Dominance hierarchies are a dominant paradigm in ant ecology (Hymenoptera: Formicidae), but should they be? And what is a dominance hierarchy anyways?

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Abstract

There is a long tradition of community ecologists using interspecific dominance hierarchies as a way to explain species coexistence and community structure. However, there is considerable variation in the methods used to construct these hierarchies, how they are quantified, and how they are interpreted. In the study of ant communities, hierarchies are typically based on the outcome of aggressive encounters between species or on bait monopolization. These parameters are converted to rankings using a variety of methods ranging from calculating the proportion of fights won or baits monopolized to minimizing hierarchical reversals. However, we rarely stop to explore how dominance hierarchies relate to the spatial and temporal structure of ant communities, nor do we ask how different ranking methods quantitatively relate to one another. Here, through a review of the literature and new analyses of both published and unpublished data, we highlight some limitations of the use of dominance hierarchies, both in how they are constructed and how they are interpreted. We show that the most commonly used ranking methods can generate variation among hierarchies given the same data and that the results depend on sample size. Moreover, these ranks are not related to resource acquisition, suggesting limited ecological implications for dominance hierarchies. These limitations in the construction, analysis, and interpretation of dominance hierarchies lead us to suggest it may be time for ant ecologists to move on from dominance hierarchies.

Key words: Aggression, ant, competition, dominance hierarchy, monopolization, network, rank, review, tradeoffs.

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Introduction

Dominance hierarchies are frequently employed in behavioral and ecological research (CHASE & SEITZ 2011). Behavioral ecologists have long used hierarchies to rank individuals based on dominance or aggression within a group. For instance, a behavioral ecologist might like to know how chimpanzee societies are organized or how food is distributed within ant colonies (e.g., COLE 1981, PUSEY & al. 1997). Community ecologists have adapted the dominance hierarchy framework and have begun to rank s p e c i e s as a function of behavioral dominance (MORSE 1974, SCHOENER 1983). These interspecific dominance hierarchies have played an important role in community ecology and are frequently employed in models, either verbal or quantitative, to explain local coexistence of species in ecological communities. But what are dominance hierarchies in the context of communities? How are they used? And what do they mean?

The dominance hierarchies created to understand ant communities are nothing more than the ranks of species based on either their numerical or behavioral dominance. N u m e r i c a l d o m i n a n c e is based on the relative abundance of a species within a community, while b e -havioral dominance is based on the outcome of interspecific encounters (DAVIDSON 1998). A combination of these two forms of dominance is often referred to as e c o l o g i c a l d o m i n a n c e, which aims to elucidate the general ecological impacts of a species (DAVIDSON 1998). Most myrmecologists mean "behavioral" dominance when they use "dominance" loosely, and this concept of behavioral dominance has been central to much of the literature on coexistence of ant species (HÖLLDOBLER & WILSON 1990) until very recently (e.g., KASPARI & al. 2012, ANDERSEN & al. 2013, FOWLER & al. 2014). Dominance hierarchies are typically constructed using field data on aggressive encounters, bait monopolization, or territoriality. The field data are then converted into ranks using a variety of methods ranging from simple counts (who won the most fights) or proportions (who won the greatest proportion of fights) to the more mathematically complex minimization of competitive reversals (DE VRIES 1998) and Colley matrix methods (discussed in the Results and Discussion section). However, a growing number of myrmecologists have suggested that dominance hierarchies may be limited in their ability to describe the structure and dy-

namics of ant communities (GORDON 2011, CERDÁ & al. 2013). In this paper, we explore whether and why that might be the case and (perhaps) offer a way forward for those intrepid myrmecologists who want to link behavioral observations to ant community structure.

Application of dominance hierarchies: The practice of classifying ant species according to their degree of behavioral aggression has been around since at least 1952 when Brian described the nesting habits of a guild of woodland ants (BRIAN 1952). GREENSLADE (1971) created a formal hierarchy to examine shifts in relative abundance within an ant community in the Solomon Islands. In the same year WILSON (1971) classified ants into hierarchies based on their foraging behavior. In a paper that ushered in modern ant community ecology in 1987, Fellers ranked ant species numerically in order to describe what she called a dominance-discovery tradeoff within a guild of woodland ants (FELLERS 1987). Since then, dominance hierarchies have been used extensively in studies of ant ecology ranging from explanations of ant coexistence to understanding ant-plant mutualisms (Tab. S1, as digital supplementary material to this article, at the journal's web pages).

As is the case with many other taxa, the most common use of dominance hierarchies is in the formal testing of tradeoffs to explain species coexistence within ant communities. In ant communities, these tradeoffs include the dominance-discovery tradeoff, the dominance-thermal tolerance tradeoff, and the dominance-colonization tradeoff (e.g., CERDÁ & al. 1998c, BESTELMEYER 2000, STANTON & al. 2002, LEBRUN & FEENER 2007, LESSARD & al. 2009, STUBLE & al. 2013). Parasites can alter dominance hierarchies, thereby disrupting tradeoffs such as the dominance-discovery tradeoff (LEBRUN 2005, LEBRUN & FEENER 2007). In addition to testing for the signature of these tradeoffs, dominance hierarchies have been used to understand a range of ecological dynamics including trail-sharing (MENZEL & al. 2010), food selection (LUQUE & REYES LÓPEZ 2007), mutualisms between ants and plants (LEAL & al. 2006, XU & CHEN 2010, ARANDA-RICKERT & FRACCHIA 2012), and spatial partitioning (PAULSON & AKRE 1991, MORRISON 1996, PALMER & al. 2000, DELSINNE & al. 2007, PALMER & al. 2013). Additionally, dominance hierarchies are used to categorize species within a guild as dominant and subordinate, primarily in attempts to elucidate the influence of dominant species on community structure and composition (e.g., ANDERSEN 1997, WARD & BEGGS 2007, BACCARO & al. 2010, ARNAN & al. 2011, CERDÁ & al. 2012).

Despite the wide use of dominance hierarchies in ant community ecology, there is a lack of consistency in the definition of dominance and, perhaps as a result, in the methods by which dominance is measured and hierarchies are constructed. These inconsistencies ultimately undermine the usefulness of dominance hierarchies in community ecology, creating disparate hierarchies that often correlate with different aspects of the behavior and life history of the ants, or are not related to behavior or life history at all. Here, we attempt to clear some of the murkiness of dominance hierarchies and how they have been used and interpreted. First we review the methods most commonly employed by myrmecologists to estimate dominance and examine how these various measures of dominance relate to important aspects of ant ecology. Second, using several previously published datasets we explore how various ranking methods relate to one another, and to community structure (relative abundances of ant species within the community) and function (the ability of ants to acquire food resources). We also discuss potential context-dependency in these hierarchies. Finally, we propose a way forward for ecologists interested in incorporating competitive relationships among ants into models aimed at understanding the structure and dynamics of ant communities.

Methods

Review: On 16March 2016 we conducted an ISI Web of Science search of the Core Collection using the terms "dominance AND hierarchy AND ant*" and "rank* AND ant*" in the topic field. From the resulting list of publications, we kept only those papers that created an interspecific dominance hierarchy of ant species. We supplemented this search with additional studies from our own knowledge of the literature and by perusing the citations of recent review papers and citations in the manuscripts that turned up in our Web of Science search. In total, our search found 55 papers meeting our criteria. See Table S1 for a full list of the literature reviewed.

Field tests of dominance: In addition to reviewing the literature, we reanalyzed three previously published dominance hierarchies from: Mediterranean Spain (CERDÁ & al. 1998a), a pine woodland in Arizona, USA (LEBRUN 2005), and a temperate forest in North Carolina, USA (STUBLE & al. 2013). All three studies monitored antagonistic interactions between ant species on baits placed in natural areas. The data in the CERDÁ & al. (1998a) and STUBLE & al. (2013) studies were collected by the authors. From each of these two datasets we had information on the number of ants per species on a bait, the outcomes of interspecific interactions on these baits, and the time of day at which these interactions took place (STUBLE & al. 2013: 288 baits; CERDÁ & al. 1998a: 30 baits sampled hourly once a month from April through November). Both of these studies involved nocturnal and diurnal baiting. The STUBLE & al. (2013) dataset also included general abundance data derived from pitfall trapping in which 98 pitfall traps were set up over the course of the experiment, each left open for 48 hours. The LEBRUN (2005) dataset provided information on the numbers of wins and losses for each pair of species and was extracted from the published literature (336 baits sampled over two days).

