



RESEARCH PAPER

Journal of
Biogeography

WILEY

Testing trade-offs and the dominance–impoverishment rule among ant communities

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Funding information

Beckett-Fonden; 15. Juni Fonden; Augustinus Fonden; Knud Højgaards Fond; Danmarks Grundforskningsfond, Grant/Award Number: DNRF96

Handling Editor: Evan Economo

[†]Raphael Boulay is deceased

Abstract

Aim: Ant communities are believed to be structured by competition, with dominant species competitively excluding subordinates (the dominance–impoverishment rule). However, a high number of seemingly similar species coexist, possibly due to interspecific trade-offs. Here, we examine the evidence for the dominance–impoverishment rule across a broad latitudinal gradient and explore whether trade-offs explain coexistence within and among ant communities.

Location: 40 sites in 19 countries across Europe, western North America and northern South America.

Taxon: Formicidae.

Methods: We conducted 2-hr baiting experiments at each site. Three dominance scores were calculated for each species at each site where it occurred. We then examined the relationship between ant dominance and diversity and tested for the generality of three trade-offs (dominance–discovery, dominance–thermal tolerance and dominance–generalism) within and among ant communities along with the possible effects of environmental variables on these trade-offs.

Results: We found no support for the dominance–impoverishment rule. Instead, overall species richness at baits was positively correlated with the number of dominant species and exhibited a unimodal relationship with the relative abundance of dominant ants. Moreover, we found little consistent evidence for the three interspecific trade-offs.

Main conclusion: Although total species richness at baits is positively correlated with species richness of dominant species and, to a point, increasing worker numbers of dominants, trade-offs among species do not appear to shape broad-scale patterns of coexistence among ants. Species richness declines only when the numbers of dominant workers are very high. Together, these results suggest that while trade-offs and the dominance–impoverishment rule might promote coexistence or shape ant communities in some locations, the evidence for their being general across communities is scant.

KEYWORDS

biogeography, competition, discovery, dominance, formicidae, resource use, thermal tolerance



1 | INTRODUCTION

Interactions among species, especially competitive interactions, are thought to be key to shaping the structure and dynamics of communities (Elton, 1946; Hölldobler & Wilson, 1990; Tilman, 1994). In ants, as in other organisms, competitively dominant species are thought to reduce the richness and abundance of subordinate species (Andersen, 1992; Duralia & Reader, 1993; Keddy, 1990), resulting in the 'dominance–impoverishment rule' (Hölldobler & Wilson, 1990; Campbell, Fellowes, & Cook, 2015). The rule predicts that species diversity should decrease linearly as the number or abundance of dominant species increases (Andersen & Patel, 1994; Hölldobler & Wilson, 1990).

However, evidence for the dominance–impoverishment rule is mixed. The diversity of ants within a community has sometimes even been found to be higher when dominant species are present (Arnan et al., 2018) or to show a unimodal relationship as the relative abundance of dominant species increases (Andersen, 1992; Parr, Sinclair, Andersen, Gaston, & Chown, 2005). It is possible that the relationship between ant dominance and diversity may depend on multiple factors, such as whether the dominant species are native or invasive or climatic conditions (Arnan et al., 2018). One mechanism that might allow subordinate species to persist even in the presence of dominant species is the existence of trade-offs (Elton, 1946; Kneitel & Chase, 2004; Tilman, 1994).

Trade-offs have been well studied and documented in plants (Huot, Yao, Montgomery, & He, 2014; Leishman, 2001; Muller-Landau, 2010; Petry, Kandlikar, Kraft, Godoy, & Levine, 2018; Tilman, 1994) but also in other taxa, including birds (Ebner, Pick, & Tschirren, 2016; Podlaskiewicz et al., 2016), marine sponges (Wulff, 2005) and ants (Cerdá, Retana, & Cros, 1998; Davidson, 1998; van Oudenhove, Cerdá, & Bernstein, 2018). However, it is not yet clear if and when trade-offs exist in a way that allows subordinate species to coexist with dominants (Adler, LeBrun, & Feener, 2007; Davidson, 1998; Feener, 1981, 2000; Holway, 1999; Human & Gordon, 1996; LeBrun, 2005; Lebrun & Feener, 2007; Morrison, Kawazoe, Guerra, & Gilbert, 2000; Parr & Gibb, 2012; Stuble, Rodriguez-Cabal, et al., 2013). Some studies suggest that trade-offs may depend on climate and are more pronounced at sites with more extreme temperatures (Bestelmeyer, 2000; Cerdá Retana, & Cros, 1997, 1998; Lessard, Dunn, & Sanders, 2009). However, studies of trade-offs in ants have typically been conducted at single sites (Cerdá, Arnan, & Retana, 2013; Cerdá, Retana, & Cros, 1997; Stuble, Rodriguez-Cabal, et al., 2013), limiting our ability to detect whether factors such as climate mediate the existence, strength or resulting consequences of trade-offs in ant communities (Chesson, 2000).

