation seasonality: F=1.8, p=0.105) differed among vegetation types. Again, this finding underscores the independence of these factors.

**Data analyses**
We used two traditional indices that have been widely used in ecological research to statistically describe the functional trait composition of a given community: the ‘trait average’ ($\bar{X}$) index reveals the most common traits in a community, and the ‘trait dissimilarity’ (FD) index indicates the extent to which species within a community differ in their traits (Díaz et al. 2007; Ricotta & Moretti 2011; Arnan et al. 2013). The trait dissimilarity index is defined as the Rao quadratic diversity coefficient, which reflects the probability that two randomly chosen individuals in a community will be different. Rao’s Q ranges from 0 to the maximum value for the Simpson index of diversity, with higher values indicating more trait dissimilarity within the community. The Rao coefficient presents several desirable properties when describing the functional diversity of a community (see Botta-Dukat 2005).

These indices were computed for each functional trait using the dbFD function in the FD package in R (R Development Core Team 2010). The trait average and trait dissimilarity of a given community might reflect similar information and thus may not be fully independent, particularly in the case of categorical traits (Ricotta & Moretti 2011). Because trait averages and dissimilarities were highly correlated ($r>0.7$) for several traits (Table S3), we conducted further analyses using only the trait dissimilarity index for two binary traits (diurnality and individual foraging strategy), three ordinal traits (number of queens, number of nests, and colony foundation type) and one fuzzy-coded variable (percentage of seeds in the diet). Preliminary analyses showed that overall functional diversity (computed taking the 10 traits together) was significantly positively related to species richness ($\beta\pm SE=0.00\pm0.00; t=3.3; p=0.001$): sites with higher species richness also have higher functional diversity. However, since species richness only demonstrated a significant association with vegetation type ($F=3.4; p=0.006$), but not with climate or productivity (all $p>0.01$; Table S2), it was excluded from further analyses.
As there was likely to be a substantial amount of spatial autocorrelation in the distribution of traits across sites, we tested how the functional composition of ant communities responded to each of the three environmental gradients using GLS models. GLS models use simultaneous autoregression to estimate means. We conducted sets of tests where the functional indices ($\bar{X}$ and FD) for each trait were the response variables and the environmental gradient was the predictor variable. For example, we conducted a set of three models where the trait average for worker size was the response variable: 1) the climate model included annual mean temperature, temperature seasonality, annual precipitation, and precipitation seasonality as predictor variables; 2) the productivity model included NDVI$_{spring+summer}$ as the predictor variable; and 3) the vegetation type model included the vegetation type category as the predictor variable. GLS models were carried out using the gls function in the nlme package in R. Due to the large number of tests we conducted, we applied the Bonferroni correction. The alpha level for test acceptance was thus established at $p<0.00076$ ($0.05/66$) to avoid finding significant effects by chance.

Little is known in animals, and even less in insects, about species-level trade-offs among functional traits. Indeed, it may be that trait patterns at the community level arise from trade-offs at the species level, which would lead to erroneous interpretations. However, the existence of correlations between traits at the community level does not necessarily imply that correlations exist at the species level, because independent traits (those not correlated at the species level) might also be influenced by the same environmental gradients (Ackerley et al. 2002). Consequently, in order to be conservative and check for potential trade-offs among functional traits at the community level, we calculated Spearman rank correlation coefficients for the trait
averages and dissimilarity values we had estimated. Within our large pool of traits, only a small number of functional traits were highly correlated (r>0.7) at the community level (Table S4).

RESULTS

Based on our results, all three environmental gradients appear to strongly filter ant species based on their functional traits (Table 2; Table S5). Variance in most trait averages or dissimilarities could be explained by at least one of gradients. However, none of the environmental gradients explained average in the percentage of seeds in the diet, and dissimilarity in worker size, worker polymorphism, behavioral dominance, utilization of a group and collective foraging strategy, and colony size. Most traits were influenced by more than one gradient, but variance in several functional traits was predicted uniquely by climate (the average worker size) or biome (the percentage of liquid food in the diet, the average colony size, and the dissimilarity in diurnality). None of the variance in the trait indices was explained exclusively by plant productivity.

*Ant functional responses to climate*

Among the trait indices that were explained by at least one of the environmental gradients, the averages of four traits (the percentage of behaviorally dominant species in the community, the percentage of liquid food in the diet, the percentage of collectively foraging species, and colony size) and dissimilarity in diurnality and the percentage of insects in the diet were not predicted by any of the climate variables (Table 2; Table S5).
Precipitation seasonality was the climate variable that influenced the largest number of functional trait indices (Table 2). Dissimilarity in the percentage of individually and collectively foraging species, the number of queens, the number of nests per colony, and colony founding types increased significantly as precipitation seasonality increased. In contrast, average worker polymorphism, and the average percentage of group foraging species decreased significantly as precipitation seasonality increased. Average worker size and worker polymorphism (Figure 1a) as well as dissimilarity in the percentage of liquid foods in the diet increased significantly as temperature seasonality increased (Table 2). Mean temperature did not influence any of the functional trait indices, while annual precipitation only negatively influenced dissimilarity in the percentage of seeds in the diet (Table 2; Figure 1b).

