COMMUNITY ECOLOGY - ORIGINAL RESEARCH

Tradeoffs, competition, and coexistence in eastern deciduous forest ant communities

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Abstract Ecologists have long sought to explain the coexistence of multiple potentially competing species in local assemblages. This is especially challenging in species-rich assemblages in which interspecific competition is intense, as it often is in ant assemblages. As a result, a suite of mechanisms has been proposed to explain coexistence among potentially competing ant species: the dominance–discovery tradeoff, the dominance–thermal tolerance tradeoff, spatial segregation, temperature-based niche partitioning, and temporal niche partitioning. Through a series of observations and experiments, we examined a deciduous forest ant assemblage in eastern North America for the signature of each of these coexistence mechanisms. We failed to detect evidence for any of the commonly suggested mechanisms of coexistence, with one notable exception: ant species appear to temporally partition foraging times such that behaviourally dominant species foraged more intensely at night, while foraging by subdominant species peaked during the day. Our work, though focused on a single assemblage, indicates that many of the commonly cited mechanisms of coexistence may not be general to all ant assemblages. However, temporal segregation may play a role in promoting coexistence among ant species in at least some ecosystems, as it does in many other organisms.

Keywords Diurnal · Niche · Nocturnal · Segregation · Woodland

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Introduction

A fundamental and long-standing goal in ecology has been to determine how seemingly similar species coexist in local communities (MacArthur 1958; Hutchinson 1959). Despite ever increasing attention on neutral processes (Hubbell 2001; Rosendell et al. 2011), evidence for the importance of three general mechanisms of coexistence drawn from niche theory continues to accumulate in the literature: environmental partitioning (Schoener 1974; Wright 2002; Levine and HilleRisLambers 2009), tradeoffs (Wright 2002; Kneitel and Chase 2004), and spatial segregation (Kunz 1973; Shigesada et al. 1979). At least since 1958 (MacArthur 1958), ecologists have sought to document how partitioning of environmental niches in communities promotes coexistence (Schoener 1974; Dueser and Shuggart 1979; Chase and Leibold 2003; Silvertown 2004). Similarly, tradeoffs (i.e. inverse relationships between functional traits among organisms) might also promote segregation among species (Tilman 1994; McPeek et al.

2001; Levine and Rees 2002; Yurewicz 2004) if conditions are such that no one species is dominant under all conditions. Finally, species may be segregated in such a way that promotes coexistence, either at small or large spatial scales (Gotelli and McCabe 2002; Gotelli et al. 2010). While each of these mechanisms for coexistence may occur in at least some systems, their relative importance within a single community has largely been unexamined.

In ants, many species often coexist in local communities. For example, Silva and Brandão (2010) reported 30 species in 1 m^2 of leaf litter in eastern Brazil, and Andersen (1983) documented more than 80 species in 0.25 ha in semi-arid northwestern Victoria, Australia. In temperate systems, 10 species can occur in 1 m^2 of litter, and 22 species might coexist in a 0.25-ha plot (Sanders et al. 2007c). Superficially, such diversity is surprising since competitive exclusion is often cited as playing a major role in controlling species density in ants, which often compete for food resources (Parr et al. 2005; Parr and Gibb 2010). Considerable research has focused on the coexistence of ant species and the factors that may be involved in promoting coexistence in ant communities (Parr and Gibb 2010).

To our knowledge, no study has simultaneously examined a suite of tradeoffs and the potential for niche partitioning in a single ant community (or a single community of any taxon for that matter). In this study, we examine evidence for a suite of mechanisms with the potential to facilitate coexistence within a deciduous forest ant community in the southeastern United States. These mechanisms, described below, include the dominance–discovery tradeoff, the dominance–thermal tolerance tradeoff, spatial partitioning, temperature-based niche partitioning, and temporal niche partitioning.

Dominance–discovery tradeoff

Tradeoffs in different ecological functions or tolerances among species are one of the most common explanations for coexistence in communities (Kneitel and Chase 2004). These tradeoffs may be universal, bounding similar taxa to the same tradeoffs despite being spatially isolated (Tilman 2011). The dominance–discovery tradeoff suggests that coexistence is promoted by a tradeoff in behavioural dominance and resource discovery ability among ant species (Fellers 1987; Davidson 1998; Adler et al. 2007). Behaviourally dominant ant species (typically defined as those species that can readily defend resources from other ant species) may find food more slowly than do subordinate species (Fellers 1987). A dominance–discovery tradeoff can promote coexistence if the species able to find resources more quickly tend to be poor at defending those resources against other ant species, while species that find

resources slowly tend to be more aggressive and are better able to dominate a food resource. A negative correlation between resource discovery ability and some measure of dominance among a suite of coexisting ant species is the signature of this tradeoff. A recent synthetic review of the subject suggests that there is only limited support for this tradeoff (Parr and Gibb 2011).

Dominance–thermal tolerance tradeoff

The dominance–thermal tolerance tradeoff posits that behaviourally dominant ant species can forage under only a relatively narrow window of temperatures, while behaviourally subordinate ants can, and indeed need do, forage over a wider range of temperatures in order to avoid interference by dominant species (Cerdá et al. 1998). The signature of this tradeoff is a negative correlation between the thermal tolerance of a species and an estimate of its behavioural dominance. Evidence for the dominance–thermal tolerance tradeoff in ant assemblages comes from a variety of ecosystems (Cerdá et al. 1997, 1998; Bestelmeyer 2000; Lessard et al. 2009).

