

A multidimensional functional trait analysis of resource exploitation in European ants

JAVIER RETANA,^{1,2,5} XAVIER ARNAN,^{1,3} AND XIM CERDÀ⁴

¹CREAF, Cerdanyola del Vallès 08193 Spain

²Universitat Autònoma Barcelona, Cerdanyola del Vallès 08193 Spain

³Departamento de Botânica, Universidade Federal Pernambuco, Ave Prof Moraes Rego s/no, Cidade Universitária, 50670 901, Recife, Brazil

⁴Estación Biológica de Doñana, CSIC, Avda Américo Vespucio, s/n, E-41092 Sevilla, Spain

Abstract. The major factors explaining ecological variation in plants have been widely discussed over the last decade thanks to numerous studies that have examined the covariation that exists between pairs of traits. However, multivariate relationships among traits remain poorly characterized in animals. In this study, we aimed to identify the main multivariate trait dimensions that explain variance in important functional traits related to resource exploitation in ants. To this end, we created a large ant trait database. This database includes information on 11 traits that are important in ant resource exploitation; data were obtained for 150 European species found in different biomes. First, we examined the pairwise correlations between the traits included in the database. Second, we used multivariate analyses to identify potential trait dimensions. Our study shows that, to a great extent, resource exploitation strategies align along two main trait dimensions. The first dimension emerged in both the overall and group-specific analyses, where it accounted for the same pairwise trait correlations. The second dimension was more variable, as species were grouped by levels of taxonomy, habitat, and climate. These two dimensions included most of the significant pairwise trait correlations, thus highlighting that complementarity, but also redundancy, exists among different pairs of traits. The first dimension was associated with behavioral dominance: dominance was associated with large colony size, presence of multiple nests per colony, worker polymorphism, and a collective foraging strategy. The second dimension was associated with resource partitioning along dietary and microhabitat lines: it ranged from species that consume liquid foods, engage in group foraging, and mainly nest in the vegetation to species that consume insects and seeds, engage in individual foraging, and demonstrate strictly diurnal activity. Our findings establish a proficient ecological trait-based animal research that minimizes the number of traits to be measured while maximizing the number of relevant trait dimensions. Overall, resource exploitation in animals might be framed by behavioral dominance, foraging strategy, diet, and nesting habitat; the position of animal species within this trait space could provide relevant information about their distribution and abundance, for today as well as under future global change scenarios.

Key words: *ants; ecological variation; Europe; foraging strategy; functional trait; resource exploitation; trait covariation.*

INTRODUCTION

Over the last decade, many studies have underscored the importance of using a functional approach to understand the link between the environment and species distribution patterns (e.g., McGill et al. 2006, Swenson and Weiser 2010, Vesik 2013, Arnan et al. 2014), because a species' traits determine whether it will successfully pass through different filters (McGill et al. 2006). While abiotic filters operate on certain traits and determine which species will be present in a local community, biotic filters operate on other traits and

determine species persistence. Among these latter traits are those that relate to resource exploitation, because they are crucial for obtaining the energy needed for survival, growth, and reproduction. Significant associations exist among an individual's physiological, life-history, behavioral, and morphological traits (Grime 2001, Westoby et al. 2002). Cross-species correlations among traits also exist; they may be positive or negative and can arise in different ways (Westoby et al. 2002). Most commonly, these correlations take the form of a trade-off, where an increase in fitness due to a change in one trait entails a decrease in fitness due to a concomitant change in a second trait (Roff and Fairbairn 2007). Such trade-offs can lead to both positive and negative correlations between traits; for instance, in plants, long leaf lifespan may be positively

Manuscript received 3 December 2014; revised 24 March 2015; accepted 30 March 2015. Corresponding Editor: D. A. Holway.

⁵ Email: Javier.Retana@uab.es

correlated with greater leaf mass per area, while propagule number may be negatively correlated with individual propagule mass. Traits may also become correlated as a result of niche features: lifestyles or habitats that select for particular traits might also tend to simultaneously select for other traits. For example, an extreme environment could select for similar adaptations, thus resulting in the correlation of several traits. While individual traits are easy to define, it is more challenging to characterize the correlations that exist among them. Yet, it is these correlations that define the phenotypes and functional ecology of organisms (Tessier et al. 2000, Westoby et al. 2002, Laughlin 2014) and that therefore influence the distribution, abundance, and ecosystem impact of different species.

Such trait associations have been extensively studied in both plants and animals. In plants, correlations have been observed between leaf traits (Wright et al. 2004), wood traits (Westoby and Wright 2006, Chave et al. 2009), seed traits (Westoby and Wright 2006), and litter traits (Freschet et al. 2012). In animals, correlations have been observed between morphological traits (e.g., Barton et al. 2011, Polidori et al. 2013), reproductive traits (e.g., Martin 1995, De Mas et al. 2009, Gómez-Mestre et al. 2012), growth rate and competitive ability (e.g., Tessier et al. 2000, Bonsall et al. 2002), growth rate and predation risk (e.g., Martin 1995, Cheng and Martin 2012), and habitat use and ecological specialization (e.g., Ribera et al. 2001, Gurd 2008, Blanchet et al. 2013). The next step is to characterize the relationships among suites of traits using multivariate analysis to identify the major trait dimensions that explain ecological variation among species (Laughlin 2014). Such analyses have frequently been carried out in plants; studies involving animals are less common (but see Barton et al. 2011). Research on plants has thus helped define what are known as dimensions of ecological variation; these dimensions reflect the mixture of direct and indirect causal relationships that exist between traits (Wright et al. 2004, Westoby and Wright 2006, Chave et al. 2009). Thus, trait associations may be analyzed at two different scales: by examining pairwise correlations between traits and by exploring broader trait dimensions that account for ecological variation. However, to date, the interactions among correlated traits and trait clustering along species-level multivariate dimensions remain largely unexplored. Therefore, ecological research should move beyond simply analyzing the correlations that exist between pairs of traits; it now needs to characterize the major dimensions into which suites of traits are organized and to determine how these dimensions enhance our understanding of ecological systems.

Ants are a particularly suitable model system when it comes to studying the factors framing trait covariation in animals. Ants monopolize space and other resources and therefore influence other species in the areas they occupy. The ecological dominance of ants (defined as their effect on other species found in the community;

Cerdá et al. 2013) is matched by their extraordinary geographic range: ants are abundant in most of the world's terrestrial habitats (Hölldobler and Wilson 1990) and display an extremely diverse array of life histories and colony traits. For instance, ant workers vary considerably in size (Geraghty et al. 2007) and colony size can range from a few individuals to over a million ants (Kaspari and Vargo 1995, Geraghty et al. 2007, Shik 2008). Some species have monomorphic workers, while others have extremely polymorphic workers or specialized subcastes (Oster and Wilson 1976, Hölldobler and Wilson 1990). Depending on the species, colonies may occupy a single nest (i.e., be monodomous) or multiple nests (i.e., be polydomous; Debout et al. 2007); species may also nest in very different substrates (Hölldobler and Wilson 1990). Ants also have extremely variable diets; there are many scavenger species, but there are also predaceous species, granivorous species, herbivorous species, and species that feed on exudates (Hölldobler and Wilson 1990). Furthermore, some ant species use individual-based foraging, while others have complex foraging strategies based on rapid recruitment or the maintenance of trunk trails (Beckers et al. 1989). Overall, this high degree of variability supports the long-standing paradigm that resource exploitation is the major underlying cause of interspecific variation in life-history patterns in ants.

Previous studies on trait covariation in ant assemblages have examined some positive relationships (e.g., worker size and colony size [Geraghty et al. 2007]; colony size and morphological specialization [Anderson and McShea 2001]), but have mainly focused on characterizing negative relationships, or trade-offs. Some trade-offs, such as the dominance–thermal-tolerance trade-off and the dominance–discovery trade-off, have been extensively discussed in the literature. The dominance–thermal-tolerance trade-off occurs when dominant ant species are largely restricted by environmental conditions, but subordinate species can remain active over a wider (or different) range of temperatures (Fellers 1989, Bestelmeyer 1997, Cerdá et al. 1997, 1998). The dominance–discovery trade-off results when ant species that are good at dominating food resources are poor at discovering them (Fellers 1987, Feener et al. 2008, Parr and Gibb 2009, 2012). The ability of such trade-offs to allow co-occurrence within local communities is contingent on the environment (Cerdá et al. 1997, Retana and Cerdá 2000, Wiescher et al. 2011). However, at present, no studies have been performed in ants that analyze how these positive and negative correlations interact within the multivariate space associated with species traits.