**Ant functional responses to productivity**

The functional indices of a large number of traits were explained by the productivity gradient (Table 2; Table S5). As productivity increased, so did the average percentage of group foraging species; in contrast, the average percentage of behaviorally dominant species (Figure 1c) and the average percentage of collectively foraging species decreased. Furthermore, increased productivity was associated with decreased dissimilarity in the percentage of each kind of food in the diet, the percentage of individually foraging species, the number of queens, the number of nests and the colony foundation type.

**Ant functional responses to vegetation type**
The vegetation type gradient was also a good predictor of patterns of ant functional diversity because it explained a significant amount of the variance in a large number of trait averages and dissimilarities (Table 2; Table S5). We observed four different patterns of trait composition across the six Mediterranean vegetation types (Figure 2): a) dissimilarity in the percentage of seeds, insects, and liquid foods in the diet and the number of queens differed between forests (broadleaf, sclerophyllous, and conifer) and open habitats (shrubland, dehesa, and grassland) (Figure 2a); b) dissimilarity in diurnality and colony foundation type differed somewhat according to forest type (conifer vs. broadleaf and sclerophyllous), but was similar across the three open habitats (Figure 2b); c) the average percentage of collectively foraging species, the average percentage of liquid foods in the diet, and average colony size were different in broadleaf forests compared to the other two forest types, but broadleaf forest values resembled those of the three open habitats (Figure 2c); and d) the average percentage of behaviorally dominant species, the average percentage of group foraging species, and trait dissimilarity in nest number differed between shrublands and the other two open habitats, but their values were similar across the three forest types (Figure 2d). The other trait indices did not differ among vegetation types (Table 2; Table S5).

DISCUSSION

In this study, we report that a strong relationship may exist between the abiotic environment and the distribution of functional traits across southwestern Mediterranean ant communities. Although climate conditions have been widely considered to be key determinants of species distribution patterns at a global scale (e.g. Gaston 1996; Pausas & Austin 2001; Hawkins et al. 2007; Dunn et al. 2009), we found that productivity and vegetation type did a better job of explaining ant functional responses than did each climate variable per se in our regional context.
Based on the climate variables we examined, it is clear that seasonality has a stronger influence on ant functional responses than do average temperature and precipitation. In contrast to the latter variables, seasonality may serve as a better indicator of resource diversity and availability. For instance, greater seasonality may indicate that a more diverse range of resources with varying availabilities is present over the course of the year; consequently, in more seasonal areas, ant species may be able to exploit a greater diversity of resources, leading to more diverse exploitation strategies. Precipitation seasonality accounted for the most variance in trait averages and dissimilarities. Although other works suggest that a strong relationship exists between temperature and ant functional responses (Diamond et al. 2012; Stuble et al. 2013), our results intimate that temperature seasonality has a more limited influence on ant functional responses. Instead, it may be that humidity is more constraining for ants than temperature (Menke & Holway 2006). However, since these works only examined thermal tolerance, not desiccation resistance, this hypothesis is difficult to evaluate. More interestingly, we found that only traits related to resource exploitation, such as worker size, polymorphism, and diet, responded to differences in temperature seasonality. Worker size may respond to temperature seasonality because, in insects in general, greater size might provide greater protection against starvation or desiccation (Chown & Gaston 1999). Furthermore, larger animals have higher levels of energy efficiency (Ellington 1999), which is an advantage in environments where low temperatures, bad weather, and starvation can be a problem. Expanding on this logic, greater worker polymorphism could be advantageous in environments characterized by varying temperatures since ant species could use within-colony variability in worker size to respond more easily to temperature fluctuations, thus lengthening the overall period of external activity and enhancing colony success (Cerdá & Retana 1997). Finally, greater temperature seasonality may generate more diverse ant diets through its action on annual
food production patterns. For instance, more seasonal environments may vary more in resource availability across the seasons. Such environments could support generalist species as well as species that specialize more or less on liquid foods and thus promote species coexistence and dietary diversity.

We found that the temperature gradient did not influence any of the ant functional responses. Contrarily, Reymond and collaborators (in press) recently found a decrease in ant functional diversity with decreasing temperature along an altitudinal gradient in the Swiss Alps. Contrasts in temperature along this gradient are probably greater than those reported in our study. Our results also suggest that communities in the wettest areas were characterized by species that consumed a lower percentage of seeds. Because more species that consumed fewer seeds were present in these communities, community dissimilarity in seed-eating was decreased. In contrast, communities in drier areas contained species that varied much more in their seed-eating habits. These overall dietary patterns might reflect the changes in food resource production that occur as precipitation changes.

However, functional traits responded much more to differences in productivity and vegetation than to differences in individual climate variables. Plant productivity influenced a large number of functional traits. The negative correlation between productivity and trait dissimilarity found for many traits suggests that functional diversity declined in the most productive areas. This result is striking since ecological theory predicts that in milder and more productive environments, species should display differentiated strategies that reduce competition for more diverse resources (Pianka 1970) and, as environmental severity increases, the number of possible successful strategies should be greatly reduced (Weiher & Keddy 1999; Swenson et al. 2012). The pattern we observed may
have a somewhat complex explanation. First, in the most productive areas, where conditions are
the most favorable and resources are abundant, dominant species are likely to become more
abundant and then even more dominant, resulting in the elimination of other species, mainly other
dominants. Second, gaps exist between the foraging areas of these hyperdominant species, and
these gaps may be occupied by many subordinate species (Savolainen, Vepsäläinen &
Wuorenrinne 1989; Arnan, Gaucherel & Andersen 2011). As a result, species pools in the most
productive areas would include a few highly dominant species and many subordinate species.
Since subordinate species within the same local community are likely to have similar functional
traits (Arnan et al. 2012), functional diversity would be expected to be lower in more productive
areas than in less productive areas. This explanation is supported by the fact that the percentage of
behaviorally dominant species in the community decreased with increasing productivity.