Spatial partitioning

As in many other species (Gotelli and McCabe 2002) ants may segregate space, thereby creating spatial mosaics, or checkerboard distributions of species within sites. Such non-random patterns of spatial distribution may indicate strong competition (Majer et al. 1994; Albrecht and Gotelli 2001), though it is also possible that such patterns simply reflect differences among species in habitat/microhabitat preference (Ribas and Schoereder 2002). Spatial segregation can promote coexistence by reducing the frequency of interspecific encounters among species. The spatial arrangement of colonies appears to be structured by competition in several systems (Levings and Traniello 1981; Ryti and Case 1992) and may influence variation in the use of patchy resources such as those mimicked by baits (Albrecht and Gotelli 2001). Spatial segregation can be particularly pronounced among behaviourally dominant ant species and has been found, for example, to produce a mosaic pattern in the distribution of dominant arboreal ants (Majer et al. 1994; Pfeiffer et al. 2008). Evidence for spatial partitioning typically includes comparison of observed co-occurrence to the null expectation of co-occurrence in the absence of the proposed mechanism (Gotelli and Graves 1996). Observed overlap among species that is lower than expected is considered evidence that species are spatially segregated. However, several studies have failed to find evidence for spatial partitioning at local scales (Gotelli and Ellison 2002; Ribas and Schoereder 2002; Blüthgen and Stork 2007; Sanders et al. 2007a).

Partitioning of environmental niches

In addition to segregating spatially, ants and other species may segregate among various aspects of microhabitat or microclimate, including temperature (Torres 1984; Kaspari 1993). For instance, species in some systems segregate among times of day at which they forage (Kronfeld-Schor and Dayan 1999; Albrecht and Gotelli 2001; Gutman and Dayan 2005). Several studies have found strong temporal segregation of ant species, and, for the most part, cite temperature as the factor regulating these patterns (Fellers 1989; Cerdá et al. 1997; Albrecht and Gotelli 2001). Temperatures themselves, independent of time of day, can also be segregated by ant species (Torres 1984; Retana and Cerdá 2000).

The importance of each of these potential coexistence mechanisms has been examined alone, but never, to our knowledge, have they all been tested simultaneously in any single system, whether of animals, plants or other taxa. Here, we use observational data to search for signatures of each of these proposed mechanisms within a single ant assemblage in an eastern deciduous forest to determine which, if any, may play a role in promoting coexistence among 12 common ground-foraging ant species.

Materials and methods

Study site

We conducted this study within the Eno River Unit of Duke Forest, North Carolina, USA (35°52′N, 79°59′W, 130 m elevation). The area consists of an 80-year-old oak–hickory forest. The mean annual temperature is 15.5 °C, and the area receives approximately 1,140 mm of precipitation annually.

Ant Baiting

We sampled the ant community in the forest at 24 randomly chosen plots, spaced at least 50 m apart, within Duke Forest. The 50-m spacing is enough to assure that ants likely do not interact among plots. Within each plot, we arranged 12 baits [approximately 50 mg of cat food (14 % protein, 3 % fat, 1.5 % fiber) on a laminated white index card] directly on the leaf litter in a 3 × 4 grid, spaced 10 m apart. Baits such as the ones we used here are commonly used in studies of ant community ecology to simulate naturally occurring, patchy, protein-rich food resources for which ants frequently compete (Fellers 1987; Andersen 1992; Cerdá et al. 1997; Albrecht and Gotelli 2001; Parr et al. 2005; Feener et al. 2008; Lessard et al. 2009).

We sampled four of the plots once an hour for 24 h during non-rainy weather in June and July of 2009, always starting trials at 0800 hours. We sampled the other 20 plots every 15 min for 3 h from May through July of 2009 between 0830 and 2000 hours. Sampling during this time period assured that our sampling would overlap the seasonal period of peak ant foraging (Dunn et al. 2007). Only one plot was sampled per day and each plot was sampled only once during the course of the study. During each observation, we counted the number of workers of each ant species present on the bait, noted the first interspecific interaction and indicated whether it was aggressive or neutral. Aggressive interactions were those in which one ant was expelled from the bait. For the aggressive interactions, we noted which species was dominant and which was subordinate. We classified a species as being behaviourally dominant (or winning) if after interacting with the other species it remained on the bait. The subordinate species was the species that left the bait following the interspecific encounter. Interactions in which neither ant left the bait following the interaction were recorded as neutral. At each bait, we also recorded the ground surface temperature of the leaf litter just outside of the four corners of the index card using a handheld infrared thermometer (Raytek® Raynger ST). These four surface temperatures were then averaged to estimate the surface temperature of the ground in the vicinity of the bait at the time of the observation. We observed baits at night using a red light that was shone on the bait for fewer than 30 s at each check.