We supplemented these datasets with the results of a new termite baiting experiment conducted in North Carolina in the same deciduous forest as in STUBLE & al. (2013). From May through July of 2010 we put out 80 caches of locally collected, freeze-killed termites on laminated index cards. One bait card was put out at a time and was observed for an hour, during which time we noted the identity of each ant removing the termites and how many termites each species removed. Bait card locations were typically more than 5 m from one another, but occasionally locations were resampled several weeks later at a different time of day. We calculated the mean number of termites removed from a bait by each species, assuming that species discovered the bait.

Finally, we created three simulated datasets of five species, which we used to examine the robustness of ranking methods to variation in the number of fights as well as

variability of fight outcomes. Using these datasets, we examined:

1. Consistency in the rankings derived by four of the most common ranking methods.
2. The relationship between dominance rankings and relative abundance within an ant community.
3. Context dependency in ranking, including diurnal variation in dominance rankings.
4. The relationship between dominance and food acquisition.
5. The prevalence of neutral interactions among ant species at baits.
6. The complications and uncertainty associated with ranking species – in particular the influence of sample size and / or intransitivities on species rank.

1) Consistency in rankings: Using the data collected on cat food baits in North Carolina (STUBLE & al. 2013), we calculated dominance in four different ways.

1. The proportion of aggressive encounters a species won, out of all of the aggressive encounters that species engaged in.
2. The Colley dominance matrix (COLLEY 2002) based on wins and losses in aggressive encounters.
3. The proportion of baits monopolized (i.e., the species was the only species on a bait card by the end of the experiment) by each species out of the total number of baits.
4. The proportion of baits monopolized by each species at the end of the experiment out of the number of baits that species encountered (i.e., the species was observed on the bait at any point in the experiment).

We used Spearman's rank correlation to examine the correlation between all possible combinations of the four measures of dominance.

2) Relationship between behavioral dominance rankings and relative abundance: Using Spearman's rank correlation, we examined the relationship between relative abundance, as measured by occurrence in pitfall traps (number of pitfalls in which a species was present), and each of our four measures of dominance calculated above using the STUBLE & al. (2013) dataset.

3) Context dependency in ranking: We also examined temporal variation in dominance hierarchies to understand the extent to which the structure of these hierarchies is context dependent. In the North Carolina system, we used only the data collected from 24-hour bait observations (STUBLE & al. 2013) to calculate dominance (based on the proportion of baits monopolized out of all baits the species encountered) individually for every hour the baits were available. Using data collected in northeastern Spain from April through November over 24-hour time periods on a variety of protein and carbohydrate-based bait types (CERDÁ & al. 1998a), we calculated dominance based on the proportion of fights won separately for the morning (07:00 to 12:00), afternoon (13:00 to 20:00), and night (21:00 to 06:00). The Spanish data were collected in three discrete habitats (Holm-oak woodland, pine forest, and grassland), and we also calculated dominance based on proportion of fights won in each habitat.

4) Relationship between dominance and food acquisition: Using linear regression, we examined the relationship between each of the four dominance hierarchies generated from the North Carolina dataset (detailed above; data from STUBLE & al. 2013) and the number of termites collected by each species. We excluded ant species from the analysis for which we had fewer than seven observations (number of bait cards visited).

5) The prevalence of neutral interactions: We examined the prevalence of coexistence on baits in both the North Carolina (data from STUBLE & al. 2013) and Spain (data from CERDÁ & al. 1998a) systems by calculating the proportion of observations in which there were two or more species on a bait and those species did not behave antagonistically toward one another. These neutral interactions included both instances in which two species directly engaged with one another, but neither species left the bait, as well as instances in which the species shared a bait but were not observed interacting. Using the dataset from Spain, we also calculated the likelihood (along with Bayesian credibility intervals) that each species would engage in a fight if it shared a bait with one or more other ant species. Credibility intervals were calculated using binom.bayes in the binom package in R (DORAI-RAJ 2014).

6) Complications and uncertainty associated with ranking species: Finally, we used simulated data to determine how sample size and / or intransitivities (lower ranked species occasionally win in fights against higher ranked species) affect both the structure of hierarchies, as well as uncertainty in ranks. For this, we calculated dominance based on the proportion of aggressive encounters won as well as the Colley matrix, across a range of sample sizes and outcomes of fights. (Exact details regarding the numbers of fights utilized can be found in Fig. 3 and Fig. S2.) Credibility intervals provide a measure of certainty associated with dominance measures and provide an indication of overlap in dominance among species.

To examine the degree of confidence in our field rankings, we calculated Bayesian credibility intervals for the proportion of fights won using binom.bayes in the binom package in R (DORAI-RAJ 2014) using data on the outcome of aggressive encounters on baits in the Arizona (LEBRUN 2005), North Carolina (STUBLE & al. 2013) and Spain (CERDÁ & al. 1998a) systems. Using the same method, we also calculated dominance based on bait monopolization (out of all baits encountered by a species) in North Carolina by counting a "win" for a species as monopolization of a bait that had been discovered, and a "loss" as failure to monopolize a bait that had been discovered.

Results and discussion

How is dominance measured? Our review of the literature revealed several commonly used methods for measuring behavioral dominance: (1) the outcome of aggressive encounters at artificial baits, (2) bait occupancy, and (3) territoriality (Tab. S1). Dominance was most frequently determined by the outcome of aggressive encounters among ants on baits (28 / 55 studies). The second most common metric was bait monopolization, typically where a single species occupied a bait station, but also where many individuals of the same species occupied a bait (13 / 55 studies). Occasionally, ants were grouped into categories based on whether they defended their nest, food resources, and / or whole territories (SAVOLAINEN & VEPSÄLÄINEN 1988, SAVOLAINEN & al. 1989, PAULSON & AKRE 1991), or turnover of territories or baits (GREENSLADE 1971, PALMER & al. 2000, STANTON & al. 2002). A few studies used other measures of dominance, such as ranking species by factors

Tab. 1: Species rankings from a North American woodland ant community based on the outcome of fights (ranked according to the Colley method and proportion of encounters won) and bait monopolization (based on total number of baits monopolized and the proportion of baits monopolized out of the number of baits encountered by the species). The ranking of species in hierarchies based on aggression were not correlated with ranks based on bait monopolization (p > 0.05).

Aggression		Bait monopolization	
Colley	Proportion wins	Baits monopolized	Proportion baits monopolized of those encountered
Camponotus castaneus	*Camponotus pennsylvanicus*	*Aphaenogaster rudis*	*Aphaenogaster rudis*
Camponotus pennsylvanicus	*Crematogaster lineolata*	*Crematogaster lineolata*	*Prenolepis imparis*
Crematogaster lineolata	*Prenolepis imparis*	*Camponotus pennsylvanicus*	*Camponotus pennsylvanicus*
Prenolepis imparis	*Camponotus castaneus*	*Prenolepis imparis*	*Crematogaster lineolata*
Formica pallidefulva	*Formica pallidefulva*	*Formica pallidefulva*	*Formica pallidefulva*
Formica subsericea	*Formica subsericea*	*Camponotus castaneus*	*Camponotus castaneus*
Aphaenogaster lineolata	*Aphaenogaster lineolata*	*Temnothorax curvispinosus*	*Formica subsericea*
Aphaenogaster rudis	*Aphaenogaster rudis*	*Formica subsericea*	*Aphaenogaster lineolata*
Nylanderia faisonensis	*Nylanderia faisonensis*	*Aphaenogaster lineolata*	*Temnothorax curvispinosus*
Temnothorax curvispinosus	*Temnothorax curvispinosus*	*Nylanderia faisonensis*	*Nylanderia faisonensis*

including the ability to deter an invasive ant species (such as *Linepithema humile*) (HOLWAY 1999), competition for nest sites in the lab (LIVINGSTON & PHILPOTT 2010), or aggressive responses toward dead ants (MENZEL & al. 2010). Though some of these studies took place under controlled conditions in the lab, most took place under natural field conditions and did not account for nest proximity or local colony size. We focus the rest of this paper on the mechanisms involving competition for food, including aggressive encounters at baits and bait monopolization.