In the most productive areas, the dissimilarity in diet-related traits declined, which means that
these areas contain more specialists, ant species that more exclusively consume insects or liquid
foods. In contrast, we found that more generalist species occurred in less productive areas: the
percentage of seeds in the diet was higher in less productive areas than in more productive areas
even though the percentage of liquid foods and insects remained the same. This shift in species
dietary patterns is probably related to food production patterns along the productivity gradient; in
the most productive areas, liquid foods (nectar and honeydew) may be more readily available
(Dixon 1975), while the seeds preferred by ants may be less readily available (Wolff & Debussche
1999). In fact, since the dissimilarities in the percentages of insects and liquid foods in the diet are
highly correlated (Table S4), the functional response related to the percentage of insects in the diet
that is observed along this gradient may potentially be spurious. Foraging strategies were also
greatly influenced by productivity: as productivity increased, the percentage of collectively and
individually foraging species declined while the percentage of group foraging species climbed. This finding suggests that vegetative structure might influence ant foraging systems (Fewell 1988), assuming that less productive areas account for less vegetative cover. Our results concur with those from a study that examined intercolonial differences in the *Pogonomyrmex occidentalis* foraging system and their relationship with vegetative cover (Fewell 1988). The collective foraging strategy was found to be more common in more open areas. This strategy seems to be more efficient in areas with less vegetative cover, which could have led species that occur in more open habitats to develop this strategy. The relationship between the percentage of group foragers and vegetation may be somewhat spurious, since the percentages of group and collectively foraging species were negatively correlated at the community level (Table S4). Moreover, in less productive areas, the increase in the percentage of monogynous species might be related to colonization processes because monogynous queens produce larger offspring, which may be better equipped to survive and colonize harsh environments (Ross & Keller 1995). Meanwhile, independent colony founding provides dispersal advantages at long distances compared with dependent colony-founding strategies (Amor et al. 2011), which could indicate that species with this kind of dispersal strategy are more likely to colonize unproductive areas. Unfortunately, we do not have a clear explanation for the relationship between monodomy and plant productivity. Across the six representative Mediterranean vegetation types that were included in this study, the ecological value of many ant functional traits in open versus closed habitats was made clear (with some exceptions). Functional diversity increased in open habitats, as reflected by the finding that dissimilarity in most traits was higher in these areas. This result clearly fits the diversity pattern previously described in Mediterranean ant communities (Retana & Cerdá 2000): behaviorally dominant and subordinate species co-occur in open habitats and clearly differ in resource
exploitation and temporal activity patterns (Arnan et al. 2012). In the Mediterranean, environmental conditions (mainly temperature) in open habitats demonstrate daily and seasonal contrasts. As a result, species have developed different strategies to cope with that variability (Retana & Cerdá 2000), and as a result, functional diversity has increased. Meanwhile (and assuming that open habitats are characterized by less plant cover), habitats with more vegetative cover and moderate environmental conditions, such as forests, contain species that are more functionally similar (Arnan et al. 2012), and functional diversity has consequently been reduced. The percentage of behaviorally dominant species was higher in open than in closed habitat types. Colony size was also larger in open habitats, probably due to the small colony size of most species that are closely associated with dense vegetation (Arnan et al. 2013). Vegetation type also influenced species dietary patterns and foraging strategies. Past studies have observed that sugar-producing insects are more abundant in forests than in open habitats (Dixon 1975) and that the production of the seeds preferred by granivorous ants is usually higher in open habitats (Wolff & Debussche 1999). We found that the percentage of seeds and liquid foods in the diet increased and decreased, respectively, in open habitats. Furthermore, as previously mentioned, different foraging strategies have been found to be differentially influenced by vegetative structure (Fewell 1988); we found that, in open habitats, the percentage of group foraging species decreased, while the percentage of collectively foraging species increased. However, these functional responses may be somewhat blurred by the negative correlation between the percentages of group and collectively foraging species, as well as by the positive correlation between the percentage of collectively foraging species and colony size at the community level (Table S4).