Discovery ability

To determine the relative ability of each species to discover food resources, we positioned six baits in a circle (a discovery array) with a diameter of approximately 60 cm and baits spaced 30 cm from one another. Bait cards were not considered independent; rather, each array served as an experimental unit. We observed baits continuously, and each time an ant discovered a bait, we recorded the time to discovery (the amount of time between the bait being placed and its discovery) and the identity of the species that discovered the bait. The bait and the discovering ant were removed from the circle for the rest of the trial to prevent recruitment to the bait, which may have influenced discovery of the bait by subsequent species. Trials were conducted for 60 min or until all six baits had been discovered, and were conducted during both the day and the night. A total of 98 discovery trials were conducted. All trials took place outside the above-described baiting plots.

In order to account for the influence of relative abundance on discovery ability (described below), we placed a single pitfall trap (55 mm diameter by 75 mm deep) in the centre of the discovery array 24 hours after the discovery trial was conducted. The pitfall trap was open for 48 h

before we collected and identified all of the ants in the trap. While pitfall traps may be slightly biased toward species that fall into traps more readily than others, pitfall traps do document the relative abundances of the species actively foraging on the surface of the ground (Gotelli et al. 2011), which is the case for the species examined here.

Analyses

For all analyses below, we considered only species that were observed on 12 or more occasions; attempting to estimate foraging conditions for rare species or species that were infrequently observed might have led us to make spurious conclusions. Except where noted, all analyses were conducted using SAS v.9.2.

Behavioural dominance rankings

We created a dominance hierarchy for the ants in the study system using two common methods: (1) the Colley dominance matrix and (2) proportion of aggressive interactions won. The Colley matrix was originally developed for the purpose of ranking American college football teams (Colley 2002) and was first applied to ant communities by LeBrun and Feener (2007). This matrix estimates dominance based on wins and losses as well as the relative strength of the opponents. A major advantage of Colley matrix relative to other methods of ranking species by dominance is that it does not require each species to have interacted with all other species in order to rank them relative to one another. For details on how the Colley matrix is calculated, see Colley (2002). We also calculated a dominance index for each species based on the proportion of aggressive encounters won by that species in the 24- and 3-h bait observations combined (Fellers 1987). We found these two methods produced quantitatively similar hierarchies ($r^2 = 0.90$, $p < 0.01$) (Supplemental Table 1), and so we use the index based on proportion of aggressive encounters won (the Fellers method) as the metric of dominance in all analyses that follow. Additionally, we calculated credible intervals for the dominance index based on the Fellers method for each species using the binom.bayes function in the binom package in R. As mentioned above, we recorded a species as winning an encounter if it remained on the bait while the losing species left the bait. We included all interspecific interactions with a clear winner and loser in the creation of these dominance rankings. Interactions without a clear winner were not included in the ranking.

Discovery ability

We used two methods to estimate discovery ability. In the first, we determined the total number of baits discovered by

a species to provide a colony-level measure of discovery ability. In the second, the number of baits discovered by a species was standardised by the foraging activity of that species (as measured by the number of pitfalls the species fell into) to provide a measure of relative discovery ability. In this second method, a null expectation for the number of baits expected to be discovered by a given species was calculated as: $(a/b) \times c$; where a is the sum of baits discovered by each species (baits discovered by species 1 + baits discovered by species 2 + ⋯); b is the sum of pitfalls from which each species was detected (species 1 pitfall occurrences + species 2 pitfall occurrences + ⋯), and c is the number of pitfalls in which a given species was detected. A line was created by plotting the expected number of baits discovered as a function of the number of pitfall traps in which the species was present, representing the number of baits predicted to be found for a given occurrence of workers. We then calculated the distance from this line to the observed number of baits discovered by each species (the residuals). A positive value for the residual would indicate that the species finds more baits than would be expected based on its abundance while a negative value would indicate that the species finds fewer baits than would be expected based on the number of occurrences. We then used the residual as a metric of discovery ability (LeBrun and Feener 2007).

We also calculated an estimate of discovery time for each species. Using the minimum discovery time for each species at each discovery array, we calculated the median time at which each species discovered baits, along with the 25th and 75th quantiles. Discovery times were not calculated for species that failed to discover baits.

Dominance–discovery tradeoff

To test the importance of the dominance–discovery tradeoff in this system, we conducted two separate linear regressions. The first of these regressions used the raw number of baits discovered by each species as the measure of discovery ability regressed against dominance while the second used the residuals described above regressed against dominance; this second method corrects for relative abundance of species. A significantly negative relationship would indicate a tradeoff between behavioural dominance and the ability to discover food items by showing that behaviourally dominant species are less able to discover new food items (Fig. 1).

