



Species occurrence and abundance in a community

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Patterns of species occurrence and abundance are influenced by abiotic factors and biotic interactions, but these factors are difficult to disentangle without experimental manipulations. In this study, we used observational and experimental approaches to investigate the role of temperature and interspecific competition in controlling the structure of ground-foraging ant communities in forests of the Siskiyou Mountains of southwestern Oregon. To assess the potential role of competition, we first used null model analyses to ask whether species partition temporal and/or spatial environments. To understand how thermal tolerances influence the structure of communities, we conducted a laboratory experiment to estimate the maximum thermal tolerance of workers and a field experiment in which we added shaded microhabitats and monitored the response of foragers. Finally, to evaluate the role of temperature and interspecific competition in the field, we simultaneously manipulated shading and the presence of a dominant competitor (*Eciton bispinosum*) for foraging activities. Species of species broadly overlapped during the diurnal range of temperature. Our results suggest that interspecific competition may not be a major factor in determining species pool (Ricklefs 2004), which in turn influence the composition of local communities (Webb et al. 2002, Wiens and Donoghue 2004). At smaller spatial scales, both abiotic filtering (pH, temperature, water availability, etc.), and biotic interactions (interspecific competition, parasites, herbivory, etc.) may operate to determine which species occur, and co-occur, together within the local community (Weiher and Keddy 1999, Cavender-Bares et al. 2009).

Species exclusion may not be a major factor in determining similar ecological traits, resulting in segregation of species with similar traits (Winston 1995). On the other hand, if tolerance to abiotic conditions is more important than biotic interactions, then species can only occur if they possess specific ecological traits. When environmental conditions primarily determine community membership, we expect to find positive associations of species with similar traits across sites (Jackson et al. 1992).

Within local communities, theory predicts either separation or aggregation of important ecological traits among closely related species, depending on the relative role of biotic interactions versus the abiotic environment, respectively, on community membership. Closely related species occurring in the same habitat often have similar requirements and share similar ecological traits. Thus, classical niche theory of limiting similarity (Hutchinson 1959, MacArthur

Ants are an ideal taxon with which to study the relative influence of biotic and abiotic environment, as there is good evidence that both interspecific competition (reviewed by Hölldobler and Wilson 1990) and thermal constraints on foraging activity and colony performance (Bestelmeyer 1997, Cerdá et al. 1998, Holway et al. 2002) control ant community structure. Ant responses to temperature and competition have been used to describe dominance–diversity patterns

on continental scales (Andersen 1992, Parr et al. 2005), responses to disturbance (Andersen 1991, York 2000, Farji-Brener et al. 2002), and the invasion success of non-native species (Holway et al. 2002).

In this study, we first measured statistical patterns of ant species co-occurrence and activity at food resources. We then measured the thermal tolerance of the eight most common ant species in a laboratory experiment. Finally, we added shade and removed a dominant ant competitor in a controlled field experiment to understand how thermal tolerance and interspecific competition inter-

the number and identity of each species and estimated the soil surface temperature under and around each bait station to the nearest 0.1°C hand-held infrared thermometer.

To assess competitive ability of each species, we quantified species interactions and behavioral dominance at the control baits. Pairwise interactions between workers of two different species were categorized as 'attacks' or 'avoidances' (Fellers 1987). An attack consisted of active participation of at least two workers in which one individual bit, chased, lunged, or used chemical spray to cause the other individual to retreat. Occasionally an attack would result in a severe injury or death. Avoidance behavior occurred when workers of one species retreated from the bait card after making contact with another in the absence of an obvious attack. A species was characterized as dominant if it attacked or if its presence elicited avoidance behavior in individuals of another species. Using the method of Fellers (1987), the dominance index for each species was defined as the percentage of times it was dominant during all instances of its attacks and avoidances (Table 1). Note that some dominance indices are based on only one observation; however, the general pattern of dominance and bait occurrence displayed in Table 1 is consistent with behavioral and occurrence data collected at 16 other sites in the region (Wittman 2007).

Thermal tolerance

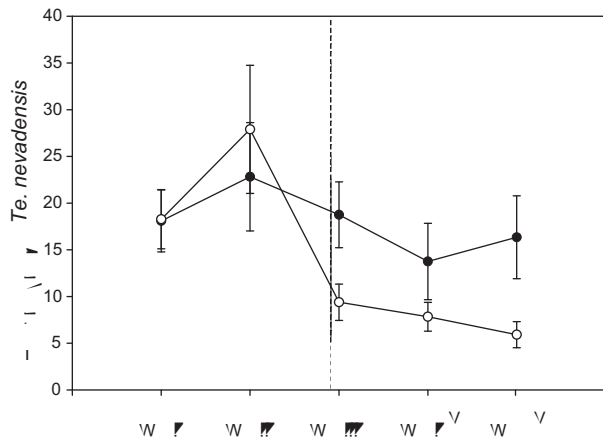
We measured thermal tolerance of all eight species observed during the BACI shading experiment (species listed in Table 1). We collected workers of each species from nest entrances and vegetation that was well beyond the area of the shading experiment. Within four hours of field collection, individual workers were exposed to slowly increasing temperatures in a heat block. Eight workers of each species were placed into individual 1.5-ml microcentrifuge tubes and randomly assigned to a well within the heat block. Temperature exposure began at 40°C and was increased in 2° intervals to 50°C. Individuals were exposed to each temperature for 10 min, and the temperature was recorded when individuals died or permanently lost muscle coordination. Each species trial was replicated six times. The mean temperature of death for the eight individual workers was calculated as an index of thermal tolerance for each species.