Converting lab and field observations into ranks: The most frequent method used to convert these behavioral observations at baits into hierarchies was to rank species based on the proportion of all observations in which the species might be considered to be dominant (Tab. S1). Proportions (of observations in which they monopolized a bait or won an encounter) were used as the basis of ranks in nearly half (23 / 55 studies) of the studies we examined. It was also common to use raw counts to construct rankings (e.g., ranking species by the number of fights they initiated, instead of the proportion of encounters in which fights were initiated). LEBRUN & FEENER (2007) attempted to account for the fact that not all species may encounter one another by borrowing a technique used to rank college teams in American football (the Colley matrix). This ranking system was developed because not all college football teams (there are more than a hundred) play against each other in a given year, but all teams still get ranked. Put very simply, this method gives more weight to wins against strong opponents and less weight to wins against weak opponents when determining a species' (or team's) rank (see COLLEY 2002 for more details). Another method was developed by DEVRIES (1998) and was designed to minimize competitive reversals within an interaction matrix of all interacting species. This method uses an algorithm to minimize the number and strength of inconsistencies within the hierarchy (that is, the number of times a lower ranked species dominates a higher ranked species).

1) Consistency in rankings: The two most common measures of dominance (outcome of aggressive encounters on baits and bait monopolization) yielded very different hierarchies for the same assemblage of ants. Focusing on the North Carolina dataset from STUBLE & al. (2013), we found that ranks of ten common ant species in dominance hierarchies were inconsistent across ranking methods (Tab. 1). While there was a positive correlation between rankings based on the proportion of fights won and the Colley matrix (both ranking methods that are based on fight data) (Spearman's $\rho = 0.93$, $p = 0.0001$), and a positive correlation between rankings based on the two bait monopolization measures (proportion of baits occupied and proportion of baits occupied out of those encountered) ($\rho = 0.90$, $p = 0.0004$), dominance measures based on aggression and bait monopolization were independent of one another (proportion wins vs. proportion monopolized: $\rho = 0.5$, $p = 0.14$; Colley versus proportion monopolized: $\rho = 0.37$, $p = 0.29$; proportion wins vs. proportion monopolized out of those encountered: $\rho = 0.6$, $p = 0.07$, Colley vs. proportion monopolized out of those encountered: $\rho = 0.49$, $p = 0.15$). That is, the species that win in head-to-head (usually one-on-one) fights do not necessarily monopolize baits. The lack of a relationship between the outcomes of these two measures of dominance is troubling because both measures are commonly used in tests of the dominance – discovery and dominance – thermal tolerance trade-offs (e.g., FELLERS 1987, LEBRUN & FEENER 2007, PARR & GIBB 2012), and both have been used to describe the structure of ant communities. But, to state the obvious, they mean very different things, or at a minimum, they suggest that winning head-to-head fights is not necessarily related to monopolizing and procuring resources. Rather, bait monopolization may be driven, at least in some systems, by factors such as colony size, density, and recruitment behavior.

2) Relationship between behavioral dominance rankings and relative abundance: In addition to the failure

Tab. 2: Dominance hierarchy based on a) bait monopolization (number of baits monopolized per number of bait the species had access to) in the North Carolina baiting study (STUBLE & al. 2013) and b) the outcome of aggressive encounters in Mediterranean Spain CERDÁ & al. (1998a). We did not include species that did not monopolize any baits in a given time period, and would technically be tied for last place in the dominance hierarchy. Here, we show that dominance hierarchies based both on bait monopolization and aggressive encounters are highly dependent on the time of day at which data are collected. Species abbreviations for the North Carolina system (a) are as follows: *Temnothorax curvispinosus* (tecu), *Nylanderia faisonensis* (nyfa), *Aphaenogaster rudis* (apru), *Aphaenogaster lineolata* (apla), *Formica pallidefulva* (fopa), *Camponotus castaneus* (caca), *Prenolepis imparis* (prim), *Camponotus pennsylvanicus* (cape), *Crematogaster lineolata* (crli).

a)

Hour																							
24	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
cape	caca	prim	prim	prim	prim	cape	apru	apru	apru	apru	apru	crli	crli	cape	crli	crli	crli	crli	crli	crli	cape	cape	cape
caca	cape	cape	cape	cape	cape	crli	cape	apla	crli	crli	crli	apru	cape	apru	cape	cape	cape	cape	cape	apru	crli	caca	caca
crli	crli	crli	crli	caca	crli	apru	prim	crli	fopa	cape	cape	cape		crli	apru	apru	apru	apru	apru	cape	prim	crli	crli
prim	prim	caca	caca	crli	caca	prim	crli		cape		apla	apla		apla	apla		prim		prim	prim	apla	prim	prim
apru	apru	apru		nyfa	apru	apla									fopa		tecu				apru		apru
				apru		caca									tecu						caca		

b)

Morning	Afternoon	Night
Camponotus foreli	*Linepithema humile*	*Tetramorium semilaeve*
Camponotus cruentatus	*Tetramorium semilaeve*	*Camponotus sylvaticus*
Camponotus sylvaticus	*Camponotus cruentatus*	*Camponotus cruentatus*
Tetramorium semilaeve	*Tapinoma nigerrimum*	*Pheidole pallidula*
Linepithema humile	*Pheidole pallidula*	*Messor capitatus*
Tapinoma nigerrimum	*Messor bouvieri*	*Cataglyphis cursor*
Pheidole pallidula	*Messor capitatus*	*Linepithema humile*
Plagiolepis pygmaea	*Camponotus foreli*	*Camponotus foreli*
Aphaenogaster senilis	*Aphaenogaster senilis*	*Tapinoma nigerrimum*
Messor bouvieri	*Plagiolepis pygmaea*	*Messor bouvieri*
Messor capitatus	*Camponotus sylvaticus*	*Plagiolepis pygmaea*
Cataglyphis cursor	*Cataglyphis cursor*	*Aphaenogaster senilis*

of aggression and monopolization dominance metrics to relate to one another, bait monopolization may be much more sensitive to a species' relative abundance than is aggression or the outcome of head-to-head encounters between ant species. In the North Carolina system, dominance estimated by bait monopolization was strongly and positively correlated with the relative abundance of ant species (estimated by occurrence in pitfall traps), with more abundant species having higher dominance rankings (proportion monopolized: Spearman's $\rho = 0.82$, $p = 0.004$; proportion monopolized of those encountered $\rho = 0.58$, $p = 0.08$; Fig. S1). Rankings based on aggressive encounters, on the other hand, were not related to abundance (proportion wins: $\rho = 0.21$, $p = 0.57$; Colley: $\rho = 0.13$, $p = 0.71$). The most abundant species in the system, *Aphaenogaster rudis*, was ranked as the most dominant ant for both bait monopolization metrics, but 8th (of 10 species) by both of the methods based on aggressive encounters. Similarly, *Camponotus castaneus*, an aggressive, but primarily nocturnal, species moved from being highly dominant (1st by Colley and 4th by proportion wins based on aggression) to being ranked 6th by both bait monopolization methods (Tab. 1). This suggests that some species (including less aggressive species) may successfully monopolize baits largely as a result of their high relative abundance within the ant community (e.g., BESTELMEYER 2000, SEGEV & ZIV 2012).