Dominance–thermal tolerance tradeoff

To assess the importance of the dominance–thermal tolerance tradeoff in this community, we first determined the mean, minimum, maximum and standard deviation of the
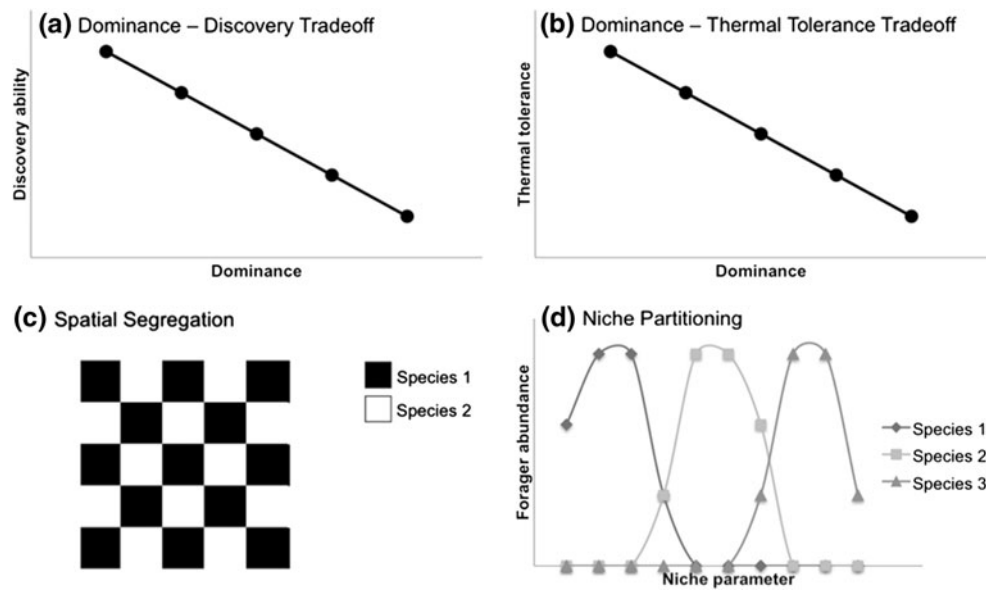
Fig. 1 Predictions of the **a** dominance–discovery tradeoff, **b** dominance–thermal tolerance tradeoff, **c** spatial segregation, and **d** niche partitioning. **a**, **b** Each *point* represents a species. In (**a**), the overall pattern indicates that behaviourally dominant species tend to be less able to discover new food resources. In (**b**), the pattern indicates that behaviourally dominant species tend to be less tolerant of temperature extremes that are behaviourally subdominant species. In (**c**), each *square* represents a patch of space. Alternating *black* and *white* colouring indicates that species 1 and 2 segregate this space. In (**d**), each *point* represents the foraging effort of a given species in a given niche. We see that the three species segregate the niche space in which they forage maximally

temperatures at which we observed each species foraging for all observations. We then used a simple linear regression to examine the relationship between each of these factors and the dominance index. A significantly negative relationship between the standard deviation of foraging temperatures and dominance indicates a tradeoff between dominance and the ability to forage at a broad range of temperatures. A positive relationship between minimum temperature and dominance would indicate a tradeoff between behavioural dominance and the ability to cope with low temperatures (Fig. 1).

Spatial analysis

We tested whether species partitioned baits by examining species co-occurrences among individual bait cards during the final hour of observations during the 3-h baiting trials. We used the final hour in order to document the outcome of both discovery and behavioural dominance. A species was considered present if it was detected on the bait at any point during the final hour of the trial. We then used these presence–absence data to calculate a C-score (Appendix 1) (Stone and Roberts 1990).

Temperature-based niche partitioning

To examine differences in foraging temperature among species, we considered foraging activity by each species in

each of nine 2 °C temperature windows ranging from the coldest temperature window observed (20–22 °C) to the warmest window at which foraging was observed (36–38 °C). For this analysis of niche space, only the 3-h baiting trails were used in order to eliminate the potentially confounding effects of dramatic shifts in temperature between day and night.

We used the mean percent of maximum number of baits occupied for each species in each temperature class as the measure of foraging activity in a "niche." We then calculated the Czechanowski index of niche overlap using EcoSim 7.72 (Gotelli and Entsminger 2010) for the community overall, as well as among the five most dominant species and among the subdominant species. We also classified each species as being either dominant or subdominant and calculated a Czechanowski index between these two groups (Appendix 2). We categorized the five most dominant species based on proportion wins as dominant and the remaining species as subdominant. We chose to make the split between dominant and subdominant species here as the dominance indices were similarly high among the first five ant species and there was a gap before the remaining species with lower Colley matrices.

Temporal niche partitioning

To examine the potential segregation of foraging times during the day, we used data from the 24-h baiting trials.

Each hour was considered an individual unit that could be used by a species, as has been done by other researchers examining temporal niches (Albrecht and Gotelli 2001). Because the 24-h trials started at 0800 hours, the observations at 0800 and 0900 hours were eliminated as they represent the first and second observations after baits were set out and many species were absent from these bait checks. Foraging-time niche analysis was conducted exactly as temperature-based niche segregation was examined above with the mean percent of maximum number of baits occupied for each species in each hour as the measure of foraging activity in a "niche."

Results

We observed a total of 22 ant species in either pitfall traps or on baits in this study, though 12 ant species were common (observed on baits at least 12 times) and subsequently used in the analyses that follow. Additionally, 371 aggressive encounters between species were observed. *Camponotus pennsylvanicus* was the most behaviourally dominant species at baits. However, the 95 % credible intervals around its dominance score overlapped considerably with those of *Crematogaster lineolata*, *Prenolepis imparis*, *Camponotus americanus* and *Camponotus castaneus*, suggesting that these five species were generally the dominant species. The least behaviourally dominant ant was *Temnothorax curvispinosus* (Fig. 2; Table 1). Further, the 95 % credible intervals around the dominance indices overlapped for many species, which is to say many species in this system have similar competitive abilities or, at the very least, more data are needed to discern subtle competitive differences between species.