In this study, we sought to (1) characterize existing pairwise correlations between traits in ant species, (2) identify the main functional trait dimensions that help explain variance in resource exploitation in ants, and (3) analyze how multivariate analyses enhance our understanding of pairwise trait correlations. We focused on 11

key morphological and behavioral traits, which, together, capture the essential features of resource exploitation in ants. To accomplish these goals, we compiled a comprehensive ant trait database that included information on 150 species from northern, western, and southern Europe; these species occur in a wide range of biomes, from boreal forests to dry grasslands. Compared to previous data sets (e.g., Cushman et al. 1993, Arnan et al. 2012, 2013), this data set spans a considerably greater range of traits, species, and biomes. First, we determined whether the traits in our data set were correlated with each other, after accounting for phylogenetic relationships among species. Second, we carried out a multivariate analysis (principal components analysis; PCoA) on all the traits to define the functional trait dimensions associated with resource exploitation. We performed two types of analyses: an overall analysis in which the total data set was used and group-specific analyses in which species were grouped by subfamily, habitat type, and climatic conditions. To determine how multivariate analyses can improve our understanding of pairwise trait correlations, we examined how such correlations scale up to define major trait dimensions that explain ecological variance among species. We asked the following two questions: (1) Can these numerous sets of correlated traits be reduced down to a smaller number of major trait dimensions, that is, do they align along multivariate axes? (2) Which sets of trait correlations are redundant vs. orthogonal? The answer to these questions is a step further to achieve more efficient ecological trait-based research in animals based on minimizing the number of traits to be measured while maximizing the number of relevant trait dimensions.

METHODS

Ant species trait data

We compiled a database of ant functional traits drawing on information for 150 Palearctic species from six subfamilies (Dolichoderinae, Formicinae, Leptanillinae, Myrmicinae, Ponerinae, and Proceratiinae); the species used are distributed throughout northern, western, and southern Europe. We focused on 11 functional traits (Table 1) recognized to be important in resource exploitation (e.g., Hölldobler and Wilson 1990, Oliver et al. 2008, Bihn et al. 2010). As in other studies of functional diversity, traits were assumed to be species specific without demonstrating intraspecific variability (e.g., Swenson and Weiser 2010, Arnan et al. 2012, 2013, 2014), although we recognize that functional traits are labile and may show variability among populations (e.g., Bolnick et al. 2011). However, because we were interested in characterizing general relationships between traits, we used the most common trait state observed in each species. Future studies should attempt to incorporate intraspecific variability. We began building the database using information obtained from various colleagues (personal data sets;

Anna Alsina, Jordi Bosch, Raphaël Boulay, Soledad Carpintero, Valentín Cavia, Sebastià Cros, Xavier Espadaler, Paqui Ruano, and Alberto Tinaut). We then exhaustively searched public databases and the scientific literature (over 1300 search hours covering more than 1000 articles). A full list of the data sources utilized is provided in Appendix A. We focused on the following 11 functional traits:

1. *Worker size*.—Worker size is an important trait because it may constrain where ants are able to forage (Gibb and Parr 2010), and in animals, body size is a prominent characteristic that affects virtually all physiological traits (e.g., Chown and Gaston 2010). As in other ant studies (e.g., Cushman et al. 1993), worker size was defined as worker body length measured from the tip of mandibles to the tip of gaster.

2. *Worker polymorphism*.—A high degree of worker polymorphism may enable a colony/species to be competitively superior because it contributes to an efficient division of labor (Oster and Wilson 1976). We used a quantitative measure of worker polymorphism: mean worker size divided by worker size range (see Arnan et al. 2013).

3. *Colony size*.—Colony size also has a clear impact on resource exploitation because, all else being equal, large colonies are competitively superior to small colonies because they can send out more workers to collect food resources or battle neighbors (McGlynn 2000, Linksvayer and Janssen 2008). We used the number of workers per colony as our measure of colony size.

4–6. *Diet*.—Ants have variable diets. They may exclusively eat one type of food resource or they may be omnivorous and eat different proportions of plant and animal matter. We described ant diets using three categories, one for each of the main food resources used by European ants: seeds, insect corpses, and liquid foods (obtained directly or indirectly from plants, including nectar and honeydew). These three variables (labeled seeds in diet, insects in diet, and liquid foods in diet) described the proportion of each of these food types in the diet of each species.

7. *Number of nests per colony*.—Many ant species are monodomous (they have only one nest per colony), but other species are polydomous (they have multiple nests per colony), which allows them to monopolize resources because parts of the colony are located nearer to food resources (Debout et al. 2007). We classified species as being monodomous, polydomous, or both.

8. *Diurnality*.—The daily activity rhythms of ants may determine the type and abundance of food resources to which they have access, the competitors with which they interact, and the predators to which they are exposed. We classified species as strictly diurnal if they are active only during the daytime and as non-strictly diurnal if they are active both during the day and at night or only at night or during the twilight hours.

TABLE 1. Description and range of values of the ant functional traits included in this study.

Trait	Data type	Range or percentage of species
Worker size	Quantitative	1.2–10.8 (mm)
Worker polymorphism	Quantitative	0.1–1.3
Colony size (number of workers/colony)	Quantitative	50–2 500 000
Proportion seeds in diet	Fuzzy coded	0–1
Proportion insects in diet	Fuzzy coded	0–1
Proportion liquid foods in diet	Fuzzy coded	0–1
Number of nests per colony		
Monodomy	Qualitative	80%
Monodomy and polydomy	Qualitative	5%
Polydomy	Qualitative	15%
Diurnality		
Non-strictly diurnal	Qualitative	79%
Strictly diurnal	Qualitative	21%
Nesting site		
Ground	Qualitative	83%
Vegetation	Qualitative	17%
Foraging strategy		
Individual	Qualitative	15%
Group	Qualitative	52%
Collective	Qualitative	33%
Behavioral dominance		
Subordinate	Qualitative	72%
Dominant	Qualitative	28%

Notes: Range is given for quantitative data, percentage of species is given for qualitative data. Worker size is defined as body size from tip of mandibles to tip of gaster, and polymorphism as mean worker size divided by worker size range. Ant diets were described utilizing fuzzy coding (Chevene et al. 1994), which uses positive scores to describe the affinity of a given species for different modalities (i.e., categories) of a given variable; the sum of the scores for a species across variable levels is set to 1. In our case, we created three new variables (seeds in diet, insects in diet, and liquid foods in diet) from one variable (diet), and the sum of these new variables was always 1. Scores ranged from 0 (no preference for a food resource) to 1 (high degree of preference for a food resource). For instance, a species that feeds mostly on seeds and less on insects would be given a score of 0.75 for the seeds-in-diet variable and a score of 0.25 for the insects-in-diet variable.

9. *Nesting site.*—Ant species nest in different substrates, which influence the way they exploit food resources. We distinguished between ground- and vegetation-nesting species.

10. *Foraging strategy.*—In ant species, the ability to exploit food resources strongly depends on the recruitment methods used (Beckers et al. 1989, Planqué et al. 2010). We distinguished among three main strategies of food collection: (1) individual, where workers of these species are unable to communicate the presence of a food resource to their nestmates, and as a consequence, they forage and collect food individually; (2) group, where workers of these species are able to communicate with nestmates and guide a small number (from a single individual to 10–25 nestmates) to a previously discovered food resource; (3) collective, where workers of these species follow chemical signals deposited by nestmates to arrive at food resources; temporary or permanent trails may be used, and mass recruitment may occur.