Here, we conducted baiting experiments at 40 sites across 19 countries to test for the existence of the dominance–impoverishment rule across ant communities, explore whether commonly proposed trade-offs explain ant species coexistence among and within sites, and evaluate how abiotic conditions influence these trade-offs. We focus on three key trade-offs previously proposed to structure ant communities:

1. *The dominance–discovery trade-off* predicts that the ants fastest at discovering resources are the worst at excluding competitors (Adler et al., 2007). Analogous trade-offs have been found in plants (Cadotte, 2007; Hastings, 1980), dogs (Kemp, 2005), mammalian carnivores (Hunter, Durant, & Caro, 2007) and finches (Herrel, Podos, Vanhooydonck, & Hendry, 2009) and could in ants be due to limited resources being allocated towards different foraging strategies (van Oudenhove et al., 2018).
2. *The dominance–thermal tolerance trade-off* predicts that dominant and subordinate species forage under different temperature conditions, allowing them to coexist under environmental fluctuations or as the result of occupying different temporal niches (Armstrong & McGehee, 1976; Chesson & Huntly, 1997; Loreau, 1992). Analogous trade-offs have been found in fish (Clark, Sandblom, Cox, Hinch & Farrell, 2008) and copepods (Willet, 2010). Mechanisms behind this trade-off are unclear but may be due to competitor or predator avoidance by subordinate species (Nonacs & Dill, 1990), heat-avoidance (Bacigalupe, Rezende, Kenagy, & Bozinovic, 2003; Stuble, Pelini, et al., 2013) or dominant species trading off heat tolerance for competitive dominance (Roze, Christen, Amerand, & Claireaux, 2013).
3. *The dominance–generalist trade-off* predicts that dominant species may be more specialized on particular resources than subordinates, allowing subordinate species to coexist by better capitalizing on a wider variety of resources (Abrams, 2002; Chesson, 1990, 2000; MacArthur, 1970). This theory is derived from classical theory of resource selection developed by Rosenzweig (1974), which has been widely studied in birds (Dhondt, 2012; Pimm & Pimm, 1982). The mechanisms behind this trade-off are unclear, but could be due to physiological adaptations in dominant ants (Davidson, 1997) or may reflect the outcome of competitive interactions between species, resulting in subordinates shifting their resource use (Sanders & Gordon, 2003).

2 | MATERIALS AND METHODS

2.1 | Study sites and sampling

We conducted baiting experiments at 40 sites of 20 × 20 m (each consisting of four 5 × 5 m subplots) during the daytime between June 29th and November 11th 2016: 20 in Spain, seven in France, five in Germany, three in Denmark, four in the United States and one in French Guiana (Figure 1). Sites were in areas with known ant activity or where ant fieldwork had previously been carried out and spanned a range of ecological biomes, including temperate forests, deserts and xeric shrublands and rainforests. Sites were separated by at least 100 m and we had local permission to work at each site.

We designed the experiments similarly to classic experiments in ant ecology (Andersen, 1992; Cerdá et al., 1997; Fellers, 1987; Perfecto, 1994; Sanders & Gordon, 2003; Savolainen & Vepsäläinen, 1988; Savolainen, Vepsäläinen, & Wuorenrinne, 1989). Specifically, we chose five different resources (canned tuna in water,