Concluding remarks
Using one of the largest databases established for animals to date, which contained information on a set of 10 functional traits for 124 ant species across 211 local communities, we found that ant communities showed a strong functional response across different environmental gradients in the southwestern Mediterranean. This finding clearly underscores that functional traits might modulate the responses of ant species to environmental gradients. Since our work was limited to the southwestern Mediterranean region, we suggest that functional composition modulation by environmental gradients might be even much higher if considering a larger geographic range. Our results provide insights into the types of traits that are most revealing when analyzing ant functional responses to variation in climate, productivity and vegetation type. Since species traits act as the link between species distributions and the environment, they could be used to predict how communities will change under future global change scenarios (Silva & Brandao 2010; Diamond et al. 2011; Angert et al. 2011; Pollock et al. 2012). Interestingly, the functional responses of ant communities to each of these gradients involve sets of traits that might impact ecosystem processes. In particular, traits related to resource exploitation are implicated, all of which might be considered to be measures of the impact that ants can have on ecosystem functioning. For instance, worker size relates to metabolic characteristics (Weber 1938) and determines the quantity of resources consumed (Bihn et al. 2010); worker polymorphism relates to the breadth of functional roles performed by colonies (Mertl & Traniello 2009); diet composition relates to the kind and quantity of resources exploited; and foraging strategy, diurnality, and behavioral dominance are directly related to the relative impact of food resource exploitation. As a consequence of the strong relationships between many of these traits and ecosystem processes, the functional diversity patterns that we detected here likely translate into important differences in ecosystem functioning. Further studies should thus clarify how changes in the functional diversity of natural ant assemblages change ecosystem functioning along environmental gradients.
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Table 1. Description of the ant traits examined in this study and their functional significance.

<table>
<thead>
<tr>
<th>Trait</th>
<th>Functional significance</th>
<th>Source</th>
<th>Data type</th>
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<tr>
<td>Worker size</td>
<td>Strongly correlates with many physiological, ecological, and life history traits such as resource use</td>
<td>Kaspari &amp; Weiser 1999</td>
<td>Continuous</td>
<td>Worker body size from the tip of mandibles to tip of the gaster (mm)</td>
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<tr>
<td>Worker polymorphism</td>
<td>Relates to the breath of functional roles performed by colony</td>
<td>Mertl &amp; Traniello 2009</td>
<td>Continuous</td>
<td>Mean worker size divided by the range of worker size</td>
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<td>Diurnality</td>
<td>Indicates when individuals are actively foraging</td>
<td>Hölldobler &amp; Wilson 1990</td>
<td>Binary</td>
<td>(0) Non-strictly diurnal; (1) Strictly diurnal</td>
</tr>
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<td>Behavioral dominance</td>
<td>Refers to the influence of one species on another when acquiring food resources and thus the ability to gain access to food resources</td>
<td>Arnan et al. 2012</td>
<td>Binary</td>
<td>(0) Subordinate; (1) Dominant</td>
</tr>
<tr>
<td>Diet: Seed-eating, Insect-eating, and Liquid-food eating</td>
<td>Refers to the type and quantity of food resources a species exploits</td>
<td>Hölldobler &amp; Wilson 1990</td>
<td>Fuzzy-coded</td>
<td>0-1 (for each of the three categories)</td>
</tr>
<tr>
<td>Foraging strategy: Individual, Group, and Collective (**)</td>
<td>Refers to how a species searches for and exploits food resources, which plays an important role in the ability to survive and reproduce</td>
<td>Traniello 1989</td>
<td>Binary</td>
<td>0-1 (for each of the three categories)</td>
</tr>
<tr>
<td>Colony size</td>
<td>The ecological advantages of large colony size include increased defense, homeostasis, work efficiency, and a greater ability to modify the surrounding environment</td>
<td>Bourke 1999</td>
<td>Continuous</td>
<td>Mean number of workers per colony</td>
</tr>
<tr>
<td>Number of queens</td>
<td>Influences a wide range of species characteristics, including group size, worker size, growth rate, competitive ability, and efficiency</td>
<td>Keller 1995; Ross &amp; Keller 1995; Rosset &amp; Chapuisat 2007</td>
<td>Ordinal</td>
<td>(0) Monogyny; (0.5) Both monogyny and polygyny; (1) Polygyny</td>
</tr>
<tr>
<td>Number of nests</td>
<td>Polydomy confers a great competitive advantage relative to monodomy</td>
<td>McGlynn 1999</td>
<td>Ordinal</td>
<td>(0) Monodomy; (0.5) Both monodomy and polydomy; (1) Polydomy</td>
</tr>
<tr>
<td>Colony foundation type</td>
<td>Independent colony foundation (ICF) strategies provide long-distance dispersal advantages relative to dependent colony foundation (DCF) strategies</td>
<td>Amor et al. 2011</td>
<td>Ordinal</td>
<td>(0) DCF; (0.5) Both DCF and ICF; (1) ICF</td>
</tr>
</tbody>
</table>

*Variable categories were coded using a fuzzy-coding technique. Scores ranged from ‘0’ (no consumption of a food resource) to ‘1’ (frequent consumption of a food resource).

**Individual: workers of these species are not able to communicate their nestmates the presence of a food source, they forage and collect food individually; Group: workers of these species are able to communicate and guide a low number of nestmates to a previously discovered food source; Collective: workers of these species follow "anonymous" chemical signals provided by other nestmates to exploit a food source, they can organize mass-recruitment or temporal or permanent trails to the food source.
Table 2. Significant effects of the environmental gradients on the trait average ($\bar{X}$) and dissimilarity (FD) found using the GLS models. Arrows indicate the direction of the effects. Significance level of p<0.00076 after the Bonferroni correction. * Note that the trait dissimilarity of these traits is highly correlated with the trait average of the same traits; for instance, a negative effect on trait dissimilarity corresponds in turn to a negative effect on trait average, and vice versa.