11. *Behavioral dominance.*—Behaviorally dominant species are aggressive, capable of exerting a strong influence on other species, and engage in interference competition to behaviorally exclude others from resources (Savolainen and Vepsäläinen 1988, Cerdá et al.

1998, Arnan et al. 2012). In this study, species were classified using the following two categories: (1) dominants, ant species located at the top of the dominance hierarchy that are capable of excluding many ant species from food resources; subdominants (Cerdá et al. 2013) were also included in this group; and (2) subordinates, ant species at the bottom of the dominance hierarchy that are excluded from food resources by dominants. Using prior research (Cerdá et al. 1997, Retana and Cerdá 2000), the threshold for distinguishing dominants from subordinates was determined for each community based on two criteria. First, dominant species were those who won more than 50% of their encounters with other species (i.e., they drove other species away). Second, dominant species had dominance index values that did not statistically differ from those of species classified as dominant based on the first criterion (according to the results of a χ^2 test). Whenever this specific type of information was available, we used these criteria. If not, as with other traits, we used the classification scheme employed by other authors when their criteria were similar enough to ours. Dominance is relative, and the dominance rank of a particular species may depend on the other species with which it interacts.

However, based on the results of our previous studies examining dominance hierarchies (e.g., Retana and Cerdá 2000, Arnan et al. 2012), it is extremely unlikely that a given species will be dominant or subdominant in one community and subordinate in another, or vice versa (we have not observed a single such case in the more than 30 communities we have analyzed).

Climate and habitat data

Climate data were obtained from the WorldClim database (*available online*).⁶ We focused on two climatic variables: mean annual temperature (MAT) and mean annual precipitation (MAP). The mean values for the two variables associated with the distributions of each species were obtained by averaging all of the species records found on two web sites with large-scale ant distribution maps (the Site for Palaearctic and Macaronesian Ants and AntWiki; *available online*).⁷ MAT values for the ant species included in this study ranged from 4.3° to 21.2°C, while MAP values ranged from 170 to 1233 mm per year; these ranges are representative of most of the MAT and MAP values experienced by ants in Europe. Based on the range of values for each variable, we placed species in one of three MAT and MAP groups. Thus, we distinguished among species with MAT values lower than 12°C (MAT_{<12}), between 12 and 15°C (MAT_{12–15}), and higher than 15°C (MAT_{>15}). Similarly, we distinguished among species with MAP values of less than 600 mm (MAP_{<600}), between 600 and 900 mm (MAP_{600–900}), and greater than 900 mm (MAP_{>900}). The MAT and MAP values for the species included in this study are given in Appendix A. There was roughly the same number of species in each category (between 39 and 56).

We identified the most common habitat in which each ant species is found as per Arnan et al. (2012), distinguishing between two main habitat types: (1) open habitat, which is characterized by the almost complete absence of tree cover and includes both grasslands and shrublands; and (2) forested habitat, which is characterized by the presence of trees, either conifers or broadleaf species, in the overstory. We then summarized the information we had for each species to determine that species' occurrence in different habitat types (Appendix B). The species' most common habitat was the one in which the species was most frequently found based on records in the literature. When a species was equally common in open and forested habitats, both were considered to be the main habitat types for that species.

Phylogeny

To account for the effect of phylogenetic history on the relationships between functional traits, we reconstructed a working phylogeny from the literature. For the basal

tree, we used a published genus-level phylogeny based on a molecular data set (Moreau et al. 2006). We mapped species onto the basal tree using information from different sources. First, we used any available molecular within-genus phylogenies, adding any missing species in accordance with their taxonomic relationships to already-included species (based on morphological similarities or comments in the original species description). Second, when molecular data were not available, we reconstructed species relationships within each genus based on taxonomic relationships. The tree was built using Mesquite v. 2.75 (Maddison and Maddison 2011). As species-level branch lengths in the Formicidae tree are mostly unknown, we assigned a value of 1.0 to all such branches. We acknowledge that this approach likely resulted in the loss of some information; however, because branch length is unavailable for many species and for some supraspecies groups, it was impossible to resolve polytomies.

Data analysis

All statistical analyses were carried out in R v. 2.14.1 (R Development Core Team 2011). As we used traits that were defined both quantitatively and qualitatively (see Table 1), we used different statistical approaches to determine the pairwise relationships between different types of traits. When the two traits were quantitatively defined, we conducted linear regressions using the *crunch* function in the *caper* package, v. 0.5 (Orme et al. 2012), which makes it possible to investigate the correlation between continuous variables using phylogenetically independent contrasts. To obtain normally distributed residuals, we used a log transformation on colony size, worker size, and worker polymorphism.

When one trait was quantitatively defined and the other was qualitatively defined, we evaluated differences in the quantitative traits among the levels of the qualitative traits. We used phylogenetic analyses of variance to account for phylogenetic history: potential phylogenetic autocorrelation in the relationships was controlled for using the *phylANOVA* function in the *phytools* package v. 0.2–20 (Revell 2012); 1000 replicates were performed.

When the two traits were qualitatively defined, we used a generalized linear mixed model (GLMM) with a binomial error distribution and a logit link function implemented with the *glmer* function in the *lme4* package (Bates et al. 2014). In these analyses, to control for phylogenetic effects, subfamily and genus nested within subfamily were included as random factors. Since only binary variables can be used as response variables in these models, the number of nests was recoded in the following way: 0 for monodomy and 1 for no monodomy, a category that included polydomous species and species that were both monodomous and polydomous. Additionally, foraging strategy was included exclusively as a predictor variable. Given the large number of analyses and data points, the threshold

⁶ <http://www.worldclim.org/bioclim>

⁷ <http://www.antwiki.org>

TABLE 2. Pairwise relationships between functional traits taking into account phylogenetic effects.

Functional trait relationship	<i>t</i>	df	<i>F</i>	χ^2	<i>P</i>	<i>R</i> ²	<i>n</i>
ln(worker size)							
ln(worker polymorphism)	2.0	131			0.047		
ln(colony size)	1.0	139			0.305		
Insects in diet	1.4	132			0.172		
Seeds in diet	1.9	132			0.064		
Liquid foods in diet	-2.6	132			0.009	0.04	
Number nests per colony			0.3		0.896		138
Diurnality			23.7		0.06		138
Nesting site			5.2		0.439		138
Foraging strategy			1.6		0.813		138
Behavioral dominance			6.6		0.271		138
ln(worker polymorphism)							
ln(colony size)	1.5	129			0.129		
Insects in diet	-0.5	131			0.654		
Seeds in diet	1.6	131			0.108		
Liquid foods in diet	-0.5	131			0.615		
Number nests per colony			5.4		0.137		138
Diurnality			3.5		0.508		138
Nesting site			4.1		0.495		138
Foraging strategy			6.4		0.416		138
Behavioral dominance			40.4		0.004		138
ln(colony size)							
Insects in diet	-1.3	130			0.209		
Seeds in diet	3.0	130			0.003	0.06	
Liquid foods in diet	-0.5	130			0.594		
Number nests per colony			15.9		0.002		138
Diurnality			0.4		0.826		138
Nesting site			6.0		0.409		138
Foraging strategy			70.0		0.001		138
Behavioral dominance			125.4		0.001		138
Insects in diet							
Seeds in diet	4.8	136			0.001	0.14	
Liquid foods in diet	-17.6	136			0.001	0.70	
Number nests per colony			0.3		0.879		138
Diurnality			8.0		0.346		138
Nesting site			0.3		0.878		138
Foraging strategy			1.6		0.785		138
Behavioral dominance			6.7		0.3		138
Seeds in diet							
Liquid foods in diet	-2.5	136			0.01		
Number nests per colony			2.3		0.432		138
Diurnality			0.2		0.891		138
Nesting site			5.8		0.409		138
Foraging strategy			10.2		0.222		138
Behavioral dominance			0.1		0.887		138
Liquid foods in diet							
Number nests per colony			1.2		0.639		138
Diurnality			5.0		0.427		138
Nesting site			7.6		0.341		138
Foraging strategy			17.7		0.050		138
Behavioral dominance			7.3		0.263		138
Number nests per colony							
Diurnality		1		5.9	0.015		140
Nesting site		1		0.6	0.447		140
Foraging strategy		2		11.6	0.003		140
Behavioral dominance		1		5.2	0.022		138
Diurnality							
Nesting site		1		0.6	0.459		148
Foraging strategy		2		10.9	0.004		141
Behavioral dominance		1		31.4	0.001		146

TABLE 2. Continued.