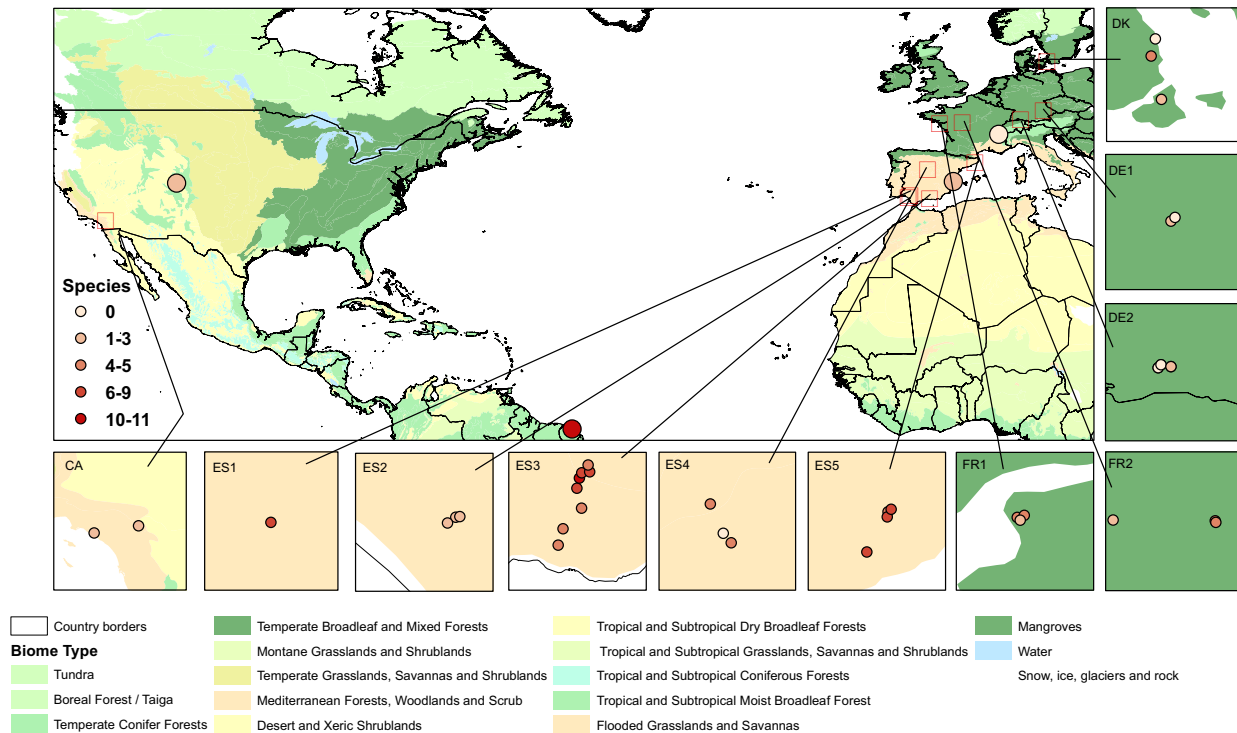


FIGURE 1 Global map of the 40 study sites for ant (Formicidae) baiting experiments included in this study (20 in Spain [ES1-5], seven in France [FR1-2], five in Germany [DE1-2], three in Denmark [DK], four in the United States [CA and CO] and one in French Guiana [FG]) with cut-outs for areas where sites were too close together to distinguish. Colours indicate the number of species recorded at each site, ranging from 0 to 11, with a total of 72 species in 27 genera. Background colours indicate the major biomes at each sites. Most experiments were carried out in areas of either Mediterranean or Temperate forests and scrub [Colour figure can be viewed at wileyonlinelibrary.com]

untoasted sesame seeds, 20% sugar water solution, 1% saltwater solution and tap water) to attract diverse species at each site. Approximately one teaspoon of solid resources and 2.5 cm diameter cotton balls soaked in the liquid resources were placed on individual ~6 cm diameter plastic discs in the middle of each subplot in a pentagonal shape, equidistant from the plot boundaries and approximately 20 cm from each other. In all, 20 baits were deployed at each site: One bait per bait type (5) per subplot (4). See Supporting Information for an illustration of the set-up (Figure S1). After deploying the baits, the numbers and identities of ants present were recorded after 5, 15, 30, 60, 90 and 120 min. Ground temperatures were measured during each observation using a handheld infrared thermometer (Raytek Raynger ST).

2.2 | Environmental data

We extracted four environmental variables from online databases for each site. Mean annual temperature (MAT) and annual precipitation (AP) data were extracted from the 1970 to 2000 average WorldClim2 dataset at a resolution of 30 arc seconds (Fick & Hijmans, 2017). Both temperature and precipitation have previously been identified as important determinants of ant distributions (Fitzpatrick et al., 2011; Kluge, Kessler, & Dunn, 2006; Lessard et al., 2009). In addition, we extracted monthly normalized difference vegetation

index (NDVI) values for each site during the month when sampling occurred from Moderate-Resolution Imaging Spectroradiometer MOD17, 30-arcsec data (Didan, 2015). NDVI is often used as a measure of productivity (Sanders, Lessard, Fitzpatrick, & Dunn, 2007), which is hypothesized to be correlated with larger population sizes and perhaps increased competition. Finally, we estimated actual evapotranspiration (AET) using Turc's formula (Kluge et al., 2006; Turc, 1954; Sanders et al., 2009), where $AET = P/[0.9 + (P/L)^2]^{1/2}$ with $L = 300 + 25T + 0.05T^3$, P = annual precipitation and T = annual mean temperature. AET is the quantity of water removed from a surface due to the processes of evaporation and transpiration and has been shown to be an important correlate of diversity at broad spatial scales (Currie et al., 2004).

A correlation matrix between the four environmental variables showed a significant correlation between MAT and AP (0.58, $p < 0.0001$), NDVI (-0.49 , $p < 0.0001$) and AET (0.72, $p < 0.001$), and AP and AET (0.98, $p < 0.0001$). However, except for the correlation between AP and AET, all correlations were nonlinear (Figure S2).

2.3 | Dominance

Ant dominance has been defined in multiple ways (Cerdá et al., 2013; Parr & Gibb, 2012), with different dominance metrics

reflecting different ecological phenomena (see Stuble, Juric, Cerdá, & Sanders, 2017). In this study, we only assess ecological dominance, which we calculated in three different ways based on the numerical abundance of workers at baits (one metric) and the monopolization of baits (two separate metrics. Andersen, 1992; Cerdá et al., 1997; Parr et al., 2005). Numerical abundance was calculated following a 6-point scale: 1, 1 ant; 2, 2–5 ants; 3, 6–10 ants; 4, 11–20 ants; 5, 21–49 ants and 6, 50+ ants (as in Andersen, 1997a). All three dominance metrics were calculated for each ant species at each site where it occurred. Monopolization was calculated as the number of observations where baits were monopolized, and we considered baits to have been monopolized if one species was present with 20 or more individuals simultaneously. We assessed two different monopolization metrics: (a) the proportion of available baits monopolized per subplot (5 baits \times 6 time periods = 30 available) and (b) the proportion of discovered baits monopolized (as in Parr et al., 2005). This differs slightly from other ways of measuring dominance, where a species only dominates a bait if it is the only species on a bait by the end of an experiment (see Stuble et al., 2017), by allowing for situations where different species could have been considered to monopolize the same bait, but at different times.

