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Living with an invader: the role of environment heterogeneity in the coexistence of competitor ant species

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Abstract In order to coexist in sympatry, subordinate species must somehow obtain resources that dominant taxa may generally control. Previous work has demonstrated that subordinate ant species may achieve coexistence via spatial separation or resource partitioning, but often these studies encompassed relatively large spatial scales. Such work fails to acknowledge that in any one environment there are likely to be multiple food items. Here, we examine the response of ant species to fine-scale variation in resource distribution. During a variety of temperatures over the course of a year, we partitioned a total of 6 g of food as 1, 8, or 64 items in five 0.4m² areas centred on nests of the ecologically dominant ant *Monomorium sydneyense* Forel. As the number of food items increased, we observed an increase in species utilizing the food and a corresponding increase in the proportion of foods being unoccupied and available for consumption. We then modelled the response of the *M. sydneyense* to temperature and a varying distribution of the same amount of resources, and examined how three other species in the community vary from this response in order to obtain food. A binary logistic regression model indicated significant main effects of density, site, species, and temperature. However, there were also significant interaction effects for these variables, making it impossible to interpret the main effects in isolation. Increasing temperatures resulted in *M. sydneyense* becoming increasingly dominant and displacing other species from large resource patches, resulting in species changing their behaviour to forage on smaller patches. Though most species were able to respond to increasing resource dispersion, species that were in low abundance apparently could not. Factors such as temperature and resource dispersion are important in coexistence patterns at small spatial scales, because different species respond differently to each of these factors.

Keywords Coexistence · sympatry · diversity · dominance · food · temperature · foraging · *Monomorium sydneyense*

Introduction

Community theory predicts that species competing for the same resource should be spatially or temporally separated in order to allow for coexistence. Subordinate species can coexist only when their niche is different from that in ecologically dominant species. This niche differentiation arises when stochastic fluctuations in the environment, such as with the

distribution of resources or temperature variation, affect each species differently (Savolainen and Vepsäläinen 1988).

Competition is thought to have a considerable role in structuring ant communities. However, the outcome of these competitive interactions is considered dependent on environmental conditions. Temperature is considered to be a key factor; so much so that resource partitioning based on thermal tolerance has frequently been demonstrated (Andersen 1995; Cerdá et al. 1997; Albrecht and Gotelli 2001). Several studies have shown ecologically dominant species to have limited thermal tolerance compared to that of subordinate species, enabling these subordinates to achieve a much higher density than would be otherwise expected (Cerdá et al. 1998). In at least some communities there even appears to be a trade-off between temperature tolerance and behavioural dominance, wherein subordinate species tolerate low temperatures (Bestelmeyer 2000). However, in several of these studies, considerable niche overlap in temperature is observed between competing and coexisting ant species (e.g. Bestelmeyer 2000; Albrecht and Gotelli 2001). In addition, daily temperature fluctuations are relatively small in habitats like those on the equator, resulting in limited potential for niche differentiation based on temperature, and yet extremely diverse ant assemblages still occur in these areas (Kaspari et al. 2004). For such communities, other mechanisms of reducing niche overlap must be acting to maintain coexistence patterns.

One such mechanism enabling coexistence is spatial niche partitioning. Greenslade (1979) demonstrated dominant species to be spatially separated with little overlap in their foraging range. This pattern in ant distribution has been described as 'ant mosaics' (Leston 1973). Such regular dispersion in ant communities is often observed and is thought to result from neighbourhood competition, where competition between established colonies is weak but established colonies interfere or inhibit new colonies from establishing (Ryti and Case 1992). Subordinate species coexist in these mosaics by fitting between the boundary gaps of the dominant species (Greenslade 1979). The size of the area that the dominant species occupies varies, but is generally of several meters (Greenslade 1971, 1979). Consequently, perhaps it is not surprising that in studies examining ant coexistence in spatial scales encompassing tens of meters (e.g. Levings and Traniello 1981; Albrecht and Gotelli 2001; Thomas and Holway 2005), considerable niche overlap is observed and the spatial segregation of species is considered a major factor enabling niche overlap and coexistence.