Functional trait relationship	<i>t</i>	df	<i>F</i>	χ^2	<i>P</i>	<i>R</i> ²	<i>n</i>
Nesting site							
Foraging strategy		2		3.5	0.176		141
Behavioral dominance		1		2.4	0.120		147
Foraging strategy							
Behavioral dominance		1		29.3	0.001		139

Notes: Relationships are shown in a nested format, i.e., relationship between ln(worker size) and ln(worker polymorphism) is shown first, followed by relationship between ln(worker size) and ln(colony size), etc. Worker size was originally measured in mm (see Table 1), and colony size was originally measured as number of workers per colony. Relationships were significant at $P < 0.01$ (bolded text). Statistics were *t* (*t* statistic from linear regressions using phylogenetically independent contrasts), *F* (*F* statistic from phylogenetic analyses of variance; note that degrees of freedom are not provided because *P* values are obtained from phylogenetic simulation), χ^2 , (χ^2 statistic from the GLMM models), and *R*² (coefficient of determination).

for statistical significance was set at $P < 0.01$ throughout.

To identify the different trait dimensions associated with resource exploitation, we used PCoA, a statistical ordination method that characterizes similarities in data sets that include both qualitative and quantitative variables. First, we carried out a PCoA using all the full data set. Then, we carried out different PCoAs in which species were grouped by subfamily (i.e., Formicinae and Myrmicinae, the two subfamilies that contained a sufficient number of species), major habitat type (open vs. forested), and MAT (<12°, 12–15°, and >15°C) and MAP classes (<600, 600–900, and >900 mm). We estimated the concordance among the different trait dimensions we identified using the amount of variation explained by the relevant PCoA axes in the different group-level analyses and the presence of correlations between traits. The PCoAs were carried out using the *dudi.mix* function in the *ade4* package (Chessel et al. 2004).

RESULTS

The values for the quantitatively defined functional traits varied by one to several orders of magnitude across the data set (Table 1). There was a high proportion of monodomous, ground-nesting, and non-strictly diurnal species. There were also many subordinate species and group-foraging species (Table 1). When it came to dietary preferences, omnivorous species were well represented (66%), but specialists that feed almost exclusively on seeds, insects, or liquid foods were also present.

Pairwise trait correlations

Certain pairs of traits (12 overall) were highly and significantly correlated after controlling for species relatedness (Table 2). Behavioral dominance and foraging strategy were the two traits that most frequently correlated with other traits (Table 2). For instance, behavioral dominance was significantly associated with worker polymorphism and colony size: dominant species demonstrated a higher degree of worker polymorphism

(worker polymorphism of 0.63 ± 0.04 vs. 0.36 ± 0.02 for subordinate species; mean \pm SE) and had larger colonies ($121\,610 \pm 65\,590$ and 2032 ± 1026 ants per colony for dominants and subordinates, respectively). Moreover, behavioral dominance was also significantly correlated with diurnality (2.4% vs. 30.0% of strictly diurnal species were dominants vs. subordinates, respectively) and foraging strategy (Fig. 1A). In turn, foraging strategy was significantly associated with the number of nests per colony (Fig. 1B), diurnality (Fig. 1C), and colony size (Fig. 1D). There was also a significant relationship between colony size and nests per colony ($24\,630 \pm 22\,505$ and $84\,114 \pm 40\,046$ workers per colony for monodomous vs. polydomous species, respectively). Furthermore, there was a significant and positive relationship between the proportion of seeds in the diet and colony size and a negative relationship between the proportion of liquid foods in the diet and worker size. As expected, proportions of different food resources were negatively correlated; the negative relationship between the proportions of insects and liquid foods consumed was particularly strong (Table 2).

Overall multivariate analysis: emergence of multiple trait dimensions

In the overall PCoA, a relatively large amount of variance (43.3%) was explained by the first two axes (Table 3). The third and fourth axes explained a much smaller amount of variance (12.4% and 11.3%, respectively) and did not include any of the correlations found in the pairwise analyses (Table 2). For this reason, they will not be discussed further.

The first axis explained 24% of the variance. The three highest-loading traits were behavioral dominance, colony size, and foraging strategy (collective foraging; Table 3). This axis can therefore be regarded as a trait dimension representing behavioral dominance differences. In Fig. 2, dominant species with large colony sizes, polymorphic workers, a collective foraging strategy, and polydomous colonies were found on the left side of the axis, while subordinate species with small colony sizes, monodomous colonies, either group or individual

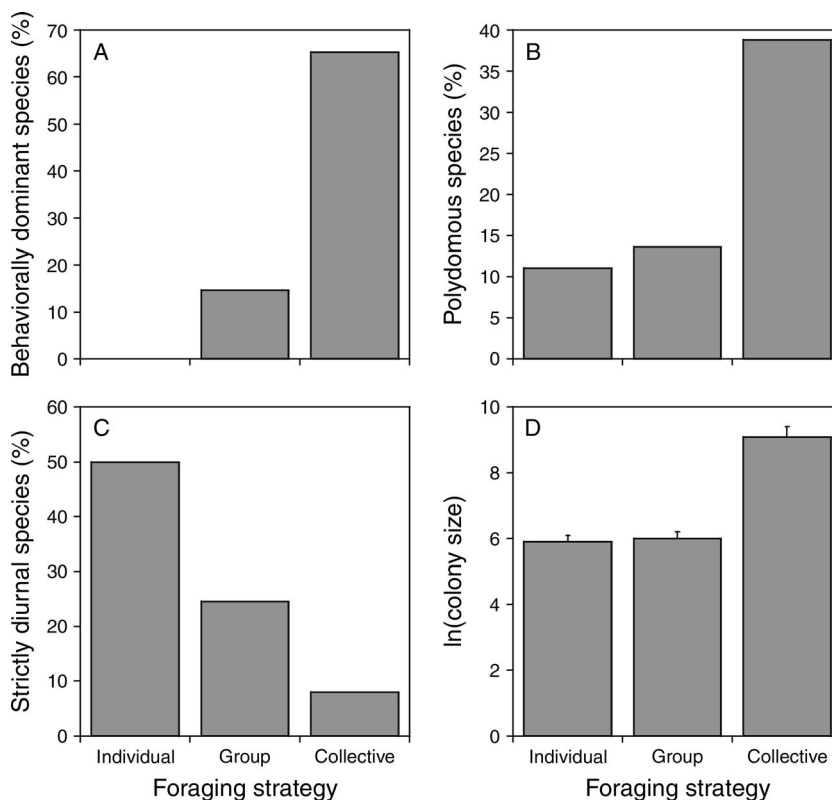


FIG. 1. Graphical representation of the relationships between foraging strategy and the different functional traits with which it shows significant ($P < 0.01$) relationships in Table 2: (A) behavioral dominance, (B) polydomy, (C) diurnality, and (D) colony size (natural-log-transformed, originally measured as number of workers per colony; mean + standard error).

foraging strategies, and diurnal activity were on the right. This first dimension included six (50%) of the significant relationships obtained in the pairwise analyses (Table 2): those between colony size and number of nests per colony, colony size and foraging strategy, colony size and behavioral dominance, worker polymorphism and behavioral dominance, foraging strategy and behavioral dominance, and diurnality and behavioral dominance.

The second axis explained 19.3% of the variance. The two highest-loading traits were proportion of liquid foods in the diet and foraging strategy (group and individual foraging). This axis can therefore be regarded as a trait dimension representing dietary partitioning and microhabitat differences. This axis, which largely (but not exclusively) included subordinate species, was characterized by a gradient along which vegetation-nesting, group-foraging, liquid-eating, non-diurnal species with small foragers were separated from individual-foraging, seed- or insect-eating, diurnal species with large foragers (Fig. 2). This second dimension included five (42%) of the significant relationships obtained in the pairwise analyses (Table 2): those between seed eating and liquid-food eating, seed eating and insect eating, liquid-food eating and worker size, foraging strategy

and number of nests per colony, and foraging strategy and diurnality.