<table>
<thead>
<tr>
<th>Functional trait</th>
<th>Climate gradient</th>
<th>Productivity gradient</th>
<th>Vegetation type gradient</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean temperature</td>
<td>Temperature seasonality</td>
<td>Precipitation</td>
</tr>
<tr>
<td>Trait average</td>
<td>-</td>
<td>$\uparrow$</td>
<td>-</td>
</tr>
<tr>
<td>Worker size</td>
<td>-</td>
<td>$\uparrow$</td>
<td>-</td>
</tr>
<tr>
<td>Worker polymorphism</td>
<td>-</td>
<td>$\uparrow$</td>
<td>-</td>
</tr>
<tr>
<td>Behavioral dominance (dominants)</td>
<td>-</td>
<td>$\uparrow$</td>
<td>-</td>
</tr>
<tr>
<td>Food resources - insects</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Food resources - liquid food</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Foraging strategy - group</td>
<td>-</td>
<td>-</td>
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</tr>
<tr>
<td>Foraging strategy - collective</td>
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<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Trait dissimilarity</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Worker size</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Worker polymorphism</td>
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<td>-</td>
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</tr>
<tr>
<td>Diurnality*</td>
<td>-</td>
<td>-</td>
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</tr>
<tr>
<td>Behavioral dominance</td>
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<td>-</td>
</tr>
<tr>
<td>Food resources - seeds*</td>
<td>-</td>
<td>-</td>
<td>$\downarrow$</td>
</tr>
<tr>
<td>Food resources - insects</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Food resources – liquid food</td>
<td>-</td>
<td>$\uparrow$</td>
<td>-</td>
</tr>
<tr>
<td>Foraging strategy - individual*</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Foraging strategy - group</td>
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<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Foraging strategy - collective</td>
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<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Colony size</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Number of queens*</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Number of nests*</td>
<td>-</td>
<td>-</td>
<td>$\uparrow$</td>
</tr>
<tr>
<td>Colony foundation type*</td>
<td>-</td>
<td>$\uparrow$</td>
<td>$\uparrow$</td>
</tr>
</tbody>
</table>
Figure legends

Figure 1. Some examples of significant relationships between functional trait indices and climate and productivity. Relationship between a) average worker polymorphism and temperature seasonality, b) dissimilarity in the % of seeds in the diet and precipitation, and c) the percentage of behaviorally dominant species and productivity.

Figure 2. A comparison of the trait averages and dissimilarities (FD) that differed significantly among the six vegetation types considered. Boxplots are ordered according to the four general patterns (see results; a-d). The different letters above the boxplots indicate the significant differences among vegetation types found using multiple contrasts of the GLS models. Abbreviations on the x-axis are: BR, broadleaf forest; SC, sclerophyllous forest; CO, conifer forest; SH, shrubland; DE, dehesa; and GR, grassland.
Figure 1
Figure 2
Appendix S1. Details on how we completed gaps in the species-trait database.

The information found in the literature for most *Solenopsis* species was very scarce and we were not able to complete the traits of these species. For this reason, we did not consider them in the analyses and the six localities with an overall abundance of *Solenopsis* spp. > 5% were eliminated. For species from which information was scarce because that have been recently described from another species or that are rare but similar to other more common species, we used the same traits of these well-known species. This applies to the following pairs of unknown/well known species: *Camponotus amaurus/Camponotus foreli, Camponotus figaro/Camponotus piceus, Lasius lasioides/Lasius alienus, Goniomma thoracicum/Goniomma hispanicum, Messor maroccanus/Messor bouvieri, Myrmica spinosior/Myrmica sabuleti, Stenamma orousetti/Stenamma westwoodi, Tetramorium impurum/Tetramorium caespitum, Tetramorium hispanicum/Tetramorium ruginode, Tetramorium fortet/Tetramorium ruginode and Tetramorium punicum/Tetramorium semilaeve*. For one trait from which we did not have information (colony founding of *Aphaenogaster dulcinea*) we assigned the value of the closest species of the genera. We did not complete another trait, that of colony founding of *Proformica ferreri* and *Proformica nasuta*, because their social structure was very different to that of the species of the genus from which this information was available. Similarly, we did not complete the values of colony size of *Messor celiæ* and *Messor hispanicus*. Finally, there were two species that were not classified in the original literature sources. In the case of *Oxyopomyrmex* sp. from five sites we assigned the values of *O. saulcyi* because the distribution area of this species includes all these sites and no other species of the genus does. In the case of *Temnothorax* sp. from two sites, different species of the genus could match this location and for this species we applied the most common trait values of the species of the genus.
Appendix S2. List of the literature sources and online databases from which functional trait data were obtained.