3) Context dependency in ranking: At local scales, the outcomes of particular pairwise interactions can be context dependent (SANDERS & al. 2001, ANDERSEN 2008, GORDON 2011), potentially influencing the structure of dominance hierarchies. These contingencies happen at two levels. First, abiotic conditions can drive daily and seasonal activity patterns of foraging activity, dictating which species directly interact (CERDÁ & al. 1998a, STUBLE & al. 2013). Second, environmental conditions have the potential to influence the outcome of these competitive interactions (LEVINS & al. 1973, FEENER 1981, SANDERS & GORDON 2003, LUQUE & REYES LÓPEZ 2007, ANDERSEN 2008). Comparing previously published hierarchies from three deciduous forests in North Carolina revealed potentially important variation in hierarchies across sites (Tab. S2a). For example, the top-ranked species, *Camponotus chromaiodes*, in FELLERS' (1987) Maryland woodland ant community was ranked in the middle of the hierarchy in LESSARD & al.'s (2009) North Carolina forest ant community. Even rankings generated in three adjacent habitats in Mediterranean Spain (CERDÁ & al. 1998a) with extensive species overlap can vary (Tab. S2b). *Messor bouvieri*, for example, was ranked last in an oak woodland, but in the middle of the hierarchy in a nearby pine forest. SANDERS & GORDON (2003) similarly uncovered variability in dominance across sites in a desert grassland system.

Dominance can also depend on the time of day (or temperature – see SANTINI & al. 2007, WITTMAN & al. 2010) at which the experiment is conducted (STUBLE & al. 2013, HOUADRIA & al. 2015). In North Carolina, strong diurnal shifts in some of the species led to higher dominance (based on bait monopolization) by cold-tolerant and nocturnal species such as *Prenolepis imparis* and *Camponotus castaneus* during the night, while heat-tolerant *Crematogaster lineolata* dominated baits in the afternoon hours and abundant *Aphaenogaster rudis* was most dominant in the morning hours (Tab. 2a). Similar findings of variability in the ability of ant species to defend food throughout day have been described in Spain as well (CERDÁ & al. 1998a). Using the Spanish dataset (CERDÁ & al. 1998a), we documented dramatic shifts in dominance based on the outcome of aggressive encounters (proportion of fights won) throughout the day (Tab. 2b). Taken together, these datasets (and likely others) show that dominance varies both temporally as well as spatially (PINTER-WOLLMAN & al. 2014).

4) Relationship between dominance and food acquisition: Regardless of how behavioral dominance is measured, its ecological relevance remains unclear. Can these hierarchies tell us anything about how communities are put together? As we showed above, ant dominance hierarchies are often based on the outcomes of aggressive encounters on baits. However, the relationship between these aggressive encounters and success at the colony level is unclear and may be limited if these interactions do not ultimately drive foraging success. It was long thought that fitness was simply related to foraging behavior – those ants that were best at procuring the most high quality resources would have the highest fitness, and become the most locally abundant species. That has turned out to be an oversimplification. Although there are a few long-term studies that link foraging behavior, intra- and inter-specific neighborhood interactions, and colony success (GORDON & WAGNER 1997, GORDON 2013), these are rare and the evidence is to date inconclusive. In other taxa, ranging from salmon to mountain goats to macaques, determining the link between dominance and fitness has been key to validating the use of rankings of individuals (e.g., NAKANO 1995, CÔTÉ & FESTA-BIANCHET 2001, ENGELHARDT & al. 2006). At a minimum, behavioral aggression (or the outcome of fights on baits) should relate to food acquisition (e.g., NAKANO 1995). However, the relationship between dominance based on behavioral aggression and food acquisition has rarely, if ever, been examined in ants.

Our examination of termite removal in North Carolina showed that behavioral dominance (as measured by each of the four methods) did not relate to food acquisition (proportion wins: F = 3.3, p = 0.13; Colley: F = 2.5, p = 0.18; proportion monopolized: F = 3.6, p = 0.12; proportion monopolized of those encountered: F = 1.6, p = 0.26). That is to say, dominant species did not collect more termites than did submissive species. This was true even though our calculations of termites removed included only the baits that the species found, thereby reducing the influence of discovery ability on these results. However, our use of termites as a food source may have influenced our results. Studies have shown that smaller and more widely dispersed food resources tend to favor foraging success by subordinate ant species (CERDÁ & al. 1998b, STRIN-

GER & al. 2007, LESTER & al. 2010). That being said, termites, and other small arthropods, are an important component of the diet of many ant species in our and other systems, and thus likely reflect the foraging dynamics in this deciduous forest. Additionally, as is often the case with observational studies of this nature, our small sample size may limit our ability to detect a relationship when the effect size is small. Similar to our failure to relate dominance to resource removal in this study, WITTMAN & GOTELLI (2011) found that pairwise aggressive interactions were not predictive of coexistence among ant species. This research, as with our baiting results, seems to suggest that aggression may not play an important role in structuring ant communities and may indicate that dominance rankings may hold limited power to explain ant community dynamics.

5) The prevalence of neutral interactions: Dominance may fail to predict food acquisition and community dynamics if aggressive interspecific ant encounters are rare. Data on neutral interactions, or coexistence between ant species at food resources, are rarely reported, and dominance hierarchies typically take into account only those instances in which there is a clear winner and loser. Based on our North Carolina dataset, we found that in more than three fourths of the bait observations (76% of observations in which we observed two or more ant species on the bait) we did not observe any antagonistic interactions among species. Data collected by CERDÁ & al. (1998a) in Mediterranean Spain revealed that in 38% of bait observations in which multiple species were present the species did not interact antagonistically toward one another. We note that our estimates for neutral interactions are likely conservative. These data were collected during experiments designed to study antagonistic interactions using large and attractive baits, which were likely to elicit defensive behavior. Other studies have similarly found a limited number of antagonistic interactions between species on baits, likely due to differences in food preferences and foraging times, which limit foraging overlap among species, and thereby reduce the importance of dominance (BARONI URBANI & AKTAC 1981, HOUADRIA & al. 2016). Considering species-specific data on coexistence and fights from CERDÁ'S (1998a) Mediterranean system, the likelihood that a species would be observed engaging in a fight if it shared a bait with another species ranged from 10% to 80% (Fig. 1). *Cataglyphis cursor* and *Plagiolepis pygmaea*, the two species least likely to engage in fights, were also the two least dominant species in the system. Neutral interactions may be particularly important in allowing access to resources by subordinate species. Further, these neutral interactions may serve to lessen the influence of dominant species on systems with behaviorally dominant species perhaps playing smaller roles in structuring communities in which neutral interactions are very common. Subordinate species in both the Spain and North Carolina systems often waited nearby baits and were skilled at quickly removing food as the opportunity arose (K.L. Stuble, unpubl.). Ants may also purposefully limit interactions with other ant species by using chemical cues to detect and avoid potential competitors (BINZ & al. 2014, WÜST & MENZEL, in press). Thus, avoiding fights may be a valid and understudied strategy that promotes species coexistence.