Concordance of trait dimensions between the overall analysis and the group-specific analyses

The same general trait dimensions, and particularly the first PCoA axis, were found in the PCoAs in which species were grouped by subfamily or habitat (Table 3). The amount of variance explained by the two principal axes was similar in the overall analysis and the subfamily- and habitat-specific analyses (first axis, 28.0% and 32.2% in the Formicinae and Myrmicinae analyses, respectively, and 23.8% and 26.4% in the analyses of open and forested habitat; second axis, 19.7% and 20.9% in the Formicinae and Myrmicinae analyses, respectively, and 16.7% and 17.4% in the analyses of open and forested habitat; Table 3). In all analyses, the highest-loading traits were colony size, behavioral dominance, and foraging strategy. There were also traits that made large contributions exclusively in certain analyses: seed eating (Myrmicinae), insect eating (Formicinae), liquid eating (both Formicinae and Myrmicinae), diurnality (Formicinae), worker size (forest), and worker polymorphism (forest).

Overall, climate had a relatively small influence on the traits grouped in the first PCoA axis, and very few

TABLE 3. Principal coordinates analyses of ant traits related to resource exploitation.

	Overall	Subfamily		Habitat		Mean annual temperature (°C)			Mean annual precipitation (mm)		
		F	M	Open	Forest	<12	12–15	>15	<600	600–900	>900
Axis 1											
Variance explained (%)	24.0	32.2	28.0	23.8	26.4	27.9	26.4	23.2	24.9	27.3	26.4
Worker size	0.00	0.02	0.39	0.00	0.42	0.37	0.02	0.00	0.02	0.15	0.28
Worker polymorphism	0.16	0.01	0.33	0.16	0.61	0.38	0.33	0.19	0.33	0.32	0.17
Colony size	0.70	0.47	0.62	0.70	0.68	0.73	0.69	0.82	0.75	0.80	0.61
Seeds in diet	0.02	-	0.46	0.02	0.01	0.00	0.01	0.00	0.10	0.12	0.00
Insects in diet	0.11	0.60	0.07	0.11	0.15	0.18	0.46	0.00	0.03	0.03	0.44
Liquid foods in diet	0.22	0.60	0.51	0.22	0.08	0.16	0.44	0.00	0.27	0.00	0.46
Number nests per colony	0.27	0.06	0.08	0.27	0.23	0.53	0.07	0.31	0.20	0.40	0.20
Diurnality	0.20	0.75	0.04	0.20	0.03	0.05	0.15	0.04	0.05	0.01	0.15
Nesting site	0.02	0.05	0.32	0.02	0.18	0.06	0.03	0.01	0.01	0.32	0.00
Behavioral dominance	0.72	0.53	0.34	0.72	0.69	0.74	0.71	0.83	0.79	0.71	0.68
Foraging strategy	0.66	0.78	0.50	0.66	0.35	0.41	0.52	0.81	0.70	0.60	0.44
Axis 2											
Variance explained (%)	19.3	20.9	19.7	17.4	16.7	22.8	17.3	18.1	16.8	18.2	18.6
Worker size	0.19	0.03	0.04	0.45	0.02	0.14	0.36	0.02	0.23	0.27	0.24
Worker polymorphism	0.09	0.21	0.12	0.37	0.02	0.19	0.32	0.02	0.17	0.12	0.37
Colony size	0.02	0.28	0.18	0.11	0.04	0.01	0.11	0.01	0.00	0.01	0.09
Seeds in diet	0.21	-	0.47	0.09	0.19	0.05	0.23	0.79	0.46	0.08	0.04
Insects in diet	0.14	0.34	0.45	0.07	0.61	0.74	0.07	0.06	0.30	0.34	0.21
Liquid foods in diet	0.57	0.34	0.10	0.31	0.84	0.73	0.29	0.54	0.03	0.47	0.38
Number nests per colony	0.01	0.41	0.28	0.01	0.15	0.03	0.00	0.16	0.28	0.08	0.11
Diurnality	0.26	0.02	0.03	0.30	0.00	0.23	0.25	0.00	0.50	0.36	0.19
Nesting site	0.28	0.12	0.01	0.12	0.08	0.17	0.33	0.18	0.00	0.09	0.24
Behavioral dominance	0.00	0.19	0.24	0.01	0.01	0.02	0.02	0.00	0.05	0.05	0.07
Foraging strategy	0.48	0.57	0.64	0.41	0.22	0.65	0.28	0.58	0.15	0.48	0.41

Notes: The variance explained by each of the first two axes and the contributions of the original variables to these axes are given. The values correspond to the squared correlation coefficients for the quantitative variables and to the correlation ratios for qualitative variables. Subfamilies are Formicinae (F) and Myrmicinae (M).

differences among trait patterns were observed along this axis when species were grouped according to MAT or MAP (Table 3). The amount of variance explained by the first and the second PCoA axes was very similar among MAT (23.2–27.9% and 17.3–22.8%, respectively) and MAP levels (24.9–27.3% and 16.8–18.6%, respectively). The first axis demonstrated a very homogenous pattern across levels: in all cases, the most important traits were colony size, behavioral dominance, and foraging strategy. Some traits were more prominent under certain climatic conditions, i.e., number of nests (MAT<12) and liquid and insect eating (MAT12–15 and MAP>900). The second axis demonstrated a more variable pattern; although foraging strategy universally made a large contribution, several traits were important only under specific conditions, i.e., seed eating (MAT>15 and MAP<600), insect eating (MAT<12), liquid food eating (MAT<12, MAT>15, and MAP600–900), and diurnality (MAP<600).

DISCUSSION

In this study, we tried to identify the main trait dimensions related to ecological variation in resource exploitation in ants. We collected data on a number of traits using the literature and obtained a representative sample of European ants that covered a wide range of climatic and habitat conditions. The results of this study provide evidence that resource-exploitation strategies

are associated with two main trait dimensions, which capture most of the covariation that exists between pairs of important traits. Similar patterns were seen in the overall analysis and in the analyses that grouped species by subfamily, habitat, and climate.

The first step in this study was to quantify the pairwise correlations between different functional traits in order to identify those that were sufficiently related to form a single dimension capable of explaining trait variance (see Westoby and Wright 2006). The trait relationships we found are consistent with those previously reported in the literature, albeit generally in smaller data sets (e.g., Beckers et al. 1989, Planqué et al. 2010, Wiescher et al. 2011, Arnan et al. 2012). Responding to the first question stated in *Introduction*, in the overall multivariate analysis, two major trait dimensions emerged (Fig. 2 and Table 3). Interestingly, this multivariate approach considerably enhanced our understanding of the interactions that exist among simple pairwise trait associations. Thus, most of these significant associations (i.e., 11 out of 12; Table 2) were also observed along the first two PCoA axes, that is, the same positive or negative significant relationships between pairs of variables were also obtained through the multivariate PCoA axes. Consequently, our results highlight that some of these trait associations are redundant (occur along the same axis), while others are complementary (occur along orthogonal axes), which responds to the second question stated in *Introduction*.