Discovery ability

Aphaenogaster rudis discovered baits the fastest, with a median discovery time of 1 min. *Camponotus castaneus* was the slowest, with a median discovery time of 12 min when it was the first species to discover the bait (Supplemental Fig. 1). After controlling for foraging activity by calculating the residuals of the relationship between abundance and bait discoveries (a metric of how far a species was from discovering the number of baits that would be expected based on its occurrences in pitfall traps), the species that discovered the highest number of new baits, given its abundance, was *Aphaenogaster rudis* while *Camponotus pennsylvanicus* discovered the fewest (Table 1). Two species, *Tapinoma sessile* and *Aphaenogaster lamellidens*, were not observed frequently enough at discovery trials to determine their discovery ability.
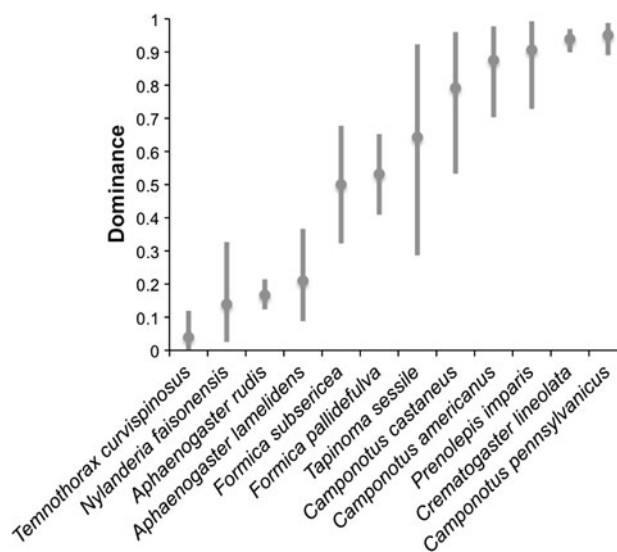
Fig. 2 Dominance (based on proportion of aggressive encounters won), plus or minus credible intervals

Table 1 Dominance (as measured by the Colley dominance matrix) and discovery abilities (residual of actual bait discovery vs. expected bait discovery) for the 12 most common ants in the study system

Species	Dominance	Discovery ability
Aphaenogaster lamellidens Mayr	0.20	N/A
Aphaenogaster rudis Enzmann	0.17	164.40
Camponotus americanus Mayr	0.89	−4.26
Camponotus castaneus (Latreille)	0.82	−21.55
Camponotus pennsylvanicus (De Geer)	0.96	−46.58
Crematogaster lineolata (Say)	0.94	−43.38
Formica pallidefulva Latreille	0.53	−16.55
Formica subsericea Say	0.50	−3.26
Nylanderia faisonensis (Forel)	0.12	6.00
Prenolepis imparis Emery	0.93	−18.03
Tapinoma sessile (Say)	0.67	N/A
Temnothorax curvispinosus Mayr	0.03	−16.80

Positive values for discovery ability indicate species that discovered more baits than expected based on worker abundance alone, while negative values indicate species that discovered fewer baits than expected based on worker abundance. Only two species, *A. rudis* and *N. faisonensis* discovered food faster than would be expected given their abundance

Dominance–discovery tradeoff

Contrary to the predictions of the dominance–discovery tradeoff, we found no relationship between dominance and discovery ability among species using either method for determining discovery ability (colony-level: $r^2 = 0.15$, $p = 0.27$; worker level: $r^2 = 0.28$, $p = 0.12$).

Dominance–thermal tolerance tradeoff

Ground surface temperatures observed during the day ranged between 19 and 52 °C (based, in part, on whether the bait was in direct sunlight or shade), and some ant species foraged across this entire range (Supplemental Fig. 2). However, 90 % of instances in which we saw ants at baits occurred between 24 and 28 °C, with a mean observed ground surface temperature of 27 °C and a median of 26 °C. We found no relationship between dominance and mean ($r^2 < 0.01$; $p = 0.96$), minimum ($r^2 = 0.01$; $p = 0.74$) or maximum foraging temperature ($r^2 = 0.02$; $p = 0.67$), nor was behavioural dominance related to the standard deviation of foraging temperature ($r^2 = 0.01$; $p = 0.83$).

Spatial analysis

We used null model analyses to determine whether species were spatially segregated from one another. We found no evidence that ant species were spatially segregated overall, among just the dominant species, or among just the subdominant species (Supplemental Fig. 3). That is, in all cases, the observed C-score (a measure of co-occurrence) did not differ from the null expectation that species co-occurred randomly with respect to one another ($p > 0.20$ in all cases).

Temperature-based niche partitioning

Considering temperature (based on 2 °C temperature classes) as a possible factor defining the foraging niche, niche overlap was greater than expected by chance for all groups compared: all ants ($p < 0.01$), dominant species only ($p < 0.01$), subdominant species only ($p < 0.01$), and dominants versus subdominants ($p < 0.01$) (Table 2).