In many ant species and communities, however, coexistence occurs at much finer scales than that of several meters. Individual traps rarely collect only individual species, indicating a variety of species are foraging the same local environment. One unstudied potential factor contributing to this result is resource number and distribution within very fine scales. Different ant species vary considerably in the way that they utilize resource patches in an environment. Some species will recruit on mass to individual resources, while others spread out over a wide area (Hölldobler and Wilson 1990). There is considerable variation between species in their ability to find food in an environment, which has been suggested to contribute to coexistence in the dominance-discovery trade-off hypothesis (Davidson 1998). In experiments on fly communities that utilize carrion resources, dominant competitors may be spatially aggregated creating spatial refuges for weaker individuals (e.g. Ives 1991). Further, the size of the resource patch may enhance or decrease the potential for coexistence (Kouki & Hanski 1995; Horgan 2005). Such influences of resource distribution on coexistence in ant communities have generally been ignored, despite the knowledge that multiple food resources occur in small habitat patches ($<1\text{m}^2$) (Wehner 1987) and not in one large patch as in most experimental studies (Albrecht and Gotelli 2001; Thomas and Holway 2005).

In this study, we sought to examine the role of fine-scale variation in food distribution and temperature enabling multiple species to utilize food resources in a small area (0.4m^2). We tested two hypotheses. Firstly, that an increasing distribution or dispersion of a constant amount of food would allow an increasing number of ant species to utilize this resource. Our second hypothesis was that with increasing temperature, dominant ant species would have a stronger influence on subordinate species (as in Bestelmeyer 2000), but these dominant species would be unable to control all resources in high resource dispersion treatments and thus allow resource use by subordinates. We examined the response of individual species to variation in food distribution and temperature, in comparison with *Monomorium sydneyense* Forel. This species is of Australian origin and is a recent invader to New Zealand (Lester 2005). In preliminary studies, *M. sydneyense* dominated food resources in study plots in New Zealand, though it appears not to have excluded other ant species from study areas (Stringer 2005). We thus used *M. sydneyense* as our reference species and compared how other ant species are able to obtain resources in its presence.

Materials and methods

Study site

Our study was undertaken at Sulphur Point, Tauranga, New Zealand (37° 39'S, 176° 11'E) in 2003 and 2004. This area experiences a sub-tropical climate with warm humid summers and mild winters. Daily temperatures range from 22-26°C in summer, with the hottest months being January and February, to 12-17°C during winter, with July being the coolest month (NIWA 2005). Annual precipitation ranges between 1250 to 1500 mm per year, with the monthly average increasing slightly during the winter months (de Lilse and Kerr 1963). The food utilization experiments were conducted in a 70 × 40 m grassed area. We located five colonies of *M. sydneyense* along the edge of the grassed area where it came into contact with an asphalt road, as nests were easier to find by following workers returning to these colonies. Colonies were separated by ~10 m and did not interact with each other.

Resource utilization experiments

We examined the effect of food dispersion on the number of ant species, as well as differences in the proportion of foods occupied by co-occurring ant species due to a change in the dispersion of the food and temperature. We divided approximately 6 g of food at three different rates within a known area simultaneously recording soil surface temperatures. Smooth, sugared peanut butter was used as a food resource, as it was found to be highly attractive to the ants in the area and retained its moisture and attractiveness for extended periods of time (Stringer 2005).

Food items were placed in 50 cm radius half circles (total area ~0.40 m²) from the edge of the asphalt centred on each of the five *M. sydneyense* colonies. The peanut butter was haphazardly placed within the trial areas at a dispersion rate of either '1' (n = 31), '8' (n = 31) or '64' (n = 30); one '64' trial was not completed due to rain. A dispersion rate of '1' meant that all six grams of the peanut butter was clumped in one spot within the half circle, whereas a rate of '64' meant that the six grams of peanut butter was distributed between 64 spots within the 50 cm radius half circle. All of the food items were uniquely identified by placing numbered flags through the centre of the food so that the presence or absence of ant species at each individual food item could be assessed. Trials were deemed to have started

once the first piece of food was placed on the ground. In the case of trials where the food was distributed in 64 spots the trials began when the first numbered flag with the peanut butter was put in the ground. At the end of a 2 h period, the species present at each food item was recorded. Soil surface temperature was recorded using an electronic thermometer with a probe that was placed under grass next to the trial site. All foods in the trials were placed on grass and never on the asphalt. Ant species in this study were readily able to be distinguished in the field, but samples of all species were taken back to the laboratory to confirm identification.