Shading and species removal

To determine if the reduction in *T. nevadensis* abundance in the shading experiment was due to the direct effect of the shade or due to the indirect effects of changes in a competitively dominant species, we conducted a full factorial shading and species removal experiment. The shading and removal experiment was conducted during June–August 2005, at the same site as the 2004 BACI shading experiment. From the census data in the BACI shading experiment, *Formica moki* was the most widespread and behaviorally dominant species (Table 1), so it was the focal removal species in 2005. We located *F. moki* nests by baiting and following workers to their nest. After locating 24 nests, we randomly assigned the area around the nest entrance to one of the four treatments: 1) shading, 2) *Ft710*

randomized matrices. Null assemblages were created in EcoSim using a fi

temperature during morning, afternoon, and evening time blocks did not vary among sites ($F_{15,47} = 0.452$, $p = 0.948$). Soil surface temperature varied significantly throughout the day ($F_{2,47} = 50.336$, $p < 0.001$) with hot afternoon temperatures (mean afternoon temperature $^{\circ}\text{C} \pm 1 \text{ SE} = 49.16 \pm 1.67$) higher than either morning (30.02 ± 1.36) or evening (26.37 ± 1.36) temperatures (Tukey $^{\circ}\text{C} \pm 1 \text{ SE} = 49.16 \pm 1.67$) higher than either morning (30.02 ± 1.36) or evening



Bait occupancy did not differ significantly between control and treatment plots for any week (week I: $F_{1,14} = 0.09$, $p = 0.769$; week II: $F_{1,14} = 0.16$, $p = 0.699$; week III: $F_{1,14} = 0.30$, $p = 0.592$; week IV: $F_{1,14} = 2.37$, $p = 0.146$; week V: $F_{1,14} = 0.95$, $p = 0.345$). Total number of workers, however, was five times greater in shaded plots than in control plots during week IV (mean workers number \pm SE = 30.9 ± 7.63 in control plots, 151.6 ± 42.3 in shade plots; $F_{1,14} = 5.36$, $p = 0.039$), and there was a trend of greater worker numbers in shaded plots during week V (45.9 ± 23.3 in control plots, 112.2 ± 31.6 in shade plots; $F_{1,14} = 4.42$, $p = 0.057$). On average, half as many *T. nevadensis* workers recruited to shaded versus control baits during shading weeks (week III: $F_{1,10} = 222.00$, $p < 0.001$; week IV: $F_{1,10} = 7.07$, $p = 0.045$; week V: $F_{1,10} = 7.57$, $p = 0.04$; Fig. 2).

There was no difference in *T. nevadensis* abundance between control and treatment baits during the two-week pre-treatment period (week I: $F_{1,10} = 1.52$, $p = 0.272$; week II: $F_{1,10} = 0.12$, $p = 0.741$; Fig. 2).

Temperature and Thermal Tolerance

The average maximum temperature tolerances ranged from 44.0 to 48.1°C (Fig. 3). *Aphaenogaster occidentalis* was the least thermally tolerant species and *T. nevadensis*, *C. coarctata* and *Liometopum luctuosum* were the most thermally tolerant (Fig. 3). Thermal tolerance measured in the laboratory was marginally associated with maximum foraging temperatures observed in the field (observed $r = 0.524$, mean of simulated = -0.025 , $p = 0.073$).

Thermal tolerances of species predicted changes in abundance in shaded plots (observed slope = -8.371 , mean of simulated slopes = -0.220 , $p = 0.007$; Fig. 4). Species with low thermal tolerances increased in abundance in shaded plots relatively more than did species with high thermal tolerance. Thermal tolerance was not associated with natural changes in abundance over time as measured in the control plots (observed slope = -3.746 , mean of simulated slopes = -0.040 , $p = 0.138$).

Similarity of thermal traits predicted patterns of co-occurrence among species pairs (observed slope = -0.3155 , mean of simulated slopes = -0.0004 , $p = 0.042$; Fig. 5). Species pairs with similar thermal tolerances were more likely to be spatially segregated (large positive SES values) within the SE site.

Shade and Removal Treatments

Removal treatments were successful, as 94.8% fewer *F. moki* workers were present at baits in removal plots than at baits in control plots (mean workers number \pm SE = 13.9 ± 2.42 in control plots, 0.69 ± 0.87 in removal plots; $F_{1,15} = 20.29$, $p < 0.001$). There was no effect of shade (7.5 ± 2.3 in control plots, 7.0 ± 2.4 in shade plots; $F_{1,15} = 3.49$, $p = 0.139$) or treatment interaction ($F_{1,15} = 3.48$, $p = 0.139$) on *F. moki* worker abundance. On average 78% more *T. nevadensis* workers recruited to baits in removal plots ($F_{1,13} = 18.58$, $p < 0.001$) and 68% fewer workers to shaded baits ($F_{1,13} = 8.92$, $p = 0.015$; Fig. 5). There was no interaction of shade and removal treatments ($F_{1,13} = 1.22$, $p = 0.290$).