Worker size and worker polymorphism


Hormigas ibéricas 2012. [http://www.hormigas.org](http://www.hormigas.org)


**Diurnality**


Behavioral dominance


**Diet**


Hormigas ibéricas 2012. [http://www.hormigas.org](http://www.hormigas.org)


Wiki La Marabunta 2012. http://www.lamarabunta.org/LaMarabuntawiki/

Foraging strategy


Colony size


Wiki La Marabunta 2012. http://www.lamarabunta.org/LaMarabuntawiki/


Number of queens


Wiki La Marabunta 2012. http://www.lamarabunta.org/LaMarabuntawiki/


**Number of nests**


Featured creatures. Entomology and Nematology. [http://entnemdept.ufl.edu/creatures/urban/ants/](http://entnemdept.ufl.edu/creatures/urban/ants/)

Hormigas ibéricas 2012. [http://www.hormigas.org](http://www.hormigas.org)

Lasius brunneus una plaga del corcho en España 2012. [http://www.creaf.uab.es/xeg/brunneus/espanol/]


Colony foundation type


Wiki La Marabunta 2012. [http://www.lamarabunta.org/LaMarabuntawiki/](http://www.lamarabunta.org/LaMarabuntawiki/)
Table S1. The Spearman rank correlation coefficients for climate variables. Abbreviations: Tmean, mean annual temperature; Tmin, minimum temperature; Tmax, maximum temperature; Tseas, temperature seasonality; Precip, Precipitation; Precip. Dry, precipitation in the driest month; Precip. Wet, precipitation in the wettest month; Precip. Seas, precipitation seasonality. Spatial autocorrelation was considered by reducing the number of degrees of freedom. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; in bold, $r > 0.7$ and at least $p < 0.05$.

<table>
<thead>
<tr>
<th></th>
<th>Tmean</th>
<th>Tmin</th>
<th>Tmax</th>
<th>Tseas</th>
<th>Precip</th>
<th>Precip. Dry</th>
<th>Precip. Wet</th>
<th>Precip. Seas</th>
<th>Altitude</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tmean</td>
<td>1</td>
<td>0.90***</td>
<td>0.48***</td>
<td>-0.54*</td>
<td>-0.50***</td>
<td>-0.51***</td>
<td>-0.18**</td>
<td>0.50*</td>
<td>-0.76***</td>
</tr>
<tr>
<td>Tmin</td>
<td>1</td>
<td>0.15***</td>
<td>-0.76***</td>
<td>-0.22***</td>
<td>-0.23**</td>
<td>0.00</td>
<td>0.27*</td>
<td>-0.78***</td>
<td></td>
</tr>
<tr>
<td>Tmax</td>
<td>1</td>
<td>0.30</td>
<td>-0.80***</td>
<td>-0.89**</td>
<td>-0.54**</td>
<td>0.81</td>
<td>-0.24*</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tseas</td>
<td>1</td>
<td>-0.14</td>
<td>-0.13</td>
<td>-0.33*</td>
<td>0.02</td>
<td>0.58***</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Precip</td>
<td>1</td>
<td>0.82***</td>
<td>0.78***</td>
<td>-0.69</td>
<td>0.31***</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Precip. Dry</td>
<td>1</td>
<td>0.51*</td>
<td>-0.93</td>
<td>0.32</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Precip. Wet</td>
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<td>-0.38</td>
<td>-0.07</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Precip. Seas</td>
<td>1</td>
<td>0.28</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Altitude</td>
<td>1</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table S2. A) The Spearman rank correlation coefficients between NDVI<sub>spring+summer</sub> and climate variables. Spatial autocorrelation was considered by reducing the number of degrees of freedom. * P < 0.05; ** P < 0.01; *** P < 0.001. B) The t statistics and significance (p) from the GLS models conducted to analyse the relationship between species richness and climate variables and NDVI<sub>spring+summer</sub>. Abbreviations: Tmean, mean annual temperature; Tseas, temperature seasonality; Precip, Precipitation; and Precip. Seas, precipitation seasonality.

A)

<table>
<thead>
<tr>
<th>NDVI&lt;sub&gt;spring+summer&lt;/sub&gt;</th>
<th>Tmean</th>
<th>Tseas</th>
<th>Precip</th>
<th>Precip. Seas</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>-0.23</td>
<td>-0.30</td>
<td>0.64*</td>
<td>-0.57</td>
</tr>
</tbody>
</table>

B)

<table>
<thead>
<tr>
<th>Species richness</th>
<th>Tmean</th>
<th>Tseas</th>
<th>Precip</th>
<th>Precip. Seas</th>
<th>NDVI&lt;sub&gt;spring+summer&lt;/sub&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>t</td>
<td>p</td>
<td>t</td>
<td>p</td>
<td>t</td>
</tr>
<tr>
<td>Species richness</td>
<td>-0.56</td>
<td>0.575</td>
<td>1.96</td>
<td>0.051</td>
<td>-0.31</td>
</tr>
<tr>
<td></td>
<td>0.756</td>
<td>0.08</td>
<td>0.938</td>
<td>1.84</td>
<td>0.066</td>
</tr>
</tbody>
</table>
**Table S3.** The Spearman correlation coefficients for trait averages and dissimilarities. For categorical traits, the reference category used in the analysis is given in parentheses. Spatial autocorrelation was taken into account by reducing the number of degrees of freedom. * Indicates $P < 0.05$; in bold, $r > 0.7$.