To investigate whether there were differences in ant species richness during a trial due to the dispersion rate of the food we compared the number of species recorded for each dispersion trial ($n = 92$, with a total number of 2196 data points). We surveyed five sites, which were sampled in March, August, October and December 2004. A Generalized Linear Model (GLM) quasi-Poisson regression was used to test for differences in ant species richness between food dispersion treatments.

We used the four most commonly occurring ant species to test for the effect of food dispersion and temperature on food utilization: *M. sydneyense*, *Pheidole rugosula* Forel, *Paratrechina vaga* (Forel) and *Iridomyrmex anceps* (Roger). These ants were observed co-occurring at the five sites. Predictions were made on the proportion of baits occupied by each species using a binary logistic regression (Agresti 2002). The dependent response variable was the presence or absence of an ant species at each of the individual food items at the end of the two hour trial modelled using four explanatory variables: ant species, food dispersion rate, site and temperature. Binary logistic regression models the data to give predicted probabilities of presence at food, given particular values of the explanatory variables. The continuous explanatory variable temperature was centred about 0 by mean-correction, making the mean temperature of 21.3°C a reference point. For the categorical explanatory variables of species, food dispersion rate and site, the reference categories, from which all other categories are fitted as deviations, are: species = *M. sydneyense*, dispersion rate = 1 and site = 1. The natural way to interpret a parameter estimate, β_i , in such models is via the direct effect that the parameter has on the odds of presence at a food item. Those odds increase multiplicatively by $\exp(\beta_i)$ for every one unit increase in the corresponding i th explanatory variable, at fixed levels of the other explanatory variables. For example, if the predicted odds ratio, $\exp(\beta)$, is 15 for one of the ant species, when comparisons are made between the

proportion of food items occupied with only species allowed to change, the odds that it is present at the food is 15 times as large as the odds of *M. sydneyense* being present. An $\exp(\beta)$ value of one implies that the predicted proportion of foods occupied by the species is not different from the reference species, *M. sydneyense*. Conversely, an $\exp(\beta)$ value of 0.5 means that the odds are half that of *M. sydneyense* being present at the food.

Results

A significantly higher mean ant species richness was observed when the 6 g amount of food was distributed in 64 patches, compared to just in an individual patch (d.f.=2; Deviance= 9.430; $P= 0.009$) (Figure 1a). There was a site effect on the number of ant species present (d.f.= 4; Deviance= 15.821; $P= 0.003$). Although we are unable to specifically state the cause of this significant site effect, it is likely to be related to spatial variation in the distribution of ant species or microclimate differences between sites. No significant food dispersal rate \times site interaction was observed (d.f.= 8; Deviance= 1.403; $P = 0.994$). A total of 9 ant species were observed foraging on the bait. These species were (in order of most to least observed over the entire study): *Pheidole rugosula* (Forel), *Monomorium sydneyense* Forel, *Paratrechina vaga* (Forel), *Iridomyrmex anceps* (Roger), *Monomorium antarcticum* (F. Smith), *Monomorium antipodum* Forel, *Tetramorium grassii* Emery, *Tetramorium bicarinatum* (Nylander), *Cardiocondyla minutior* Forel. The following analysis will focus on the first four of these species, as only these provided sufficient data for the logistic regression analysis. At the time of choosing the study sites, all four species were observed to be present at all of the five study sites used below.

The proportion of foods occupied by ants declined with increasing food dispersion (Figure 1b). An initial binary logistic regression model that contained only the main effects of food dispersion, site, species and temperature, was relatively poor at correctly classifying food occupation by ants (percentage correct classification= 88.3% overall; 9.5% for ants at food; 98.7% for ants not being present) (d.f.= 10; Deviance= 4911.7). Our selected model included all 2-way interactions of the main effects except temperature \times site, and temperature \times density (these factors were excluded from the analysis as they did not improve classification success). This selected model improved the correct classification rate relative to the initial model, particularly for ants present at food (percentage correct classification= 89.2% overall; 49.2% for ants at food; 94.5% for ants not being present) (d.f.= 39; Deviance= 4159.4). The

change in deviance from the initial model of 752.3 on 29 d.f. ($P < 0.001$) is indicative of a substantial improvement in model fit. The addition of 3-way interactions did not improve classification success (as well as being difficult to interpret).