6) Complications and uncertainty associated with ranking species: Converting field data based on bait oc-
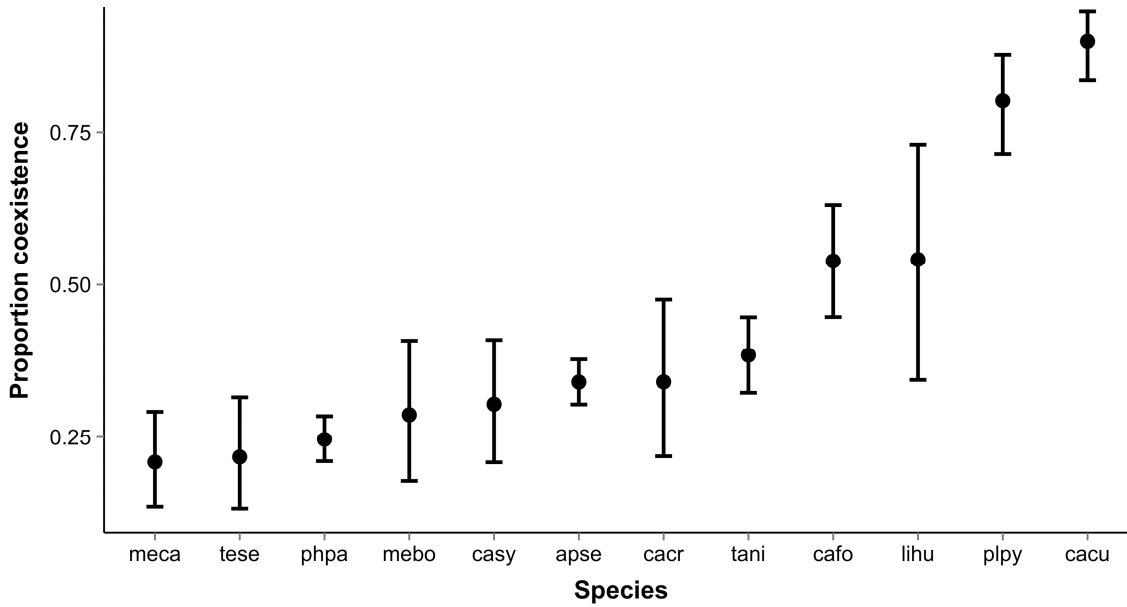
Fig. 1: Proportion of observed encounters in which species were found to coexist on baits out of total encounters (peaceful coexistence + antagonistic interactions).
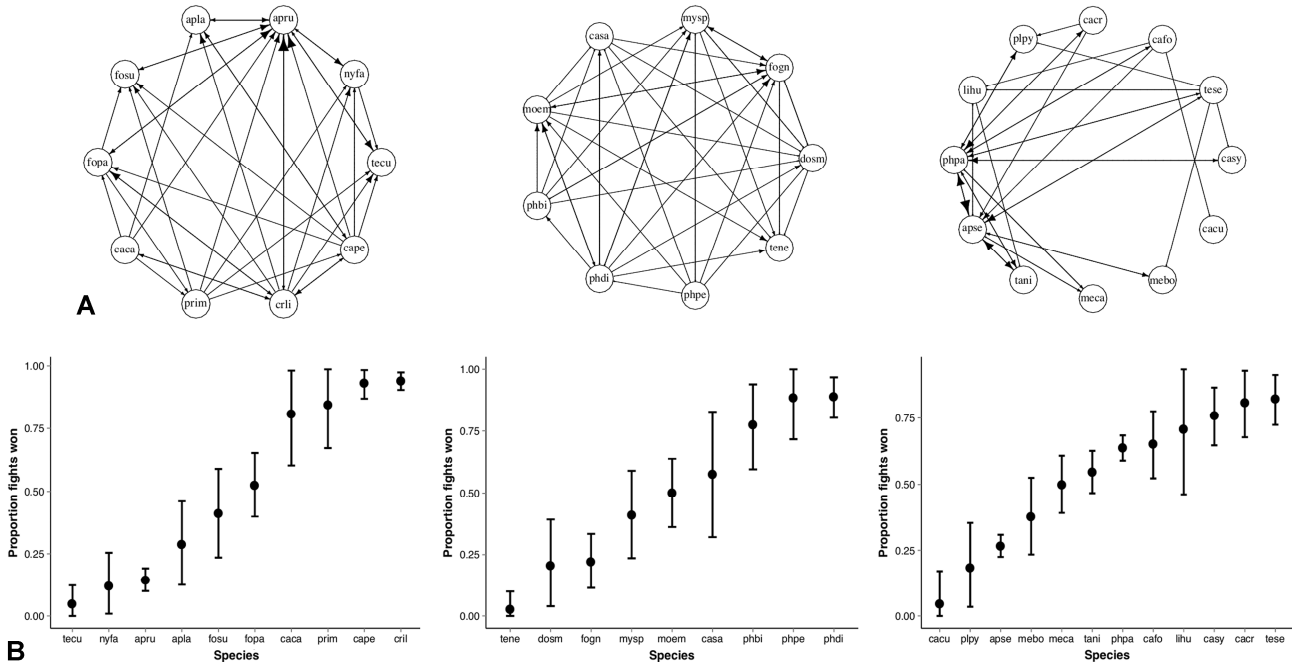

Fig. 2: A) These networks represent all interactions between ants within three ant assemblages. The left column represents data derived from STUBLE & al. (2013), the center column comes from LEBRUN (2005), and the right is from CERDÁ & al. (1998). Arrows connect species that were observed in antagonistic interactions with one another. The size of arrowheads is proportional to the number of fights won by the species being pointed to against the species at the other end of the arrow. B) These figures take the same network of data and collapse it into point estimates of dominance along with Bayesian credibility intervals. Species abbreviations are as follows: *Temnothorax curvispinosus* (tecu), *Nylanderia faisonensis* (nyfa), *Aphaenogaster rudis* (apru), *Aphaenogaster lineolata* (apla), *Formica subsericea* (fosu), *Formica pallidefulva* (fopa), *Camponotus castaneus* (caca), *Prenolepis imparis* (prim), *Camponotus pennsylvanicus* (cape), *Crematogaster lineolata* (crli), *Temnothorax neomexicanus* (tene), *Dorymyrmex smithi* (dosm), *Formica gnava* (fogn), *Myrmica* sp. (mysp), *Monomorium emersoni* (moem), *Camponotus sansabeanus* (casa), *Pheidole bicarinata* (phbi), *Pheidole perpilosa* (phpe), *Pheidole diversipilosa* (phdi), *Cataglyphis cursor* (cacu), *Plagiolepis pygmaea* (plpy), *Aphaenogaster senilis* (apse), *Messor bouvieri* (mebo), *Messor capitatus* (meca), *Tapinoma nigerrimum* (tani), *Pheidole pallidula* (phpa), *Camponotus foreli* (cafo), *Linepithema humile* (lihu), *Camponotus sylvaticus* (casy), *Camponotus cruentatus* (cacr), *Tetramorium semilaeve* (tese).

cupancy or the outcome of aggressive encounters among multiple species into dominance hierarchies poses its own set of challenges. Interactions between any number of pairs of species can be effectively represented by a two-dimensional network (Fig. 2). However, to perfectly rank species by behavioral dominance measurements in a way con-
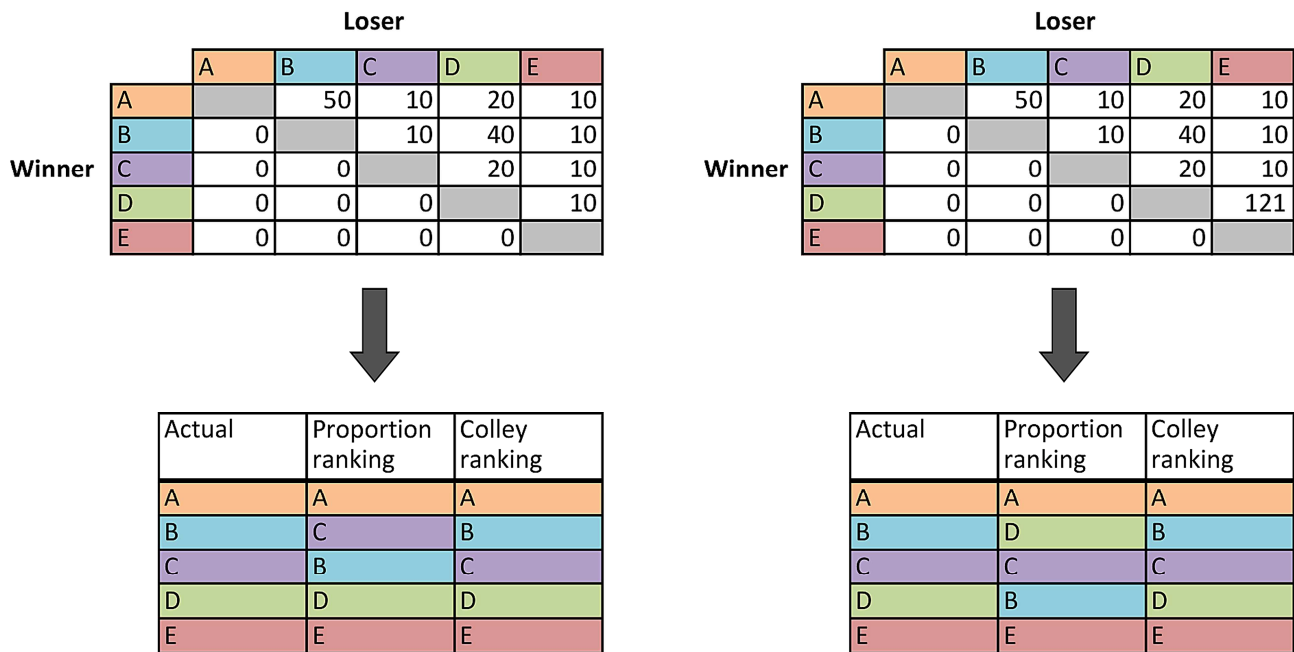
Loser