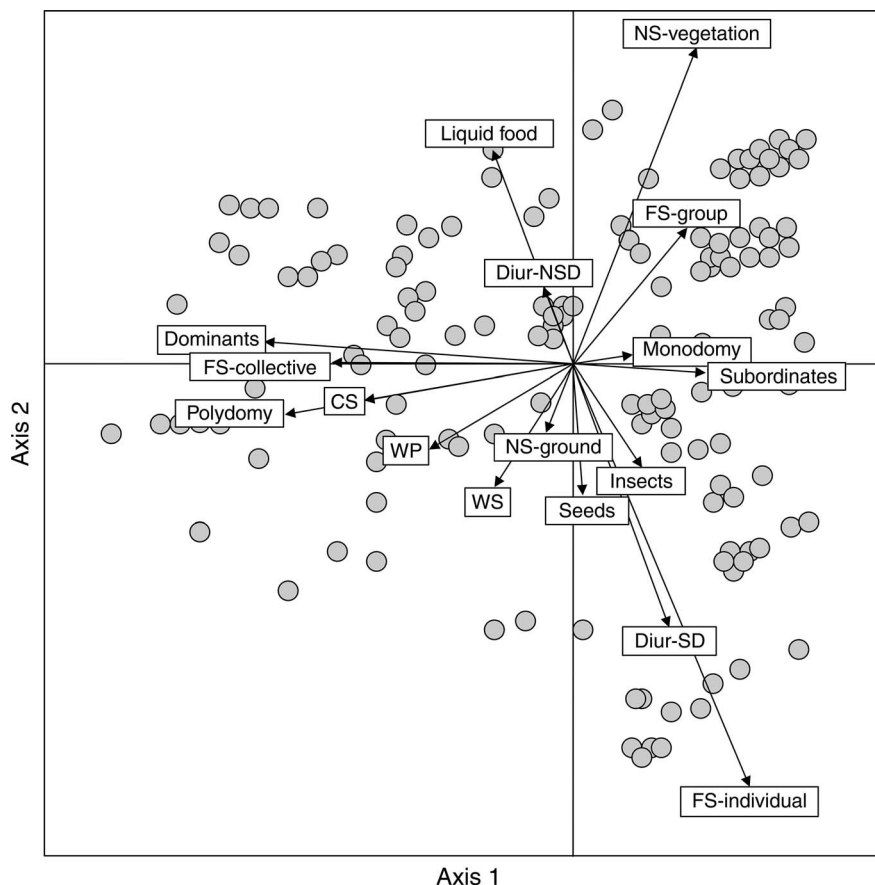


FIG. 2. Overall principal components analysis (PCoA; i.e., including all traits and species). Functional traits aligned along two trait dimensions. The first (axis 1) was associated with behavioral dominance; it included behavioral dominance, colony size, polydomy, worker polymorphism, and a collective foraging strategy. The second (axis 2) was associated with group and individual foraging strategies and dietary preferences; it included diet, foraging strategy, worker size, and diurnality. The abbreviations of the variables are as follows: Dominants and subordinates are the two levels of behavioral dominance; polydomy and monodomy are the two levels of number of nests per colony; FS-collective, FS-group, and FS-individual are the three levels of foraging strategy; diur-NSD and diur-SD are the two levels of diurnality (non-strictly diurnal and strictly diurnal, respectively); NS-ground and NS-vegetation are the two levels of nesting site; seeds is the relative proportion of seeds in the diet; insects is the relative proportion of insects in the diet; liquid food is the relative proportion of liquid foods in the diet; CS is colony size; WP is worker polymorphism; and WS is worker size. The grey circles are the different ant species.

This finding should help render ecological trait-based research more efficient because it means that a minimal number of traits can be measured while still maximizing the number of trait dimensions present.

The first dimension accounting for variance in resource exploitation traits related primarily to behavioral dominance and included the following mixed group of closely correlated traits: behavioral dominance, foraging strategy, polydomy, colony size, and to a lesser extent, worker polymorphism. Thus, dominant ants are frequently characterized by larger colony sizes, multiple nests per colony, worker polymorphism, and collective foraging strategies. Large colony size may enhance species ability to discover and defend resources (Holway and Case 2001, Palmer 2004). Having multiple nests may result in energy savings because it can reduce the distance ants need to travel to reach resources (Davidson 1997, Debout et al. 2007). The presence of

polymorphic workers (including a soldier caste) may allow these species to have a more efficient division of labor (Oster and Wilson 1976, Arnan et al. 2011), and collective foraging allows large numbers of workers to be recruited to concentrated food resources (Cerdá et al. 1997, Arnan et al. 2012). Using this suite of characteristics, behaviorally dominant species can expand their foraging areas and more efficiently dominate and exploit large and rich food resources, which in turn means that they can pay the high energetic costs associated with these characteristics. In contrast, subordinates may invest energy in other strategies that might allow them to co-occur with dominants. For instance, Mediterranean subordinate ants have higher levels of thermal tolerance than do dominants (Cerdá et al. 1998, Arnan et al. 2012) and can thus forage when dominants are inactive. Thermal tolerance mechanisms might be associated with high energy costs. The central role

played by behavioral dominance in the primary, and thus most important, trait dimension related to resource exploitation in ants supports the assertion that competition is a hallmark feature of ant ecology when it comes to explaining species coexistence. The importance of behavioral dominance as a central trait in ant ecology has been underscored by a large number of publications and numerous recent reviews (e.g., Cerdá et al. 2013, Soares 2013).

The second trait dimension reflected resource partitioning along dietary and microhabitat lines and explained variance related to taxonomy, habitat type, and climate. This second dimension included the following traits that were, in some cases, closely correlated: foraging strategy, worker size, diet, and diurnality. It also included most of the significant pairwise relationships (Table 2) that were not included in the first trait dimension. It revealed the strong, negative relationship between the dietary proportions of liquid foods and insects (Table 2); this result suggests that species may trade off between the efficient consumption of different resource types (Kneitel and Chase 2004). Moreover, in this trait dimension, species were separated along a microhabitat gradient (which included different times of the year and types of nesting sites). It comprised species that eat liquid foods, forage in groups, and nest mainly in the vegetation and species that eat insects and seeds, forage individually, have large workers, and demonstrate strictly diurnal activity. Species that are active at higher temperatures (i.e., at midday) have been found to be individual foragers that do not use chemical signals to recruit nestmates (Ruano et al. 2000), probably because high soil temperatures limit the effectiveness of such signals (Billen and Morgan 1998, van Oudenhove et al. 2012). High temperatures are also associated with the scavenging of insect corpses because arthropod corpses are considered to be a limited resource, given their rapid disappearance in many habitats (Fellers and Fellers 1982, Retana et al. 1991). The high energy costs associated with thermal tolerance in strictly diurnal species might also force such species to adopt more complex foraging strategies. Group foragers are more likely to monopolize resources and form close associations with sugar-producing insects (Blüthgen et al. 2004, Oliver et al. 2008) because they are able to recruit higher numbers of workers to food resources. Group and individual foraging strategies were key components in the second trait dimension, highlighting that they were essentially orthogonal to collective behavior, the third foraging strategy considered that is a key trait in the first dimension of the analysis. This makes sense physiologically, as group foraging might be easily derived from individual foraging with some minor modifications in forager behavior, but evolving collective foraging requires the evolution of a whole communication system (Traniello 1989).

The fact that the overall analysis and the subfamily- and habitat-specific analyses found similar

primary axes when explaining trait variance (Table 3) is of special significance. This coincidence indicates that certain key traits are consistently important. Furthermore, traits present in the first axis were similar across climatic gradients (both temperature and precipitation), suggesting that climate plays a limited role in explaining trait relationships. This result was rather surprising because ant communities commonly vary in composition along environmental gradients (e.g., Hölldobler and Wilson 1990) and because, more specifically, some of the traits examined in this study vary significantly along climatic gradients. For instance, Cushman et al. (1993) found that ant body size (i.e., worker length) increased significantly with increasing latitude (i.e., decreasing temperature), and Arnan et al. (2014) observed that the relative importance of liquid food in the diet increases along a precipitation gradient. The relatively small contribution made by these traits to the trait dimensions we identified possibly explains why the general patterns observed across all climates were more or less similar. At any rate, because we included a highly diverse range of habitats and environmental conditions in our study, we propose that the trait dimensions we identified may be of general importance, especially the dimension associated with behavioral dominance. However, in order to test the universality of their relevance, we would need to conduct similar analyses using data from other biogeographic regions, especially those located outside of western Europe. Also, although our study included species from the world's three largest ant subfamilies, it would be ideal to conduct analyses using additional clades.