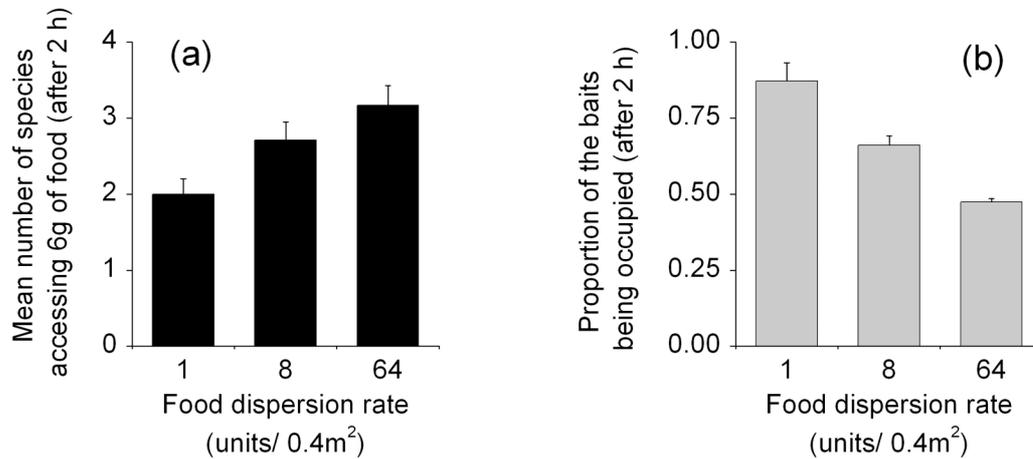


Figure 1. (a) Mean species richness (\pm S.E.; $n=31, 31, 30$) of ants at the 6 g of bait, distributed in either 1, 8 or 64 patches; and (b) the proportion (\pm S.E.; $n=31, 248, 1920$) of baits occupied by the four main species at different temperatures and bait dispersal rates.

The binary logistic regression model indicated significant main effects of density, site, species, and temperature ($P \leq 0.029$). However, there were also significant interaction effects for these variables, making it impossible to interpret the main effects in isolation. For example, the model with 2-way interactions indicated that the odds, $\exp(\beta)$, that *Pheidole rugosula* would occupy a food item were $34 \times$ greater than the odds for *M. sydneyense*, when other factors were fixed at reference levels ($P < 0.001$; Table 1). However, the odds ratios for *M. sydneyense* were higher at all four other study sites and the site \times *P. rugosula* interaction terms were significantly negative at all other sites, indicating a relative reduction in the odds ratio for *P. rugosula* at all other sites (i.e. the odds ratios were less than $34 \times$ that for *M. sydneyense* at the other sites).

As food dispersion was increased from 1 to 64 items, the odds of food being occupied decreased for all species (Figure 1b). The food dispersion \times species interaction terms indicated that both *P. rugosula* and *I. anceps* responded in a similar manner to increasing food dispersion as did *M. sydneyense*. However, the odds of food occupation by *P. vaga*

declined significantly faster, being $33 \times$ lower at a food dispersion of 64 per arena than for *M. sydneyense*. Thus, the probability of *P. vaga* occupying food at higher resource dispersion rates declined at a faster rate than for the other species.