We used Spearman rank correlation with a 0.70 threshold to test for correlation between the dominance metrics (Hinkle, Wiersma, & Jurs, 2003). Monopolization of discovered baits was highly correlated with monopolization of all possible baits ($r = 0.98$, $p < 0.001$) and mean abundance score ($r = 0.71$, $p < 0.001$). Monopolization of all possible baits was also highly correlated with mean abundance score ($r = 0.70$, $p < 0.001$). Therefore, we used monopolization of discovered baits as representative of dominance in all further analyses.

Finally, we classified species as dominant or subordinate at each site based on mean monopolization score of discovered baits. Species with dominance scores higher than the upper 95% confidence interval of the mean dominance scores of all ants combined across all sites were considered to be dominant. All other species were classified as subordinate. The mean monopolization percentage of discovered baits (the number of observations where a species monopolized a bait divided by the total number of times that species was observed in that plot) was $8.6 \pm 2.44\%$ 95% CI, and dominant species thus had a monopolization score above 11.04%. Site-level dominance calculations allowed a species to be dominant at one site but subordinate at another.

2.4 | Discovery ability

Discovery ability was assessed based on the number of times a species was first to occur at a bait (Lebrun & Feener, 2007; Parr & Gibb, 2012). Species that occurred first were assigned '1', and all subsequent species to arrive were assigned '0'. If two or more species arrived at a bait at the same time, they were both assigned '1'. We then divided the total number of baits a species discovered first by the total number of baits that the species discovered (a maximum of 20 if a species discovered all baits) to determine its discovery ability.

While this allowed us to assess the discovery ability of species that were actively foraging during the time of the experiment, it did not account for any potential differences in species abundances or their peak foraging times.

2.5 | Thermal activity range

For each species at each plot, we calculated the ground temperature range during which that species was foraging, and use this as an approximation of the species' thermal activity range. While not a reflection of a species' thermal tolerance or fundamental niche, this is a commonly used method to determine whether subordinate species have the ability to persist because they forage under broader temperature ranges than dominant species (Bestelmeyer, 2000; Cerdá, 2001; Cerdá, Angulo, Boulay, & Lenoir, 2009).

2.6 | Resource use

We calculated resource generalism for each species at a site using Hurlbert's probability of an interspecific encounter index (PIE): $PIE = \frac{N}{N-1} \times 1.0 - \sum_{i=1}^S (p_i)^2$, where S is the number of bait types, p_i is the proportion of workers found on bait i and N is the total number of workers observed (Ellison & Gotelli, 2009; Gotelli & Graves, 1996; Hurlbert, 1971). PIE ranges from 0 to 1, where a value close to 0 indicates that the species is a resource specialist and a value close to 1 indicates that the species uses multiple resources equally and is a generalist. Species that were only present at a site with a single worker were excluded from the resource use analysis.

2.7 | Is there evidence for the dominance–impoverishment rule?

Species richness or abundance of dominant ants has been shown to be correlated with total species richness in different ways, depending on how dominance is measured and whether dominant species are native or non-native (e.g. unimodal; Andersen, 1992; Arnan et al., 2018; Parr, 2008; Parr et al., 2005, logarithmic; Baccaro, De Souza, Franklin, Landeiro, & Magnusson, 2012, negative linear; Andersen & Patel, 1994; Morrison, 1996). To test whether there is a negative linear or unimodal relationship between apparent species richness and the abundance or number of dominant species at baits across multiple sites, we carried out two separate mixed effects linear and second-order polynomial models with the total number of observed species at each site as the dependent variable in both models, either the number of dominant species or the abundance of dominant species as the independent variable, and locality as a random effect to account for possible spatial autocorrelation in both models. Model performance was evaluated using the AIC score and we used variance inflation factors (VIF) to test for multicollinearity (Borenstein, Hedges, Higgins, & Rothstein, 2009; Craney & Surles, 2002). We acknowledge that actual species diversity



at sites may differ from the observed diversity at baits, but are in this study only considering interacting species.

2.8 | Do trade-offs promote coexistence within and among ant communities?