Winner	A	B	C	D	E
A		50	10	20	10
B	0		10	40	10
C	0	0		20	10
D	0	0	0		10
E	0	0	0	0	

Loser

Winner	A	B	C	D	E
A		50	10	20	10
B	0		10	40	10
C	0	0		20	10
D	0	0	0		121
E	0	0	0	0	

Actual	Proportion ranking	Colley ranking
A	A	A
B	C	B
C	B	C
D	D	D
E	E	E

Actual	Proportion ranking	Colley ranking
A	A	A
B	D	B
C	C	C
D	B	D
E	E	E

Fig. 3: We provide an example of a transitive network of interspecific interactions in which A > B > C > D > E and winners win 100% of fights against losers (i.e., there is no uncertainty in the outcome of interactions among species). In the top tables, rows represent wins and columns represent loses. The column labeled "Actual" ranks species according to the number of species dominated. Here we show that a) the proportion method can rank the species incorrectly when the number of fights engaged in is not equal among species pairs while b) the Colley ranking method is consistent with the "actual" ranking.

sistent with the definition of dominance, two criteria must be met: (1) all species pairs must interact with one another and (2) for all species triplets a, b, c, if a is dominant over b and b is dominant over c then a must be dominant over c (mathematical criteria for ranking: MIRIMANOFF 1917). In reality, both of these conditions are often violated when ranking ant species. Frequently, certain species pairs do not interact (or are never observed interacting), making behavioral dominance for these species undefined. Further, interactions between ant species may be circular rather than transitive (GREENSLADE 1971, LEBRUN 2005, SOLIVERES & al. 2015). Ecologists use various rules to transform behavioral dominance data into forms that can be ranked. These transformations can be as simple as calculating the proportion of fights won for each species, or by the use of more elaborate rules such as those used in the Colley or de Vries methods. As such, there is no "correct" ranking method, but these different ranking methods can be more or less informative when considering different features of ant communities, as well as the nature of the data itself (i.e., sample size).

By far the most common ranking method bases rank on proportion wins. The appeal of this method is its simplicity as the proportion of wins is an easily understood summary statistic to describe behavioral dominance. Here behavioral dominance is implicitly defined as the ability to win fights, regardless of who the fight is against. In addition to allowing common encounters to drive dominance patterns, the consequence of this is that dominance is driven by the number of observed fights, while the number of opponent species that a given species dominates is inconsequential. For example, a higher ranked species can do-minate fewer species than a lower ranked one, as long as the species wins a larger number of fights (Fig. 3). As such, rankings are very sensitive to number of fights observed per species pair. Altering the number of fights observed among species can yield deviant rankings even when there is no uncertainty in the outcome of fights (i.e., A beats B 100% of the time, and so on).

Additionally, the uncertainty associated with these rankings is almost always ignored (but see LEBRUN & FEENER 2007, STUBLE & al. 2013). Field data typically used to construct dominance hierarchies are complex, containing variable numbers of observed fights across species, species pairs that never meet, and subordinate species occasionally winning fights against dominant species (Fig. 2a). These factors generate a great deal of uncertainty associated with species ranks (Fig. S2). Using actual field data on wins and losses in the three study systems (CERDÁ & al. 1998a, LEBRUN & FEENER 2007, STUBLE & al. 2013) we used Bayesian confidence intervals to explore the uncertainty associated with a species dominance rank, and ultimately the composition of the dominance hierarchy itself. In all three of the study systems, the numbers of fights each species engaged in varied, and there were intransitivities in those interactions (occasions in which a lower ranked species won a fight against a higher ranked species). These factors contributed to the uncertainty in the placement of each species within the dominance hierarchy, which can be observed in the wide and overlapping credibility intervals among species that were observed in all three of the study systems (Fig. 2b). This uncertainty is substantial not only in fight-based hierarchies but also in rankings based on monopolization (Fig. S3).

A way forward: The ranking of ant species based on dominance is plagued by several issues, not least of which are the: (1) lack of consistency in the definition of dominance, (2) failure of scientists to acknowledge the uncertainty associated with dominance rankings, (3) strong contingencies, yielding dominance hierarchies that are variable both in space and time, and (4) uncertain association between dominance and fitness. There is also a lack of information on the prominence of neutral interactions and other potentially important foraging strategies. While dominance hierarchies have had their place in the field of myrmecology over the past decades, we suggest that the time has come for the field to take a deeper look at their use and construction.

While there has been some important work seeking to understand ant coexistence and community dynamics without relying on dominance hierarchies (e.g., YU & al. 2001, SARTY & al. 2006, FOWLER & al. 2014, HOUADRIA & al. 2016), there is still much more to be done. The role of neutral processes is under-developed in the field of myrmecology compared to other areas of community ecology (e.g., CHESSON 2000, HUBBELL 2001, LEIBOLD & MCPEEK 2006, but see ANDERSEN 2008). Based on our findings that dominance hierarchies may be limited in their ability to predict food acquisition among ant species, we also recommend additional research into successful foraging strategies in ant communities. While behavioral dominance may play a role in food acquisition, foraging success is almost certainly a complex interplay of ant behavior, community structure, and ecological context, as evidenced, in part, by the strong contingencies often observed in food acquisition (e.g., SANDERS & GORDON 2003). Further, while ant ecologists have fixated on aggressive encounters, the influence of aggression is uncertain at best, and may play a limited role in many systems.

So are there dominant ant species in local communities? And are some species more dominant than others? Yes, of course, on both counts. For instance, in boreal systems, *Formica* species can have dramatic impacts on the rest of the community, and perhaps in some instances, those species appear to be arranged into dominance hierarchies (SAVOLAINEN & VEPSÄLÄINEN 1988). Similarly, in Mediterranean systems, some species are dominant under specific conditions (CERDÁ & al. 1998a). But in other systems (e.g., tropical or temperature forests) species appear not to be arranged in dominance hierarchies, or if they are, those dominance hierarchies are so context dependent as to be fluid entities. Instead of forcing dominance hierarchies on all systems, we should be working toward ways to understand and compare the organization of communities across sites, habitats, climates, etc.

For studies that may still benefit from the incorporation of interspecific dominance hierarchies, we have four recommendations. First, researchers should understand the purpose of using dominance hierarchies in their study and should select a measure of dominance best suited to their goals. They should then clearly state how they define dominance in their research. We think that doing so would eliminate the current need to infer such information, perhaps incorrectly, from methods sections, and should introduce much needed clarity. Second, we believe that researchers should calculate credibility intervals on dominance rankings. Doing so would give researchers and readers alike the ability to see whether two species differed statistically in their rankings. Third, we would recommend that researchers provide information on the prevalence of neutral or non-aggressive interactions in their study system. This information helps to estimate the probable significance of aggressive encounters. Finally, shaking off the confines of thinking about species as being arranged in transitive hierarchies may also be valuable. Considering ant communities as networks of interacting species rather than linear hierarchies in which species can easily be ranked from most to least dominant may be more accurate description of reality in ant communities. The adoption of methods from network analysis (reviewed in PINTER-WOLLMAN & al. 2014, SHIZUKA & MCDONALD 2015) provides a promising avenue. Such a framework may allow us to step past the thinking that a single species must be behaviorally dominant within a system and instead consider the more nuanced and diverse interactions and behaviors (both aggressive and not) within communities that may act to structure them. If the goal is to understand how ant communities are assembled in space and time, then new approaches, or thinking critically about old approaches, can certainly help.