Table 2 Niche segregation for temporal and thermal niches

| Class	Obs. niche overlap	Simulated	p
Thermal niche overlap			
All	**0.63**	0.56	<0.01
Dominant	**0.66**	0.53	<0.01
Subdominant	**0.72**	0.63	<0.01
Dominant versus subdominant	**0.89**	0.76	<0.01
Temporal niche overlap			
All	0.44	**0.46**	0.02
Dominant	**0.49**	0.45	<0.01
Subdominant	**0.59**	0.45	<0.01
Dominant versus subdominant	0.67	**0.73**	<0.01

Bold text indicates which index of niche overlap (observed or expected) was larger

Temporal niche partitioning

We observed significant niche-differentiation when time of day was examined as the focal niche axis. In the overall ant community, significant niche segregation of foraging-time was apparent ($p = 0.02$) (Table 2). The five most dominant species, however, showed greater niche overlap than the null expectation ($p < 0.01$) (Fig. 3a). Subdominant species also overlapped in foraging times with one another more than would be expected ($p < 0.01$) (Fig. 3b). Additionally, dominant ants occupied a different niche space than did subdominant ants ($p < 0.01$). Dominant ants in the study system focused the bulk of their foraging effort at night while subdominant ants foraged more during the day (Fig. 4).

Discussion

The idea that interspecific competition drives community assembly and limits local coexistence has been at the core of community ecology (Kneitel and Chase 2004; Tilman 2011). Numerous mechanisms promoting the maintenance of coexistence have been proposed in a wide array of taxa (MacArthur 1958; Wright 2002; Silvertown 2004). In ants, competitive interactions and a suite of tradeoffs associated with competitive ability and thermal tolerance have long been thought to structure communities (Hölldobler and
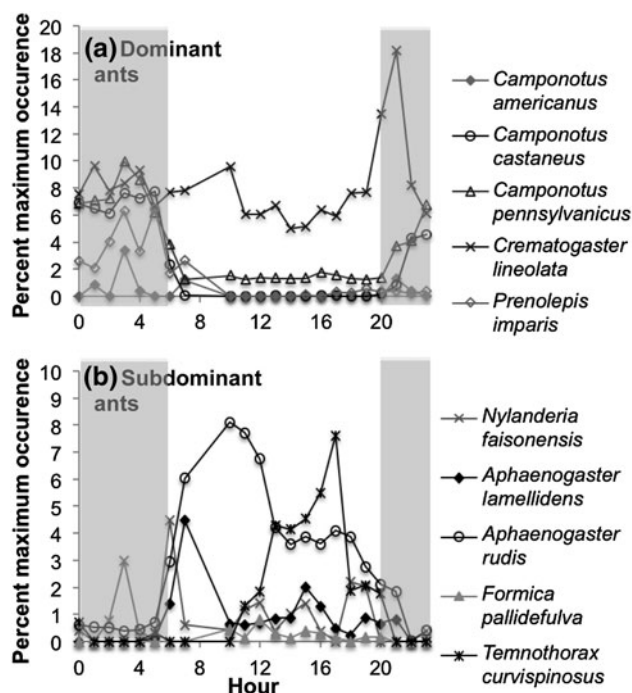
Fig. 3 Percent maximum occurrence of abundance of **a** dominant ants and **b** subdominant ants on baits over the course of the day. *Shaded areas* indicate nighttime. Hour *0* indicates midnight
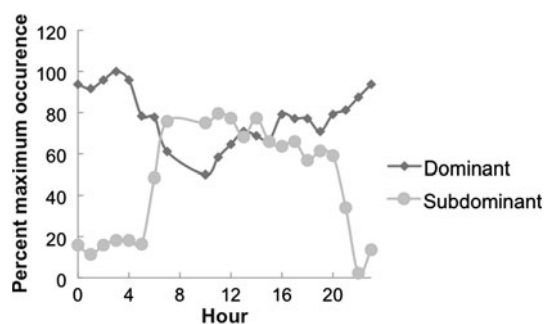
Fig. 4 Percent maximum occurrence of abundance of dominant ants (combined) and subdominant ants (combined) on baits the course of the day. Hour *0* indicates midnight

Wilson 1990; Parr and Gibb 2010). Generally speaking, four common mechanisms have been proposed for coexistence among ant species. These are the dominance–discovery tradeoff (Fellers 1987), the dominance–thermal tolerance tradeoff (Cerdá et al. 1997, 1998; Bestelmeyer 2000; Lessard et al. 2009), spatial segregation (Albrecht and Gotelli 2001), and partitioning of thermal niches (Torres 1984; Albrecht and Gotelli 2001). We found no support for any of these coexistence mechanisms. However, our results suggest that foraging times of species are temporally partitioned, which may promote coexistence in forest ant communities. Admittedly, however, temporal niche partitioning in this system may have also arisen for reasons entirely unrelated to interspecific interactions and coexistence.