To test for the existence of the dominance–discovery, dominance–thermal tolerance and dominance–generalist trade-offs across sites, we used generalized linear mixed models fit by maximum likelihood (Adaptive Gauss-Hermite Quadrature, with 25 iterations) with monopolization as the response variable, discovery ability, temperature range and resource generalism as fixed effect and locality as a random effect. As before, we tested for multicollinearity between the three independent variables using VIF. In the analysis, each point is a specific species at a specific site. A significantly negative relationship between dominance and discovery ability would provide evidence for the dominance–discovery trade-off, with dominant species being slower to discover resources than subordinate species. A significantly negative relationship between dominance and the activity temperature range would provide evidence for the dominance–thermal tolerance trade-off, with subordinate species foraging over a broader range of temperatures than dominant species. A significant negative relationship between resource generalism (measured as PIE) and dominance would provide evidence for the dominance–generalism trade-off, with dominant species being more specialized in their resource use than subordinate species. To determine if there was a significant difference between dominant and subordinate species in discovery ability, thermal tolerance and specialization, we compared the mean values of each variable for species classified as dominant and subordinate using Student's *t* tests.

To test for the effect of environmental variables on the presence of trade-offs in ant communities, we conducted Spearman rank correlations between dominance and discovery, dominance and thermal tolerance and dominance and generalism for each site where three or more species were present. We then use the correlation coefficients (*r*-values) as an effect size index (Borenstein et al., 2009) to explore the effect of mean annual temperature (MAT), annual precipitation (AP), actual evapotranspiration (AET) and monthly NDVI on the trade-offs using a linear mixed model. Because of high correlation between some of the climatic variables, we first ran a model containing all variables and evaluated this using VIF. We then ran a second model in which we dropped the variable with the highest score (AET). This did not change the performance of the model (Table S1). Finally, we corrected for multiple comparisons by Bonferroni correction (Bonferroni, 1935). A significant positive effect would suggest that a factor strengthens the tested trade-off.

2.9 | Data and analyses

All analyses were conducted in 'R' (R Core Team, 2018) using the packages 'raster' (Hijmans (2019), 'lme4' (Bates, Maechler, Bolker,

& Walker, 2015), 'jtools' (Long, 2019), 'car' (Fox & Weisberg, 2019) and 'MASS' (Venables & Ripley, 2002). Figures were created using the R packages 'ggplot2' (Wickham, 2016), 'ggpubr' (Kassambara, 2019) and 'cowplot' (Wilke, 2019) and the map was created using 'ArcGIS' (ESRI, 2010). All data used in this study have been made publicly available through Sheard et al. 2020. Code has been made freely available through Github (<https://github.com/JKSheard/Tradeoffs.git>). An overview of all analyses is shown in Table S1.

3 | RESULTS

Across all sites, we observed 72 species in 27 genera. The number of species present at the baits at each site ranged from zero at one site each in Denmark and in Germany to 14 in French Guiana (mean: 4.45 ± 2.73 SD; Figure 1; Table S2). The two sites where no ants were present were excluded from all analyses. The most common species in the dataset were *Aphaenogaster senilis* (209 observations, 6 localities), *Aphaenogaster iberica* (175 observations, 10 localities), *Camponotus cruentatus* (98 observations, 2 localities) and *Pheidole pallidula* (76 observations, 9 localities; Table S3). We identified 26 ant species as dominant at one or more sites in which they occurred (mean monopolization score $>11.04\%$). Eight of these species were dominant at all sites in which they occurred (Table S3). On average, dominant species monopolized baits during $31.14\% \pm 2.76$ SE of all observations.

3.1 | Is there evidence for the dominance–impoverishment rule?

We found a significant linear relationship between dominant species richness and overall species richness ($R^2 = 0.10$ [fixed effects], $R^2 = 0.59$ [total], $p = 0.03$, Figure 2a), but this relationship was positive rather than negative (slope = 0.79), a pattern opposite to that expected by the dominance–impoverishment rule. We found a unimodal relationship between overall species richness and the relative number of dominant workers ($R^2 = 0.19$ [fixed effect] and 0.29 [total], $p = 0.01$; Figure 2b).

3.2 | Do trade-offs promote coexistence within and among ant communities?

3.2.1 | The dominance–discovery trade-off

If ants adhere to the dominance–discovery trade-off, we would expect a negative relationship between dominance and discovery ability such that subordinate species persist because they are faster at discovering baits than are dominant species. However, we found no relationship between monopolization and the percentage of baits discovered first ($R^2 = 0.15$, $p = 0.32$,