We found clear evidence that resource exploitation strategies, which are essential in fueling life, align to a great extent along two different trait dimensions, and that traits show similar overall and group-specific correlation patterns. The behavioral interactions and diet- and microhabitat-related resource partitioning reveal that there is a mixture of direct and indirect causal relationships among traits. Overall, because ants serve as bioindicators for other animal groups (at least for other arthropods; Andersen and Majer 2004, Leal et al. 2010) and because variation in traits related to resource exploitation plays a key role in species persistence in animals, we propose that resource exploitation in animal species is framed by the following four functional traits: behavioral dominance, foraging strategy, diet, and nesting habitat. The position of any given animal species within this trait space could be used to predict its distribution and abundance, and this approach could yield substantial benefits for global meta-analyses of field experiments, comparative eco-physiology studies, and studies of how animal dynamics are responding to global change (Westoby 1998).

ACKNOWLEDGMENTS

We wish to dedicate this study to Francis Bernard because his extraordinary and stimulating book "Les fourmis d'Europe occidentale et septentrionale" yielded information about many of the functional traits included in our database. This study was

partly funded by the Spanish Ministry for Science and Innovation (Ministerio de Ciencia e Innovación; project Consolider MONTES CSD 2008-00040 to J. Retana and projects CGL2009-09690/BOS and CGL2012-36181 to X. Cerdá, who also received funding from FEDER). Thanks are due to our colleagues and friends Anna Alsina, Jordi Bosch, Raphaël Boulay, Soledad Carpintero, Sebastià Cros, Valentín Cavia, Xavier Espadaler, Paqui Ruano, and Alberto Tinaut for providing us with ant trait data and to Iván Gómez-Mestre for his help with the phylogenetic analyses. Finally, we wish to thank Jean-Philippe Lessard and three anonymous referees for their very helpful comments on a draft of the manuscript.

LITERATURE CITED

- Andersen, A. N., and J. D. Majer. 2004. Ants show the way down under: invertebrates as bioindicators in land management. *Frontiers in Ecology and the Environment* 2:291–298.
- Anderson, C., and D. W. McShea. 2001. Individual versus social complexity, with particular reference to ant colonies. *Biological Reviews* 76:211–237.
- Arnan, X., X. Cerdá, and J. Retana. 2012. Distinctive life traits and distribution along environmental gradients of dominant and subordinate Mediterranean ant species. *Oecologia* 170: 489–500.
- Arnan, X., X. Cerdá, and J. Retana. 2014. Ant functional responses along environmental gradients. *Journal of Animal Ecology* 83:1398–1408.
- Arnan, X., X. Cerdá, A. Rodrigo, and J. Retana. 2013. Response of ant functional composition to fire. *Ecography* 36:1182–1192.
- Arnan, X., M. Ferrandiz-Rovira, C. Pladevall, and A. Rodrigo. 2011. Worker size-related task partitioning in the foraging strategy of a seed-harvesting ant species. *Behavioral Ecology and Sociobiology* 65:1881–1890.
- Barton, P. S., H. Gibb, A. D. Manning, D. B. Lindenmayer, and S. A. Cunningham. 2011. Morphological traits as predictors of diet and microhabitat use in a diverse beetle assemblage. *Biological Journal of the Linnean Society* 102: 301–310.
- Bates D., M. Maechler, B. Bolker, and S. Walker. 2014. lme4: linear mixed-effects models using eigen and S4. R package version 1.1-7. <http://CRAN.R-project.org/package=lme4>
- Beckers, R., S. Goss, J. L. Deneubourg, and J. M. Pasteels. 1989. Colony size, communication and ant foraging strategy. *Psyche* 96:239–256.
- Bestelmeyer, B. T. 1997. Stress tolerance in some Chacoandolichoderine ants: implications for community organization and distribution. *Journal of Arid Environments* 35:297–310.
- Bihn, J. H., G. Gebauer, and R. Brandl. 2010. Loss of functional diversity of ant assemblages in secondary tropical forests. *Ecology* 91:782–792.
- Billen, J., and E. D. Morgan. 1998. Pheromone communication in social insects: sources and secretions. Pages 3–33 in R. K. Vander Meer, M. D. Breed, K. E. Espelie, and M. L. Winston, editors. *Pheromone communication in social insects*. Elsevier, London, UK.
- Blanchet, F. G., J. A. C. Bergeron, J. R. Spence, and F. He. 2013. Landscape effects of disturbance, habitat heterogeneity and spatial autocorrelation for a ground beetle (Carabidae) assemblage in mature boreal forest. *Ecography* 36:636–647.
- Blüthgen, N., N. E. Stork, and K. Fiedler. 2004. Bottom-up control and co-occurrence in complex communities: honeydew and nectar determine a rainforest ant mosaic. *Oikos* 106: 344–358.
- Bolnick, D. I., P. Amarasekare, M. S. Araújo, R. Bürger, J. M. Levine, M. Novak, V. H. W. Rudolf, S. J. Schreiber, M. C. Urban, and D. A. Vasseur. 2011. Why intraspecific trait variation matters in community ecology. *Trends in Ecology and Evolution* 26:183–191.
- Bonsall, M. B., M. P. Hassell, and G. Asefa. 2002. Ecological trade-offs, resource partitioning, and coexistence in a host-parasitoid assemblage. *Ecology* 83:925–934.
- Cerdá, X., A. Arnan, and J. Retana. 2013. Is competition a significant hallmark of ant (Hymenoptera: Formicidae) ecology? *Myrmecological News* 18:131–147.
- Cerdá, X., J. Retana, and S. Cros. 1997. Thermal disruption of transitive hierarchies in Mediterranean ant communities. *Journal of Animal Ecology* 66:363–374.
- Cerdá, X., J. Retana, and S. Cros. 1998. Critical thermal limits in Mediterranean ant species: trade-off between mortality risk and foraging performance. *Functional Ecology* 12:45–55.
- Chave, J., D. Coomes, S. Jansen, S. L. Lewis, N. G. Swenson, and A. E. Zanne. 2009. Towards a worldwide wood economics spectrum. *Ecology Letters* 12:351–366.
- Cheng, Y. R., and T. E. Martin. 2012. Nest predation risk and growth strategies of passerine species: grow fast or develop traits to escape risk? *American Naturalist* 180:285–295.
- Chessel, D., A. B. Dufour, and J. Thioulouse. 2004. The ade4 package—I: one-table methods. *R News* 4:5–10.
- Chevone, F., S. Dolédec, and D. Chessel. 1994. A fuzzy coding approach for the analysis of long-term ecological data. *Freshwater Biology* 31:295–309.
- Chown, S. L., and K. J. Gaston. 2010. Body size variation in insects: a macroecological perspective. *Biological Reviews* 85: 139–169.
- Cushman, J. H., J. H. Lawton, and B. F. J. Manly. 1993. Latitudinal patterns in European ant assemblages: variation in species richness and body size. *Oecologia* 95:30–37.
- Davidson, D. W. 1997. The role of resource imbalances in the evolutionary ecology of tropical arboreal ants. *Biological Journal of the Linnean Society* 61:153–181.
- De Mas, E., C. Ribera, and J. Moya-Laraño. 2009. Resurrecting the differential mortality model of sexual size dimorphism. *Journal of Evolutionary Biology* 22:1739–1749.
- Debout, G., B. Schatz, M. Elias, and D. McKey. 2007. Polydomy in ants: what we know, what we think we know, and what remains to be done. *Biological Journal of the Linnean Society* 90:319–348.
- Feener, D. H., Jr., M. R. Orr, K. M. Wackford, J. M. Longo, W. W. Benson, and L. E. Gilbert. 2008. Geographic variation in resource dominance–discovery in Brazilian ant communities. *Ecology* 89:1824–1836.
- Fellers, G. M., and J. H. Fellers. 1982. Scavenging rates of invertebrates in an eastern deciduous forest. *American Midland Naturalist* 107:389–392.
- Fellers, J. H. 1987. Interference and exploitation in a guild of woodland ants. *Ecology* 68:1466–1478.
- Fellers, J. H. 1989. Daily and seasonal activity in woodland ants. *Oecologia* 78:69–76.
- Freschet, G. T., R. Aerts, and J. H. C. Cornelissen. 2012. A plant economics spectrum of litter decomposability. *Functional Ecology* 26:56–65.
- Geraghty, M. J., R. R. Dunn, and N. J. Sanders. 2007. Body size, colony size and range size in ants (Hymenoptera: Formicidae): are patterns along elevational and latitudinal gradients consistent with Bergmann's rule? *Myrmecological News* 10:51–58.
- Gibb, H., and C. L. Parr. 2010. How does habitat complexity affect ant foraging success? A test using functional measures on three continents. *Oecologia* 164:1061–1073.
- Gómez-Mestre, I., R. A. Pyron, and J. J. Wiens. 2012. Phylogenetic analyses reveal unexpected patterns in the evolution of reproductive modes in frogs. *Evolution* 66: 3687–3700.
- Grime, J. P. 2001. *Plant strategies, vegetation processes, and ecosystem properties*, Second edition. John Wiley, Chichester, UK.
- Gurd, D. B. 2008. Mechanistic analysis of interspecific competition using foraging trade-offs: implications for duck assemblages. *Ecology* 89:495–505.