Ant species in our system are temporally segregated, with behaviourally dominant ants occupying baits during the night and subdominant ants more prevalent during the day. Of course, further investigation is needed to be sure that these species-level interactions scale up to promote coexistence. However, evidence for the importance of temporal niches in ant communities has been found in other systems. For example, Fellers (1989) found that ant species segregated time in another eastern deciduous forest. In the Maryland forest system she worked in, *Prenolepis imparis* foraged primarily during the night in summer, while *Formica subsericea* foraged during the day. We also found *Prenolepis imparis* to be primarily nocturnal during the study periods and *Formica subsericea* and *F. pallidefulva* to be strictly diurnal in our study system. Likewise, diurnally active *Formica* species in Europe have been found to shift occupation of baits by subdominant species to the night (Vepsäläinen and Savolainen 1990). Diurnal segregation of species has also been observed in other ecosystems. In a classic study on a sand ridge in Michigan, Talbot (1946) observed diurnal variation in ant activity among three ant species. Additionally, Cerdá et al. (1997, 1998) also found variability in daily patterns of foraging among ant species in Spain. Similarly, diurnal niche partitioning was found to be

important in an Oklahoma grassland, while seasonal niche partitioning was not a factor due to the clustering of species during the warmer part of the year (Albrecht and Gotelli 2001). Temperature is commonly suggested as the proximate cue for temporal niche segregation. However, considering only the baiting observations occurring during the day, we found no evidence that temperature explained temporal niche segregation within the studied ant community despite the 33 °C range in temperatures observed among baiting stations (though we admit that the hottest temperatures observed across this spectrum were associated with light flecks on the forest floor and, as such, were short-lived). This suggests that temperature is not the cue for foraging. We should note that these daytime temperatures did not encompass the cooler end of the nighttime temperatures, which dropped to as low as 14 °C in this study, though the range of daytime temperatures did overlap the average observed nighttime temperature of 21 °C. However, using only the daytime temperature data in this analysis allowed us to avoid confounding temperature and time.

If the temporal cue that ants use to decide when to forage is not temperature, it is reasonable to wonder what it might be. Recent studies suggest that light levels may play a role in determining the timing of foraging in some ant species (Narendra et al. 2010; Amor et al. 2011), while other species may switch between vision and chemical cues depending on light levels (Beugnon and Fourcassié 1988). The bigger question, though, is what factors have favoured the evolution of differences in foraging times. Perhaps competition has favoured such segregation, though it is interesting that the species that are most similar to each other behaviourally (which is to say dominant *Camponotus* species) tend to forage at the same time. Another factor that could shape temporal foraging patterns may be food availability. For example, there is evidence in other systems that honeydew quality and availability may vary over the course of a day; such variation in availability of this key resource could shape daily activity patterns (Degan and Gersani 1989; Pekas et al. 2011). Thus, segregation of food resources may also influence temporal foraging patterns. Alternatively, and not exclusively, phorid flies and other parasites may limit the activity of dominant species during the day. During the study, phorid flies were frequently observed attacking *Camponotus* species during the day. Phorid flies have been found to limit daytime foraging by a species of leaf-cutter ants in Costa Rica (Orr 1992) and to cause shifts in *Pheidole titanis* toward nocturnal foraging in a dry season deciduous thorn forest in Mexico (Feener 1988). Beyond regulating diurnal patterns, phorid flies are known to alter competitive interactions between species (LeBrun and Feener 2007).

The dominance–discovery tradeoff does not seem to mediate the coexistence of ant species in our study system.

Previous studies in eastern deciduous forests on the dominance–discovery tradeoff have found support for this mechanism (Fellers 1987), while others have not (Lessard et al. 2009). However, the substantial overlap in the credible intervals among species indicates that a strict linear dominance hierarchy does not exist in this system. This lack of a true linear hierarchy may lessen the role of tradeoffs in functional traits in promoting coexistence. Additionally, intransitivities under certain environmental conditions or for some resources may also lead to coexistence (Sanders and Gordon 2003). Further, our failure to find evidence of this tradeoff may be, at least in part, because one ant species (*A. rudis*) dominated bait discoveries over all other species. The ability of this single species to find food resources more efficiently than any other ant species in the system may alter the predictive power of the dominance–discovery tradeoff for other subdominant species in this system. *A. rudis* was also present in Fellers's (1987) system and was also the species most adept at discovering baits in that system. However, Fellers's system had two other commonly observed species that were fairly close to *A. rudis* in discovery ability. Interestingly, one of these species was *Temnothorax curvispinosus* (ex *Leptothorax curvispinosus*), a species which we found to be a relatively poor discoverer of food resources in our study. Variability in community composition may cause this tradeoff to be important in some systems but not in others. However, a recent review (Parr and Gibb 2011) suggests that the dominance–discovery tradeoff may not be general among ant assemblages in a variety of systems.

We also found little evidence for the dominance–thermal tolerance tradeoff in maintaining species coexistence. A dominance–thermal tolerance tradeoff may be more important in systems in which temperatures are high or low enough to limit foraging in intolerant species (Cerdá et al. 1997, 1998; Bestelmeyer 2000; Lessard et al. 2009; Wiescher et al. 2011). In hot, arid systems, the only species foraging during the hottest periods of the day are often the subordinate species (Cerdá et al. 1997, 1998), while in relatively more benign systems, the reverse has been found, with subordinate ants foraging more frequently at cooler, and across a broader range of, temperatures, relative to dominant ants (Lessard et al. 2009). Additionally, Lynch et al. (1980) found evidence for seasonal niche segregation in a Maryland deciduous forest, suggesting the importance of temperature in this system on an annual timescale.