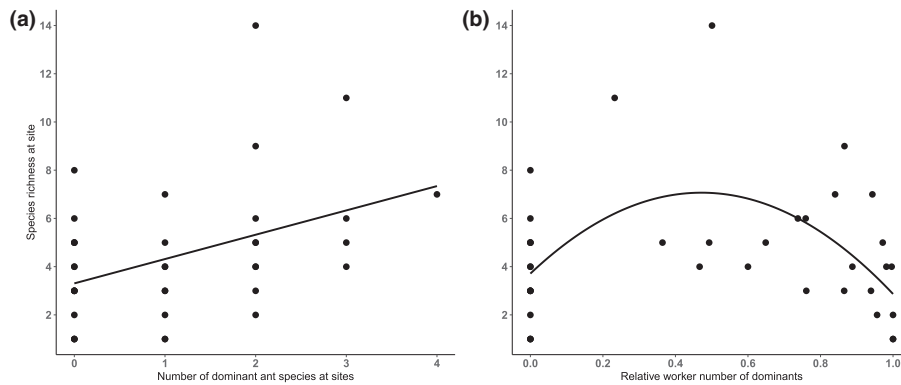


FIGURE 2 Test of the dominance–diversity relationship of ants across 40 sites in North America, South America and Europe. (a) Relationship between species richness and number of dominant species ($R^2 = 0.10$ [fixed effects], $R^2 = 0.59$ [total], $p = 0.03$). (b) Relationship between species richness and the relative number of workers of dominant ants at site level ($R^2 = 0.19$ [fixed effect] and $R^2 = 0.29$ [total effects], $p = 0.01$). Species richness increased linearly with number of dominant species and unimodally with relative number of dominant workers. Relative number of dominant workers was calculated as the number of dominant workers at a site divided by the total number of workers observed at a site

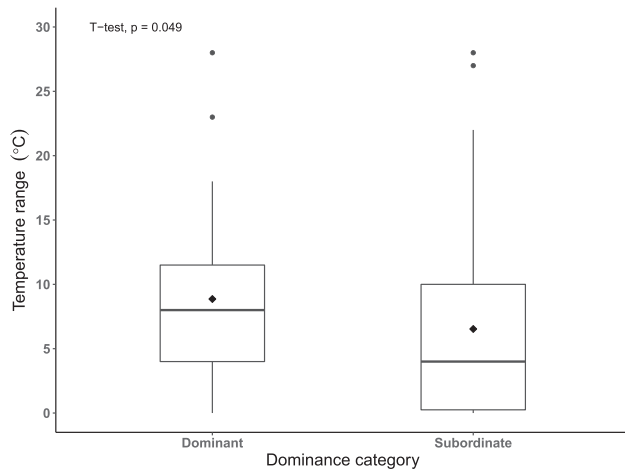


FIGURE 3 Boxplots showing the median, interquartile range, minimum and maximum temperature ranges for foraging workers of dominant and subordinate ant species from 40 sites across Europe, North America and South America. Black diamonds represent the mean. There was a significant difference in temperature range ($p = 0.049$), with dominant species having a higher range than subordinate species

Est. = 0.01). On average, dominant species discovered baits first $61 \pm 37\%$ SD of the time and subordinate species discovered baits first $59 \pm 37\%$ SD of the time with no difference between the two groups ($t_{73.27} = 0.27$, $p = 0.79$). In fact, only one site (Lower Blue Jay Campground in Cleveland National Forest, USA with three species present) showed a significant relationship between dominance and discovery ($r = 1$, $p < 0.0001$; Table S4), but the pattern was opposite that predicted by the dominance–discovery trade-off. We found no significant drivers of the dominance–discovery trade-off based on MAT, AP, AET or NDVI ($p > 0.4$ in all cases).

3.2.2 | The dominance–thermal tolerance trade-off

If ants adhere to the dominance–thermal tolerance trade-off, here represented by activity temperature range, then dominance and activity temperature range should be negatively correlated, with dominant species foraging at a narrower temperature range than do subordinate species. However, we found no trade-off between monopolization and activity temperature range ($R^2 = 0.15$, $p = 0.86$, Est. = 0.01). There was a slight difference in mean observed foraging temperature range, but this was the opposite of what the trade-off predicts, with dominant species having a broader activity temperature range than subordinate species ($8.86^\circ\text{C} \pm 6.50$ SD and $6.53^\circ\text{C} \pm 6.80$ SD, respectively, $t_{75.68} = 2.0042$, $p = 0.049$, Figure 3). Overall, only two sites showed a significant relationship between dominance and activity temperature. These were Regensburg Universität in Germany ($r = 1$, $p < 0.0001$) and La Turleda in Spain ($r = 0.96$, $p = 0.0005$, Table S4). In both cases, dominant species had a higher temperature range than subordinate species. We found no significant drivers of the dominance–thermal tolerance trade-off based on MAT, AP, AET or NDVI ($p > 0.96$ in all cases).

3.2.3 | The dominance–generalist trade-off

There was a significant relationship between monopolization and resource generalism measured as Hurlbert's PIE ($R^2 = 0.15$, $p = 0.02$, Est. = -2.89). Dominant species were more specialized in their resource use than were subordinate species (PIE = 0.37 ± 0.23 SD and 0.54 ± 0.25 SD, respectively, $t_{82.21} = -3.94$, $p = 0.0002$, Figure 4). Two sites showed a significant correlation between dominance and resource generalism (Girona forest, $r = -0.94$, $p = 0.0005$ and Girona Universidad, $r = -0.89$, $p = 0.04$, Table S4), with dominant species being more specialized in both cases. We found a significant positive effect of annual precipitation on the dominance–generalist trade-off



(Est. = 0.004, $p = 0.04$), but upon removing the outlier (French Guiana) this effect disappeared (Est. = 0.004, $p = 0.16$). There was no effect of MAT, AET or NDVI ($p > 0.08$ in all cases).