Acknowledgments

References

ANDERSEN, A.N. 1997: Functional groups and patterns of organization in North American ant communities: a comparison with Australia. – Journal of Biogeography 24: 433-460.

ANDERSEN, A.N. 2008: Not enough niches: non-equilibrial processes promoting species coexistence in diverse ant communities. – Austral Ecology 33: 211-220.

ANDERSEN, A.N., ARNAN, X. & SPARKS, K. 2013: Limited niche differentiation within remarkable co-occurrences of congeneric species: *Monomorium* ants in the Australian seasonal tropics. – Austral Ecology 38: 557-567.

ARANDA-RICKERT, A. & FRACCHIA, S. 2012: Are subordinate ants the best seed dispersers? Linking dominance hierarchies and seed dispersal ability in myrmecochory interactions. – Arthropod-Plant Interactions 6: 297-306.

ARNAN, X., GAUCHEREL, C. & ANDERSEN, A.N. 2011: Dominance and species co-occurrence in highly diverse ant communities: a test of the interstitial hypothesis and discovery of a three-tiered competition cascade. – Oecologia 166: 783-794.

BACCARO, F.B., KETELHUT, S.M. & WELLINGTON DE MORAIS, J. 2010: Resource distribution and soil moisture content can regulate bait control in an ant assemblage in Central Amazonian forest. – Austral Ecology 35: 274-281.

BARONI URBANI, C. & AKTAÇ, N. 1981: The competition for food and circadian succession in the ant fauna of a representative Anatolian semi-steppic environment. – Bulletin de la Société Entomologique Suisse 54: 33-56.

BESTELMEYER, B.T. 2000: The trade-off between thermal tolerance and behavioural dominance in a subtropical South American ant community. – Journal of Animal Ecology 69: 998-1009.

Binz, H., Foitzik, S., Staab, F. & Menzel, F. 2014: The chemistry of competition: exploitation of heterospecific cues depends on the dominance rank in the community. – Animal Behaviour 94: 45-53.

Brian, M.V. 1952: The structure of a dense natural ant population. – Journal of Animal Ecology 21: 12-24.

Cerdá, X., Angulo, E., Caut, S. & Courchamp, F. 2012: Ant community structure on a small Pacific island: only one native species living with the invaders. – Biological Invasions 14: 323-339.

Cerdá, X., Arnan, X. & Retana, J. 2013: Is competition a significant hallmark of ant (Hymenoptera: Formicidae) ecology? – Myrmecological News 18: 131-147.

Cerdá, X., Retana, J. & Cros, S. 1998a: Critical thermal limits in Mediterranean ant species: trade-off between mortality risk and foraging performance. – Functional Ecology 12: 45-55.

Cerdá, X., Retana, J. & Cros, S. 1998b: Prey size reverses the outcome of interference interactions of scavenger ants. – Oikos 82: 99-110.

Cerdá, X., Retana, J. & Manzaneda, A.J. 1998c: The role of competition by dominants and temperature in the foraging of subordinate species in Mediterranean ant communities. – Oecologia 117: 404-412.

Chase, I.D. & Seitz, K. 2011: Self-structuring properties of dominance hierarchies: a new perspective. In: Huber, R., Bannasch, D.L. & Brennan, P. (Eds.): Advances in genetics: aggression. – Academic Press, San Diego, CA, pp. 51-75.

Chesson, P. 2000: Mechanisms of maintenance of species diversity. – Annual Review of Ecology and Systematics 31: 343-366.

Cole, B.J. 1981: Dominance hierarchies in *Leptothorax* ants. – Science 212: 83-84.

Colley, W. 2002: Colley's bias free college football ranking method. – <http://www.colleyrankings.com/%3E>, retrieved on 3 March 2016.

Côté, S. & Festa-Bianchet, M. 2001: Reproductive success in female mountain goats: the influence of age and social rank. – Animal Behaviour 62: 173-181.

Davidson, D.W. 1998: Resource discovery versus resource domination in ants: a functional mechanism for breaking the trade-off. – Ecological Entomology 23: 484-490.

de Vries, H. 1998: Finding a dominance order most consistent with a linear hierarchy: a new procedure and review. – Animal Behaviour 55: 827-843.

Delsinne, T., Roisin, Y. & Leponce, M. 2007: Spatial and temporal foraging overlaps in a Chacoan ground-foraging ant assemblage. – Journal of Arid Environments 71: 29-44.

Dorai-Raj, S. 2014: binom: binomial confidence intervals for several parameterizations. R package version 1.1-1. – <https://cran.r-project.org/web/packages/binom>, retrieved on 15 May 2015.

Engelhardt, A., Heistermann, M., Hodges, J.K., Nürnberg, P. & Niemitz, C. 2006: Determinants of male reproductive success in wild long-tailed macaques (*Macaca fasicularis*) – male monopolization, female mate choice or post-copulatory mechanisms? – Behavioral Ecology and Sociobiology 59: 740-752.

Feener, D.H. 1981: Competition between ant species: outcome controlled by parasitic flies. – Science 214: 815-817.

Fellers, J.H. 1987: Interference and exploitation in a guild of woodland ants. – Ecology 68: 1466-1478.

Fowler, D.A., Lessard, J.-P. & Sanders, N.J. 2014: Niche filtering rather than partitioning shapes the structure of temperate forest ant communities. – Journal of Animal Ecology 83: 943-952.

Gordon, D.M. 2011: The fusion of behavioral ecology and ecology. – Behavioral Ecology 22: 225-230.

Gordon, D.M. 2013: The rewards of restraint in the collective regulation of foraging by harvester ant colonies. – Nature 498: 91-93.

Gordon, D.M. & Wagner, D. 1997: Neighborhood density and reproductive potential in harvester ants. – Oecologia 109: 556-560.

Greenslade, P.J.M. 1971: Interspecific competition and frequency changes among ants in Solomon Islands coconut plantations. – Journal of Applied Ecology 8: 323-352.

Hölldobler, B. & Wilson, E.O. 1990: The ants. – Harvard University, Cambridge, MA, 732 pp.

Holway, D.A. 1999: Competitive mechanisms underlying the displacement of native ants by the invasive Argentine ant. – Ecology 80: 238-251.

Houadria, M., Blüthgen, N., Salas-Lopez, A., Schmitt, M.-I., Arndt, J., Schneider, E., Orivel, J. & Menzel, F. 2016: The relation between circadian asynchrony, functional redundancy, and trophic performance in tropical ant communities. – Ecology 97: 225-235.

Houadria, M., Salas-Lopez, A., Orivel, J., Blüthgen, N. & Menzel, F. 2015: Dietary and temporal niche differentiation in tropical ants – can they explain local ant coexistence? – Biotropica 47: 208-217.

Hubbell, S.P. 2001: The unified neutral theory of biodiversity and biogeography. – Princeton University Press, Princeton, NJ, 392 pp.

Kaspari, M., Donoso, D., Lucas, J.A., Zumbusch, T. & Kay, A.D. 2012: Using nutritional ecology to predict ant community structure: a field test in Neotropical ants. – Ecosphere 3: art. 93.

Leal, I.R., Fischer, E., Kost, C., Tabarelli, M. & Wirth, R. 2006: Ant protection against herbivores and nectar thieves in *Passiflora coccinea* flowers. – Ecoscience 13: 431-438.