Removal of *F. moki* increased the likelihood of bait occupancy by two of the seven other ant species: *T. nevadensis* occupied more baits in the removal treatment during three sampling periods (= times of day), and *T. sessile* occupied more baits in the removal treatment during two sampling periods (Table 2). Shading increased the likelihood that *A. occidentalis* occupied baits during two sampling periods but decreased the likelihood that *Temnothorax nevadensis* occupied baits (Table 2). Shade and removal treatments had no effect on bait occupancy by *S. molesta*.

Discussion

In the Siskiyou Mountains, community organization and foraging abundance of ants at the local scale appears to be

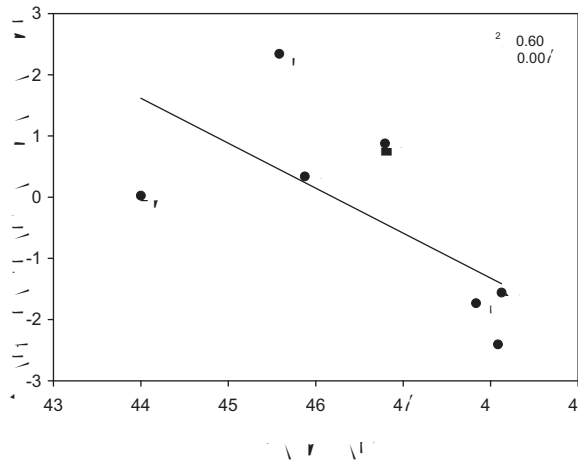


Figure 4. Thermal tolerance values predict percent changes in abundance after the addition of shade (observed slope = -8.371 , mean of simulated slopes = -0.220 , $p = 0.007$). Points represent individual species (see Table 1 for species abbreviations).

controlled primarily by the thermal environment, and secondarily by biotic interactions. Species aggregate foraging activity across the diurnal timeframe, with activity levels dropping in the hottest part of the day and increasing during cooler hours (Wittman 2007). In our study area, diurnal temperature fluctuates widely, likely setting hard boundaries to activity levels. Temperature is a cue for ants to leave the nest to forage (Muser et al. 2005, Azcarate et al. 2007), and ants generally forage within a limited thermal range (Garcia-Perez et al. 1994, Cerdà et al. 1997, Pol and de Casenave 2004). Humidity may also interact with temperature to form a ‘temperature-humidity envelope’ (Hölldobler and Wilson 1990) that dictates when workers can be active (Talbot 1946, Kuate et al. 2008).

Our study provides evidence that physiological thermal tolerance predicts how ant species respond to changes in their thermal environment: the less thermally tolerant a species was, the greater was its change in abundance after shade additions (Fig. 4). Due to the short duration of the shading experiment, the abundance changes we documented likely are not measures of change in population size of ant colonies, but rather measures of changes in foraging behavior at baits. Because abundance was quantified as the sum of workers

observed throughout the day, if a species increased recruitment or total time spent foraging at a bait, it would be recorded as an overall increase in abundance. Thus, we conclude that shading most greatly impacted the foraging behavior of species most physiologically restricted by temperature (Fig. 4).

That thermal tolerance predicted changes in foraging abundance to shade additions is striking, considering the relatively small differences in thermal tolerance (Fig. 3), the small size of shade tarps (0.25 m^2), which rarely covered nest entrances, and that physiologically driven responses were not drastically altered by any competitive interactions. Thermal control of foraging activity is also very apparent in *T. nevadensis*, as evident in both the BACI shading experiment (Fig. 2) and the shading and removal experiment (Table 2, Fig. 6). Although its abundance increased in the removal experiment

Table 2. Results of nominal logistic analysis of the effects of shading and *F. moki* removal on bait occurrence data collected during four separate sampling periods (08:00–11:00). Analyses were run separately for each species. *Crematogaster coarctata* and *L. luctuosum* did not occur at sufficient baits for the analysis. Cells boxed with a solid line indicate a greater chance of bait occupancy, while cells boxed with a dashed line indicate a reduced chance of bait occupancy. No interactions between shading and removal treatments were found ($p > 0.05$). Species abbreviations as in Table 1.

Species	8:00		9:00		10:00		11:00	
	Removal	Shade	Removal	Shade	Removal	Shade	Removal	Shade
Ao	0.162	0.046	0.167	0.004	1.000	1.000	0.958	0.945
Cc
Fm	0.570	0.767	0.002	1.000	0.047	0.999	<0.001	0.063
Ll
Sm	0.328	0.328	0.098	1.000	0.098	1.000	0.345	0.262
Tn	0.307	0.019	0.034	0.034	0.046	0.162	0.014	0.932
Ts	0.047	0.999	0.887	0.887	0.047	0.999	0.098	1.000

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