4 | DISCUSSION

Trade-offs can promote species coexistence in many taxa (Chesson, 2000), including ants (Bestelmeyer, 2000; Hölldobler & Wilson, 1990). In the absence of other factors, dominant species would be expected to outcompete subordinate species (Andersen & Patel, 1994; Hölldobler & Wilson, 1990). Yet, species diversity is sometimes higher where more dominant species are present (Arnan et al., 2018) or can increase at least up to a certain point before decreasing, leading to unimodal relationship (Andersen, 1992; Parr et al., 2005).

We found that across sites, species richness increased linearly with the number of dominant species present (Figure 2a) and had a unimodal relationship with the number of workers of dominant species present at a bait (Figure 2b), as in previous studies (Andersen, 1992; Parr et al., 2005). This suggests that rather than dominant species playing a strong role in suppressing the diversity of other species, habitat quality and favourable environmental conditions may instead be more important for determining species richness, as has previously been found by others on smaller scales (Andersen, 1995, 1997b). However, our study and others (Andersen, 1992; Morrison, 1996; Parr et al., 2005) also show that species richness at baits decreases when the number of workers of dominant species becomes so high that dominant species can competitively exclude

subordinates from resources. Such relationships are common in the case of non-native dominant species (Arnan et al., 2018).

Furthermore, we failed to find strong evidence for any of the three trade-offs commonly proposed to mediate species coexistence within ant communities. In the late 1900s and early 2000s, there was a broad consensus that trade-offs in ant communities were common, and the ability of a species to break a trade-off was sometimes thought to be an explanation for its global success or invasibility (Holway, Lach, Suarez, Tsutsui, & Case, 2002). However, as more data from field work across systems accrued, the generality of especially the dominance–discovery trade-off as an explanation for coexistence seemed to be called into question (Jordan & Blüthgen, 2007; Parr & Gibb, 2012). Indeed, our results also fail to point to any sort of dominance–discovery trade-off or dominance–thermal tolerance trade-off. Although we do find some evidence that dominant species may be more specialized in their resource use than subordinate species.

The dominance–discovery trade-off was not supported by our study. Only one site showed a trade-off between dominance and discovery ability. While previous studies have found support for this trade-off (Adler et al., 2007; Feener et al., 2008; Fellers, 1987; Lebrun & Feener, 2007), these were typically context-specific (Lessard et al., 2009; Parr & Gibb, 2012; Stuble, Pelini, et al., 2013). Even in studies where trade-offs occur or might occur, such community-wide trade-offs are easily disrupted, whether by the presence of parasitoids (Feener et al., 2008; Lebrun & Feener, 2007) or by shifts in the availability of resources (Sanders & Gordon, 2003).

The dominance–thermal tolerance trade-off was also not supported by our study. We observed ants at a site six times over a 2-hr period. During these periods, dominant ants foraged within significantly broader temperature ranges than subordinates (Figure 3), in contradiction with the proposed trade-off. Other studies using similar methods have also failed to find support for the dominance–thermal tolerance trade-off (Stuble, Rodriguez-Cabal, et al., 2013). However, this trade-off has some support in the literature when ants are observed using methods different from ours. Some studies have identified opposite diurnal activity patterns in dominant and subordinate ants of Spain (Cerdá et al., 1997; Cerdá, Retana, & Cros, 1998; Cerdá, Retana, & Manzaneda, 1998), Argentina (Bestelmeyer, 2000), North America (Albrecht & Gotelli, 2001) or differing thermal tolerance ranges along an elevational gradient (Lessard et al., 2009).

The dominance–generalism trade-off was the only trade-off detectable across all sites combined. Dominant species were more specialized in their resource use than subordinate species (Figure 4). This may also explain why overall dominance, measured as monopolization, was low (only 30% of bait × observation time combinations were monopolized). Our results line up with theories stating that dominant species may specialize on certain large, high-reward resources (Pearce-Duvet & Feener, 2010) and that ants partition resources both spatially and temporally (Delsinne, Roisin, & Leponce, 2007). Another study found that subordinate species shift their foraging preferences in the presence of dominant species (Sanders &

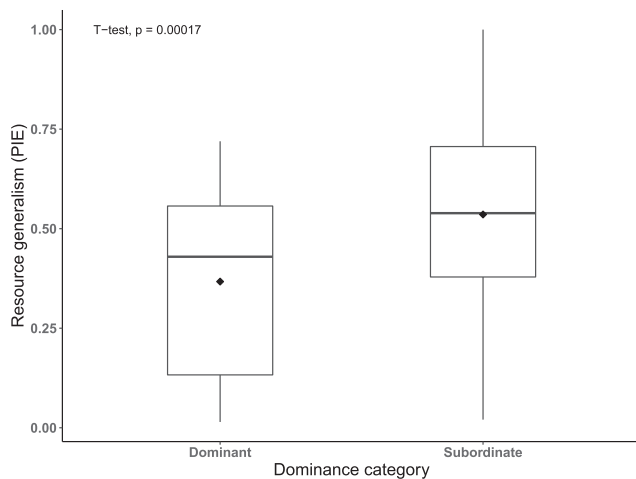


FIGURE 4 Test of the dominance–generalism relationship of ants across 40 sites in Europe, North America and South America, where dominance is calculated as the percentage of discovered baits which were monopolized and generalism is calculated as Hurlbert's probability of an interspecific encounter index (PIE). Boxplot showing the median, interquartile range, minimum and maximum generalism values for foraging workers of dominant and subordinate ant species. Black diamonds represents the mean. Dominant species are significantly more specialized than subordinates ($p = 0.0002$)