LeBrun, E.G. 2005: Who is the top dog in ant communities? Resources, parasitoids, and multiple competitive hierarchies. – Oecologia 142: 643-652.

LeBrun, E.G. & Feener, D.H., Jr. 2007: When trade-offs interact: balance of terror enforces dominance discovery trade-off in a local ant assemblage. – Journal of Animal Ecology 76: 58-64.

Leibold, M.A. & McPeek, M.A. 2006: Coexistence of the niche and neutral perspectives in community ecology. – Ecology 87: 1399-1410.

Lessard, J.-P., Dunn, R.R. & Sanders, N.J. 2009: Temperature-mediated coexistence in temperate forest ant communities. – Insectes Sociaux 56: 149-156.

Lester, P.J., Stringer, L.D. & Haywood, J. 2010: The role of resource dispersion in promoting the co-occurrence of dominant and subordinate ant species. – Oikos 119: 659-668.

Levins, R., Pressick, M.L. & Heatwole, H. 1973: Coexistence patterns in insular ants: in which it is shown that ants travel a lot from island to island, and what they do when they get there. – American Scientist 61: 463-472.

Livingston, G.F. & Philpott, S.M. 2010: A metacommunity approach to co-occurrence patterns and the core-satellite hypothesis in a community of tropical arboreal ants. – Ecological Research 25: 1129-1140.

Luque, G.M. & Reyes López, J. 2007: Effects of experimental small-scale spatial heterogeneity on resource use of a Mediterranean ground-ant community. – Acta Oecologia 23: 42-49.

Menzel, F., Woywod, M., Blüthgen, N. & Schmitt, T. 2010: Behavioural and chemical mechanisms behind a Mediterranean ant-ant association. – Ecological Entomology 35: 711-720.

MIRIMANOFF, D. 1917: Les antinomies de Russell et de Burali-Forti: et le probleme fondamental de la theorie des ensembles. – Enseignement mathematique 19: 37-52.

MORRISON, L.W. 1996: Community organization in a recently assembled fauna: the case of Polynesian ants. – Oecologia 107: 243-256.

MORSE, D.H. 1974: Niche breadth as a function of social dominance. – The American Naturalist 108: 818-830.

NAKANO, S. 1995: Individual differences in resource use, growth and emigration under the influence of a dominance hierarchy in fluvial red-spotted masu salmon in a natural habitat. – Journal of Animal Ecology 64: 75-84.

PALMER, T.M., STANTON, M.L., YOUNG, T.P., LEMBOL, J.S., GOHEEN, J.R. & PRINGLE, R.M. 2013: A role for indirect facilitation in maintaining diversity in a guild of African acacia ants. – Ecology 94: 1531-1539.

PALMER, T.M., YOUNG, T.P., STANTON, M.L. & WENK, E. 2000: Short-term dynamics of an acacia ant community in Laikipia, Kenya. – Oecologia 123: 425-435.

PARR, C.L. & GIBB, H. 2012: The discovery-dominance trade-off is the exception, rather than the rule. – Journal of Animal Ecology 81: 233-241.

PAULSON, G.S. & AKRE, R.D. 1991: Behavioral interactions among Formicid species in the ant mosaic of an organic pear orchard. – Pan-Pacific Entomologist 67: 288-297.

PINTER-WOLLMAN, N., HOBSON, E.A., SMITH, J.E., EDELMAN, A.J., SHIZUKA, D., DE SILVA, S., WATERS, J.S., PRAGER, S.D., SASAKI, T., WITTEMYER, G., FEWELL, J. & MCDONALD, D.B. 2014: The dynamics of animal social networks: analytical, conceptual, and theoretical advances. – Behavioral Ecology 25: 242-255.

PUSEY, A., WILLIAMS, J. & GOODALL, J. 1997: The influence of dominance rank on the reproductive success of female chimpanzees. – Science 277: 828-831.

SANDERS, N.J., BARTON, K.E. & GORDON, D.M. 2001: Long-term dynamics of the distribution of the invasive Argentine ant, Linepithema humile, and native ant taxa in northern California. – Oecologia 127: 123-130.

SANDERS, N.J. & GORDON, D.M. 2003: Resource-dependent interactions and the organization of desert ant communities. – Ecology 84: 1024-1031.

SANTINI, G., TUCCI, L., OTTONETTI, L. & FRIZZI, F. 2007: Competition trade-offs in the organization of a Mediterranean ant assemblage. – Ecological Entomology 32: 319-326.

SARTY, M., ABBOTT, K.L. & LESTER, P.J. 2006: Habitat complexity facilitates coexistence in a tropical ant community. – Oecologia 149: 465-473.

SAVOLAINEN, R. & VEPSÄLÄINEN, K. 1988: A competition hierarchy among boreal ants: impact on resource partitioning and community structure. – Oikos 51: 135-155.

SAVOLAINEN, R., VEPSÄLÄINEN, R.K. & WUORENINNE, H. 1989: Ant assemblages in the taiga biome: testing the role of territorial wood ants. – Oecologia 81: 481-486.

SCHOENER, T.W. 1983: Field experiments on interspecific competition. – The American Naturalist 122: 240-285.

SEGEV, U. & ZIV, Y. 2012: Consequences of behavioral vs. numerical dominance on foraging activity of desert seed-eating ants. – Behavioral Ecology and Sociobiology 66: 623-632.

SHIZUKA, D. & MCDONALD, D.B. 2015: The network motif architecture of dominance hierarchies. – Journal of the Royal Society Interface 12: art. 20150080.

SOLIVERES, S., MAESTRE, F.T., ULRICH, W., MANNING, P., BOCH, S., BOWKER, M.A., PRATI, D., DELGADO-BAQUERIZO, M., QUERO, J.L., SCHÖNING, I., GALLARDO, A., WEISSER, W., MÜLLER, J., SOCHER, S.A., GARCÍA-GÓMEZ, M., OCHOA, V., SCHULZE, E.-D., FISCHER, M. & ALLAN, E. 2015: Intransitive competition is widespread in plant communities and maintains their species richness. – Ecology Letters 18: 790-798.

STANTON, M.L., PALMER, T.M. & YOUNG, T.P. 2002: Competition-colonization trade-offs in a guild of African acacia-ants. – Ecological Monographs 72: 347-363.

STRINGER, L.D., HAYWOOD, J. & LESTER, P.J. 2007: The influence of temperature and fire-scale resource distribution on resource sharing and domination in an ant community. – Ecological Entomology 32: 732-740.

STUBLE, K.L., RODRIGUEZ-CABAL, M.A., MCCORMICK, G.L., JURIĆ, I., DUNN, R.R. & SANDERS, N.J. 2013: Tradeoffs, competition, and coexistence in eastern deciduous forest ant communities. – Oecologia 171: 981-992.

WARD, D. & BEGGS, J. 2007: Coexistence, habitat patterns and the assembly of ant communities in the Yasawa islands, Fiji. – Acta Oecologica 32: 215-223.

WILSON, E.O. 1971: The insect societies. – Harvard University Press, Cambridge, MA, 562 pp.

WITTMAN, S.E. & GOTELLI, N.J. 2011: Predicting community structure of ground-foraging ant assemblages with Markov models of behavioral dominance. – Oecologia 166: 207-219.

WITTMAN, S.E., SANDERS, N.J., ELLISON, A.M., JULES, E.S., RATCHFORD, J.S. & GOTELLI, N.J. 2010: Species interactions and thermal constraints on ant community structure. – Oikos 119: 551-559.

WÜST, M. & MENZEL, F. in press: I smell where you walked – how chemical cues influence movement decisions in ants. – Oikos: doi 10.1111/oik.03332.

XU, F.F. & CHEN, J. 2010: Competition hierarchy and plant defense in a guild of ants on tropical Passiflora. – Insectes Sociaux 57: 343-349.

YU, D.W., WILSON, H.B. & PIERCE, N.E. 2001: An empirical model of species coexistence in a spatially structured environment. – Ecology 82: 1761-1771.