In ants, both the dominance–discovery and dominance–thermal tolerance tradeoffs are problematic as general explanations for coexistence because of the lack of an agreed measure of dominance (for example: Fellers 1987; LeBrun and Feener 2007). In addition, dominance hierarchies can vary based on additional variables such as temperature and time of day (Cerdá et al. 1997), resource availability (Sanders and Gordon 2003), or simply due to unmeasured or stochastic factors, making it challenging to demonstrate whether such tradeoffs promote coexistence. The uncertain status of tradeoffs as a general explanation for coexistence in ants stands in contrast to the case for many other taxa where tradeoffs seem to be common (Tilman 2011).

Finally, we did not find any evidence that ant species partition space, in contrast to the results of many studies that have shown ant species are often spatially segregated within communities (Adams 1994; Majer et al. 1994; Blüthgen et al. 2004). Many of the studies examining spatial segregation among ants have dealt with arboreal species (but see Albrecht and Gotelli 2001; Sanders et al. 2007b), while our study focused on ground-dwelling species. Additionally, temperature may mediate patterns of co-occurrence within sites, if interspecific competition and microhabitat preferences result in spatial segregation of microsites that differ in temperature (Vepsäläinen and Savolainen 1990; Wittman et al. 2010). Spatial segregation can be particularly common among dominant ants. However, we did not observe spatial segregation even among the five most dominant ant species. This result agrees with the findings of Sanders et al. (2007a), who considered dominant arboreal ant species within a tropical forest and found them to co-occur randomly. However, Sanders et al. (2007a) did find that, in a tropical agro-ecosystem, all species co-occurred less frequently than expected by chance, suggesting that, overall, arboreal species in that tropical system segregate space. Perhaps the result most similar to ours comes from a study of ant assemblages in the northeastern US. Gotelli and Ellison (2002) found spatial segregation to be important in ant communities at regional scales (essentially among sites separated by tens of km), but failed to find evidence for spatial segregation at local scales within sites. In our study (and in others), the lack of spatial segregation likely points to the importance of other factors in limiting competitive interactions among ant species.

In our study system, the only niche-based difference among species that might facilitate coexistence was temporal niche segregation. In general, dominant ant species foraged during the night, while subdominant ants tended to recruit to baits more commonly during the day. Such segregation might result from competitive displacement, but it may simply be a result of other ecological or evolutionary processes (such at the influence of parasitism). An important implication of these results is the need to conduct more ecological research during periods traditionally less well studied (i.e. night). The vast majority of ecological studies on ants as well as other organisms are conducted during the day. However, there may be important differences in species activity during the night versus

the day, and these differences may, in large part, determine the structure of some ant assemblages.

We should be clear that this study does not exhaustively test all potential mechanisms of coexistence. For example, all the mechanisms we tested assume that interspecific competition is important in the structuring of ant communities (Hölldobler and Wilson 1990; Parr and Gibb 2010). However, intraspecific interactions also have the potential to regulate community composition if the influence of intraspecific competition for some species is greater than the influence in interspecific competition (Shorrocks et al. 1984; Shorrocks and Sevenster 1995). While we did not explicitly quantify intraspecific interactions during this experiment, we observed interspecific interactions much more frequently than intraspecific interactions. However, the relative impacts of intraspecific competition in ants are poorly understood (but see Boulay et al. 2010). Additionally, we consider only mechanisms that involve competition for food. Competition for nest sites (Andersen 2008) and the perturbation of foraging by parasitoids (LeBrun and Feener 2007) may also play a role in structuring these communities. Even considering competition for food, another possible driver of coexistence could include segregation of particular types of food resources (Bernstein 1979; Sanders and Gordon 2003). The ants observed in this study tend to be generalist omnivores, but we do not know the extent to which their diets overlap. Additional testing, perhaps with stable isotopes, would provide more information on potential dietary differences among these species (Blüthgen et al. 2003; Tillberg et al. 2006; Fiedler et al. 2007). It should also be noted that the mechanisms examined in this study all assume that populations are in equilibrium. However, as with many other studies, we do not explicitly test this assumption. Thus, it is possible that the focal community is not at equilibrium (Siepielski and McPeek 2010). Finally, we examined temporal segregation on only a diurnal timescale, but segregation on seasonal timescales could also be important (Lynch 1981). However, while it is possible that partitioning of activity times among months or seasons throughout the year is possible, we have found little evidence of such a mechanisms in this system (Stuble, unpublished data).

Our results point not only to the possible importance of temporal niche partitioning in at least some ecosystems but also to the potential for temporal niche segregation to operate outside the influence of temperature. Temporal segregation has also been suggested as a mechanism of coexistence in assemblages of other species (Carothers and Jaksić 1984; Kronfeld-Schor and Dayan 1999). However, even if temporal segregation leads to non-random temporal overlap of the activity patterns of species, temporal segregation may have evolved for other reasons (such as avoidance of parasitism) that have very little to do with interspecific competition and coexistence. Taken together, our approach of testing multiple competing hypotheses for coexistence among ant species is beginning to rule out some mechanisms while finding support for others, at least in this study system. Replicating this work in other systems, be they ant assemblages or otherwise, will provide much needed answers to one of the most vexing questions in ecology—how so many seemingly similar species coexist in local communities.

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