- Hölldobler, B., and E. O. Wilson. 1990. *The ants*. Springer, Berlin, Germany.
- Holway, D. A., and T. J. Case. 2001. Effects of colony-level variation on competitive ability in the invasive Argentine ant. *Animal Behaviour* 61:1181–1192.
- Kaspari, M., and E. L. Vargo. 1995. Colony size as a buffer against seasonality: Bergmann's rule in social insects. *American Naturalist* 145:610–632.
- Kneitel, J. M., and J. M. Chase. 2004. Trade-offs in community ecology: linking spatial scales and species coexistence. *Ecology Letters* 7:69–80.
- Laughlin, D. C. 2014. The intrinsic dimensionality of plant traits and its relevance to community assembly. *Journal of Ecology* 102:186–193.
- Leal, I. R., A. G. D. Bieber, M. Tabarelli, and A. N. Andersen. 2010. Biodiversity surrogacy: indicator taxa as predictors of total species richness in Brazilian Atlantic forest and Caatinga. *Biodiversity Conservation* 19:3347–3360.
- Linksvayer, T. A., and M. A. Janssen. 2008. Traits underlying the capacity of ant colonies to adapt to disturbance and stress regimes. *Systems Research and Behavioral Science* 26(3):315–329.
- Maddison, W. P., and D. R. Maddison. 2011. *Mesquite: a modular system for evolutionary analysis*. Version 2.75. <http://mesquiteproject.org>
- Martin, T. E. 1995. Avian life history evolution in relation to nest sites, nest predation, and food. *Ecological Monographs* 65:101–127.
- McGill, B. J., B. J. Enquist, E. Weiher, and M. Westoby. 2006. Rebuilding community ecology from functional traits. *Trends in Ecology and Evolution* 21:178–185.
- McGlynn, T. P. 2000. Do Lanchester's laws of combat describe competition in ants? *Behavioral Ecology* 11:686–690.
- Moreau, C. S., D. B. Charles, R. Vila, S. B. Archibald, and N. E. Pierce. 2006. Phylogeny of the ants: diversification in the age of angiosperms. *Science* 312:101–104.
- Oliver, T. H., S. R. Leather, and J. M. Cook. 2008. Macroevolutionary patterns in the origin of mutualisms involving ants. *Journal of Evolutionary Biology* 21:1597–1608.
- Orme, C. D. L., et al. 2012. *Caper: comparative analyses of phylogenetics and evolution in R*. R package version 0.5. cran.r-project.org/package=caper
- Oster, G. F., and E. O. Wilson. 1976. *Caste and ecology in the social insects*. Princeton University Press, Princeton, New Jersey, USA.
- Palmer, T. M. 2004. Wars of attrition: colony size determines competitive outcomes in a guild of African acacia ants. *Animal Behaviour* 68:993–1004.
- Parr, C. L., and H. Gibb. 2009. Competition and the role of dominant ants. Pages 77–96 in L. Lach, C. L. Parr, and K. L. Abbott, editors. *Ant ecology*. Oxford University Press, Oxford, UK.
- Parr, C. L., and H. Gibb. 2012. The discovery-dominance trade-off is the exception, rather than the rule. *Journal of Animal Ecology* 81:233–241.
- Planqué, R., J. B. van den Berg, and N. R. Franks. 2010. Recruitment strategies and colony size in ants. *PLoS ONE* 5: e11664.
- Polidori, C., A. Crottini, L. Della Venezia, J. Selfa, N. Saino, and D. Rubolini. 2013. Food load manipulation ability shapes flight morphology in females of central-place foraging Hymenoptera. *Frontiers in Zoology* 10:36.
- R Development Core Team. 2011. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. www.r-project.org
- Retana, J., and X. Cerdá. 2000. Patterns of diversity and composition of Mediterranean ground ant communities tracking spatial and temporal variability in the thermal environment. *Oecologia* 123:436–444.
- Retana, J., X. Cerdá, and X. Espadaler. 1991. Arthropod corpses in a temperate grassland: a limited food supply? *Holarctic Ecology* 14:63–67.
- Revell, L. J. 2012. *Phytools: an R package for phylogenetic comparative biology (and other things)*. *Methods in Ecology and Evolution* 3:217–223.
- Ribera, I., S. Dolédec, I. S. Downie, and G. N. Foster. 2001. Effect of land disturbance and stress on species traits of ground beetles assemblages. *Ecology* 82:1112–1129.
- Roff, D. A., and D. J. Fairbairn. 2007. The evolution of trade-offs: where are we? *Journal of Evolutionary Biology* 20:433–447.
- Ruano, F., A. Tinaut, and J. J. Soler. 2000. High surface temperatures select for individual foraging in ants. *Behavioral Ecology* 11:396–404.
- Savolainen, R., and K. Vepsäläinen. 1988. A competition hierarchy among boreal ants: impact on resource partitioning and community structure. *Oikos* 51:135–155.
- Shik, J. Z. 2008. Ant colony size and the scaling of reproductive effort. *Functional Ecology* 22:674–681.
- Soares, S. A. 2013. The role of competition in structuring ant communities: a review. *Oecologia Australis* 17:81–91.
- Swenson, N. G., and M. D. Weiser. 2010. Plant geography upon the basis of functional traits: an example from eastern North American trees. *Ecology* 91:2234–2241.
- Tessier, A. J., M. A. Leibold, and J. Tsao. 2000. A fundamental trade-off in resource exploitation by *Daphnia* and consequences to plankton communities. *Ecology* 81:826–841.
- Traniello, J. F. A. 1989. Foraging strategies of ants. *Annual Review of Entomology* 34:191–210.
- van Oudenhove, L., R. Boulay, A. Lenoir, C. Bernstein, and X. Cerdá. 2012. Substrate temperature constrains recruitment and trail following behavior in ants. *Journal of Chemical Ecology* 38:802–809.
- Vesk, P. A. 2013. How traits determine species responses to environmental gradients. *Journal of Vegetation Science* 24: 977–978.
- Westoby, M. 1998. A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil* 199:213–227.
- Westoby, M., D. S. Falster, A. T. Moles, P. A. Vesk, and I. J. Wright. 2002. Plant ecological strategies: some leading dimensions of variation between species. *Annual Review of Ecology and Systematics* 33:125–159.
- Westoby, M., and I. J. Wright. 2006. Land-plant ecology on the basis of functional traits. *Trends in Ecology and Evolution* 21:261–268.
- Wiescher, P. T., J. M. C. Pearce-Duvel, and D. H. Feener, Jr. 2011. Environmental context alters ecological trade-offs controlling ant coexistence in a spatially heterogeneous region. *Ecological Entomology* 36:549–559.
- Wright, I. J., et al. 2004. The world-wide leaf economics spectrum. *Nature* 428:821–827.

SUPPLEMENTAL MATERIAL

Ecological Archives

Appendices A and B are available online: <http://dx.doi.org/10.1890/14-2326.1.sm>