Gordon, 2000). To determine the generality of this, a global scale competitor removal experiment across multiple taxa would be of high value. There is some evidence that invasive species break the dominance–generalism trade-off by being both dominants and generalists (Davidson, 1997, 1998; Davidson & Patrell-Kim, 1996; Human & Gordon, 1996; McPeck, 1996; Pearce-Duvet & Feener, 2010), which opens up the need for comparing the resource use of dominant natives and dominant exotics.

Environmental drivers might promote trade-offs in ant communities. For example, the dominance–thermal tolerance trade-off might be more prevalent under extreme temperatures (Bestelmeyer, 2000; Cerdá et al., 1997; Cerdá, Retana, & Cros, 1998; Lessard et al., 2009). Although we were unable to detect any significant environmental drivers of the tested trade-offs, we mainly carried out experiments in Mediterranean and Temperate forests, woodlands and scrub. Future studies should therefore focus on sampling biomes across a broad range of environmental conditions.

We conclude that, although local evidence has previously been found for trade-offs in some ant communities (see e.g. Adler et al., 2007; Bestelmeyer, 2000; Fellers, 1987), there is no clear evidence for the role of these three trade-offs as mechanisms for coexistence on a larger geographical scale. Other studies have shown that trade-offs can interact (Lebrun & Feener, 2007) and may be context-specific, which makes detecting trade-offs and their drivers a complicated task. It could be the case that we did not examine activity over a wide enough range of temperatures to detect a dominance–thermal tolerance trade-off, or we did not work in sites with high enough levels of dominance, or we might have gotten different results with pitfall or winker traps instead of baiting experiments (Baccaro et al., 2012). Not only may there be trade-offs in species communities, but there are also trade-offs in how ant ecologists can address questions. Focusing on a single site for many months (e.g. Albrecht & Gotelli, 2001; Fellers, 1987; Stuble, Rodriguez-Cabal, et al., 2013) may provide in-depth understanding of that site; or one could examine the evidence for multiple trade-offs at multiple sites with the hope of gaining a breadth of understanding of those sites. Our approach was the latter approach. Moving forward, we suggest that removal experiments (e.g. Gibb, 2011; Sanders & Gordon, 2000) or highly controlled experiments in constructed communities, like those in freshwater cattle tanks (e.g. Chase, 2007), may bring further understanding to the field. While we of course realize that some trade-offs might exist at some sites (indeed across our sites, we found occasional, but limited, evidence for a particular trade-off at a particular site), we found that three trade-offs previously proposed to play an important role in structuring ant communities are not broadly supported.

ACKNOWLEDGEMENTS

We would like to thank Jes S e Pedersen, Catherine Parr and Xim Cerda for helping develop the field protocol and Elena Angulo, Irene Villalta Alson, Javier Seoane, Francisco Martin Azc arate, N uria Roura-Pascual, Cristina Borr as, Crisanto Gomez, Abel Bernabou, Dietrich Klimetzek and Pol Lannes for help with fieldwork. We

thank Anders P. T ottrup for discussions on earlier versions of this paper. Julie Sheard was funded by the Danish National Research Foundation (DNRF96), 15th of June Foundation, Knud H jgaard Foundation, Augustinus Foundation and Beckett Foundation.

DATA AVAILABILITY STATEMENT

All data have been uploaded to Dryad (<https://doi.org/10.5061/dryad.crjdfn31r>). All code has been uploaded to Github (<https://github.com/JKSheard/Tradeoffs>).

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BIOSKETCH

Julie Koch Sheard is broadly interested in how the environment affects community composition on a global and local scale. This work represents a component of her PhD work at Copenhagen University on the biogeography, community composition and conservation of ants using citizen science. She and the other authors collaborate across institutions on questions relating to ant biodiversity.

Authors' contributions: JKS, RB, RRD and NJS conceived the ideas; JKS, JDB, ASN and NJS conducted the fieldwork; JKS and JDB analysed the data and JKS led the writing with assistance from ASN, RB, RRD and NJS.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Sheard JK, Nelson AS, Berggreen JD, Boulay R, Dunn RR, Sanders NJ. Testing trade-offs and the dominance-impoverishment rule among ant communities. *J Biogeogr.* 2020;47:1899–1909. <https://doi.org/10.1111/jbi.13911>