<table>
<thead>
<tr>
<th>Trait</th>
<th>Data type</th>
<th>Spearman’s r</th>
</tr>
</thead>
<tbody>
<tr>
<td>Colony size</td>
<td>Quantitative</td>
<td>$r = -0.366; p &lt; 0.001$</td>
</tr>
<tr>
<td>Number of queens (polygyny)</td>
<td>Ordinal</td>
<td>$r = 0.868; p &lt; 0.001$</td>
</tr>
<tr>
<td>Number of nests (polydomy)</td>
<td>Ordinal</td>
<td>$r = 0.938; p &lt; 0.001$</td>
</tr>
<tr>
<td>Worker size</td>
<td>Quantitative</td>
<td>$r = 0.609; p &lt; 0.001$</td>
</tr>
<tr>
<td>Worker polymorphism</td>
<td>Quantitative</td>
<td>$r = 0.446; p &lt; 0.001$</td>
</tr>
<tr>
<td>Diurnality (strictly diurnal)</td>
<td>Binary</td>
<td>$r = 0.970; p &lt; 0.001$</td>
</tr>
<tr>
<td>Behavioral dominance (dominant)</td>
<td>Binary</td>
<td>$r = 0.298; p &lt; 0.001$</td>
</tr>
<tr>
<td>Diet - Seed-eating</td>
<td>Fuzzy-coded</td>
<td>$r = 0.941; p &lt; 0.001$</td>
</tr>
<tr>
<td>Diet - Insect-eating</td>
<td>Fuzzy-coded</td>
<td>$r = -0.044; p = 0.631$</td>
</tr>
<tr>
<td>Diet - Liquid food-eating</td>
<td>Fuzzy-coded</td>
<td>$r = -0.419; p = 0.010$</td>
</tr>
<tr>
<td>For. strategy – individual</td>
<td>Binary</td>
<td>$r = 1; p &lt; 0.001$</td>
</tr>
<tr>
<td>For. strategy – group</td>
<td>Binary</td>
<td>$r = -0.516; p = 0.214$</td>
</tr>
<tr>
<td>For. strategy - collective</td>
<td>Binary</td>
<td>$r = 0.312; p = 0.016$</td>
</tr>
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<td>Colony foundation type (ICF)</td>
<td>Ordinal</td>
<td>$r = -0.858; p &lt; 0.001$</td>
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</table>
Table S4. The Spearman rank correlation coefficients for the trait averages and the trait dissimilarities at the community level for the different functional traits considered in the study. Abbreviations: WS, worker size; WP, worker polymorphism; Diurn., Diurnality; Dom., dominance; pSeeds, proportion of seeds in diet; pInsects, proportion of insects in diet; pLF, proportion of liquid foods in diet; FSind, individual foraging strategy; FSgr, group foraging strategy; FScol, collective foraging strategy; CS, colony size; NQ, number of queens; NN, number of nests; CFT, colony foundation type. Spatial autocorrelation was considered by reducing the number of degrees of freedom. * P < 0.05; ** P < 0.01; *** P < 0.001; in bold, r>0.7; in grey, correlations between those traits that were significantly affected at the same time by any of the environmental gradients.

<table>
<thead>
<tr>
<th>Trait average</th>
<th>WS</th>
<th>WP</th>
<th>Dom.</th>
<th>pInsects</th>
<th>pLF</th>
<th>FSgr</th>
<th>FScol</th>
<th>CS</th>
</tr>
</thead>
<tbody>
<tr>
<td>WS</td>
<td>1</td>
<td>0.50***</td>
<td>0.25</td>
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<td>-0.22</td>
<td>0.02</td>
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<tr>
<td>WP</td>
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<td>-0.10</td>
<td>-0.09</td>
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<tr>
<td>Dom.</td>
<td></td>
<td></td>
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<td>-0.22*</td>
<td>-0.16</td>
<td>-0.32**</td>
<td>0.42***</td>
<td>0.63***</td>
</tr>
<tr>
<td>pInsects</td>
<td></td>
<td></td>
<td></td>
<td>1</td>
<td>-0.40***</td>
<td>-0.15</td>
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<td>0.01</td>
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<tr>
<td>pLF</td>
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<td></td>
<td></td>
<td>1</td>
<td>0.45**</td>
<td>-0.34*</td>
<td>-0.26*</td>
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<td>FSgr</td>
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</tr>
<tr>
<td>Trait dissimilarity</td>
<td>WS</td>
<td>WP</td>
<td>Diurn.</td>
<td>Dom.</td>
<td>pSeeds</td>
<td>pInsects</td>
<td>pLF</td>
<td>FSind</td>
</tr>
<tr>
<td>---------------------</td>
<td>------</td>
<td>------</td>
<td>--------</td>
<td>-------</td>
<td>--------</td>
<td>----------</td>
<td>--------</td>
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</tr>
<tr>
<td>WS</td>
<td>1</td>
<td>0.63***</td>
<td>0.03**</td>
<td>0.21***</td>
<td>0.14</td>
<td>0.19*</td>
<td>0.22**</td>
<td>0.03</td>
</tr>
<tr>
<td>WP</td>
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<td>0.06**</td>
<td>0.24**</td>
<td>0.37***</td>
<td>0.33***</td>
<td>0.34***</td>
<td>-0.01</td>
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<td>0.34**</td>
<td>0.43***</td>
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<td>0.40**</td>
<td>0.05**</td>
<td>0.03</td>
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<tr>
<td>Dom.</td>
<td>1</td>
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<td>0.30***</td>
<td>0.22</td>
<td>0.20*</td>
<td>0.25***</td>
<td>0.17***</td>
<td>0.06**</td>
</tr>
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<td>pSeeds</td>
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<td>0.58***</td>
<td>0.66***</td>
<td>0.32***</td>
<td>0.22**</td>
<td>0.16</td>
<td>0.01</td>
<td>0.21</td>
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<td>pInsects</td>
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<td>0.51***</td>
<td>0.14*</td>
<td>0.13</td>
<td>-0.17*</td>
<td>-0.39**</td>
<td>-0.34*</td>
</tr>
<tr>
<td>pLF</td>
<td>1</td>
<td>0.17*</td>
<td>0.14*</td>
<td>0.14*</td>
<td>-0.34***</td>
<td>0.40*</td>
<td>0.31*</td>
<td>0.50***</td>
</tr>
<tr>
<td>FSind</td>
<td>1</td>
<td>0.12*</td>
<td>0.25</td>
<td>0.24*</td>
<td>0.01</td>
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<td>0.17*</td>
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Table S5. Statistical output from the GLS models analyzing the effect of different environmental gradients (climate, productivity, and vegetation type) on ant functional diversity based on 10 functional traits. In bold, statistically significant differences (p<0.00076) after the Bonferroni correction.

<table>
<thead>
<tr>
<th>TRAIT AVERAGE</th>
<th>Climate gradients</th>
<th>Productivity gradient</th>
<th>Vegetation type gradient</th>
</tr>
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<tbody>
<tr>
<td>Functional trait</td>
<td>Mean temperature</td>
<td>Temperature seasonality</td>
<td>Precipitation</td>
</tr>
<tr>
<td>Worker size</td>
<td>t=1.13, p=0.2613</td>
<td>t=3.51, \textbf{p=0.0005}</td>
<td>t=2.11, p=0.0365</td>
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<tr>
<td>Worker polymorphism</td>
<td>t=3.31, p=0.0011</td>
<td>t=4.78, \textbf{p&lt;0.0001}</td>
<td>t=1.67, p=0.0955</td>
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<tr>
<td>Behavioral dominance (dominants)</td>
<td>t=1.32, p=0.1870</td>
<td>t=2.04, p=0.0424</td>
<td>t=0.47, p=0.6392</td>
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<tr>
<td>Food resources - insects</td>
<td>t=-2.12, p=0.0348</td>
<td>t=1.56, p=0.1198</td>
<td>t=-0.32, p=0.7433</td>
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<tr>
<td>Food resources – liquid food</td>
<td>t=1.48, p=0.1398</td>
<td>t=1.56, p=0.1196</td>
<td>t=3.15, p=0.0019</td>
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<tr>
<td>Foraging strategy - group</td>
<td>t=2.07, p=0.0395</td>
<td>t=0.23, p=0.8189</td>
<td>t=1.79, p=0.0755</td>
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<tr>
<td>Foraging strategy - collective</td>
<td>t=-1.30, p=0.1937</td>
<td>t=-0.12, p=0.9024</td>
<td>t=-0.37, p=0.7098</td>
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<tr>
<td>Colony size</td>
<td>t=-0.41, p=0.6831</td>
<td>t=1.36, p=0.1752</td>
<td>t=1.31, p=0.1907</td>
</tr>
<tr>
<td>TRAIT DISSIMILARITY</td>
<td>Climate gradients</td>
<td>Productivity gradient</td>
<td>Vegetation type gradient</td>
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<td>----------------------</td>
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<tr>
<td></td>
<td>Mean temperature</td>
<td>Temperature seasonality</td>
<td>Precipitation</td>
</tr>
<tr>
<td>Worker size</td>
<td>t=0.96, p=0.3399</td>
<td>t=2.43, p=0.0159</td>
<td>t=1.78, p=0.0769</td>
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<td>Worker polymorphism</td>
<td>t=1.22, p=0.2236</td>
<td>t=2.79, p=0.0057</td>
<td>t=0.25, p=0.8048</td>
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<td>Diurnality</td>
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<td>t=2.21, p=0.0283</td>
<td>t=0.15, p=0.8802</td>
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<td>Behavioral dominance</td>
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<td>t=0.17, p=0.8652</td>
<td>t=-0.79, p=0.4305</td>
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<td>Food resources - seeds</td>
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<td>t=2.13, p=0.0343</td>
<td>t=-4.38, p&lt;0.0001</td>
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<td>Food resources - insects</td>
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<td>Food resources - liquid food</td>
<td>t=2.08, p=0.0391</td>
<td>t=4.75, p&lt;0.0001</td>
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<td>Foraging strategy - individual</td>
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<td>t=-0.24, p=0.8091</td>
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<td>Foraging strategy - group</td>
<td>t=-1.50, p=0.1314</td>
<td>t=0.11, p=0.9099</td>
<td>t=1.54, p=0.1315</td>
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<td>Foraging strategy - collective</td>
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<td>t=0.21, p=0.8339</td>
<td>t=-0.52, p=0.6057</td>
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<td>Colony size</td>
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<td>Number of queens</td>
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<td>t=-0.44, p=0.6616</td>
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<tr>
<td>Number of nests</td>
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<td>t=-0.75, p=0.4529</td>
<td>t=1.64, p=0.1021</td>
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<tr>
<td>Colony foundation type</td>
<td>t=-0.66, p=0.5073</td>
<td>t=1.77, p=0.0784</td>
<td>t=-0.86, p=0.3928</td>
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</table>