Factor	β	S.E.	Wald	d.f.	<i>P</i>	exp(β)
Species			39.68	3	0.000	
<i>P. rugosula</i>	3.533	0.693	25.98	1	0.000	34.236
<i>I. anceps</i>	-1.442	1.322	1.19	1	0.275	0.236
<i>P. vaga</i>	-0.870	1.267	0.47	1	0.492	0.419
Dispersion			7.11	2	0.029	
Dispersion (8)	-0.147	0.937	0.02	1	0.875	0.863
Dispersion (64)	-0.976	0.902	1.17	1	0.279	0.377
Dispersion \times Species			18.92	6	0.004	
Dispersion (8) \times <i>P. rugosula</i>	-0.355	0.687	0.27	1	0.605	0.701
Dispersion (8) \times <i>I. anceps</i>	-1.128	0.947	1.42	1	0.234	0.324
Dispersion (8) \times <i>P. vaga</i>	-1.371	0.931	2.17	1	0.141	0.254
Dispersion (64) \times <i>P. rugosula</i>	0.066	0.649	0.01	1	0.919	1.068
Dispersion (64) \times <i>I. anceps</i>	-1.565	0.890	3.10	1	0.079	0.209
Dispersion (64) \times <i>P. vaga</i>	-2.641	0.882	8.96	1	0.003	0.071
Dispersion \times Site			18.39	8	0.018	
Temperature	0.152	0.013	135.29	1	0.000	1.164
Temperature \times Species			102.77	3	0.000	
Temperature \times <i>P. rugosula</i>	-0.150	0.016	91.53	1	0.000	0.860
Temperature \times <i>I. anceps</i>	-0.075	0.029	6.78	1	0.009	0.928
Temperature \times <i>P. vaga</i>	-0.214	0.038	32.43	1	0.000	0.807
Site			12.53	4	0.014	
Site \times Species			339.44	12	0.000	
Constant	-2.585	0.917	7.95	1	0.005	0.075

Table 1. Primary results from the binary logistic regression on the predicted probability that bait would be occupied dependent on species, temperature, site and dispersion rate of the food item. Further results on differences between sites, and dispersion \times site and site \times species interactions, are not shown for brevity.

For each degree of increase in temperature, the odds ratio of food occupation by *M. sydneyense* increased by 1.16 (Table 1). This result is demonstrated by increasing probability of foods being occupied by *M. sydneyense* with increasing temperatures. At the highest

temperature range (30-40°C), fewer species were observed on the food items at all dispersion rates and no other species were observed on the food at a dispersal rate of 1 (Figure 2). The influence of temperature on *M. sydneyense* foraging was exemplified in one trial where *M. sydneyense* and *P. rugosula* were observed to repeatedly displace each other from baits when there was a change in the amount of insolation. With cloud cover *P. rugosula* quickly displaced *M. sydneyense* from the food, however, when the cloud was not in front of the sun *M. sydneyense* rapidly returned to the foods that it occupied by displacing *P. rugosula*. In contrast, the regression model indicated that *P. rugosula* showed no significant change in the odds ratio for food occupation over the range of temperatures observed in this study (8.0 to 39.8°C). This result is apparent from the graphical analysis, as in all temperature ranges *P. rugosula* occupied approximately 50% of the baits in at least one of the dispersion treatments (Figure 2). For the other ant species, the logistic regression model predicted an increase in odds ratio of food occupation by *I. anceps* as temperatures increased (1.08 per 1°C) but a decrease for *P. vaga* (0.94 per 1°C).

Species	Site					Total
	1	2	3	4	5	
<i>M. sydneyense</i>	16 (12)	90 (465)	115 (423)	58 (323)	26 (89)	305 (1312)
<i>P. rugosula</i>	267 (1121)	63 (355)	69 (256)	204 (927)	35 (207)	638 (2866)
<i>I. anceps</i>	1 (0)	2 (0)	60 (20)	0 (0)	1 (0)	64 (20)
<i>P. vaga</i>	1 (1)	7 (56)	1 (0)	0 (0)	12 (14)	21 (71)
Total	285 (1134)	162 (876)	245 (699)	262 (1250)	74 (310)	1028 (4269)

Table 2. The number of baits occupied by each of four ant species after two hours, at each of the five study sites. The total number of ants observed at each site is shown in brackets; however, counts for one of the four sampling periods are missing, when only presence-absence data were taken.

The logistic regression model also showed a significant effect of site and site × species interaction (Table 1), indicating a significantly variable odds ratio for *M. sydneyense* occupying a bait at different sites. These results are related to differences in the observed relative abundance of ants between sites (Table 2). For example, almost all observations of *I. anceps* were at site 3, where a nest of this species was observed close to the study arena. Similarly, almost all observations of *P. vaga* were at sites 2 and 5. *P. rugosula* was at all sites, but its relative number of baits occupied differed substantially between sites. With these

differences in ant abundance between sites, it was not surprising to also observe a significant density \times site interaction term. The relative abundance of ants at each site seems likely to have influenced the number of baits any one ant species is able to control.

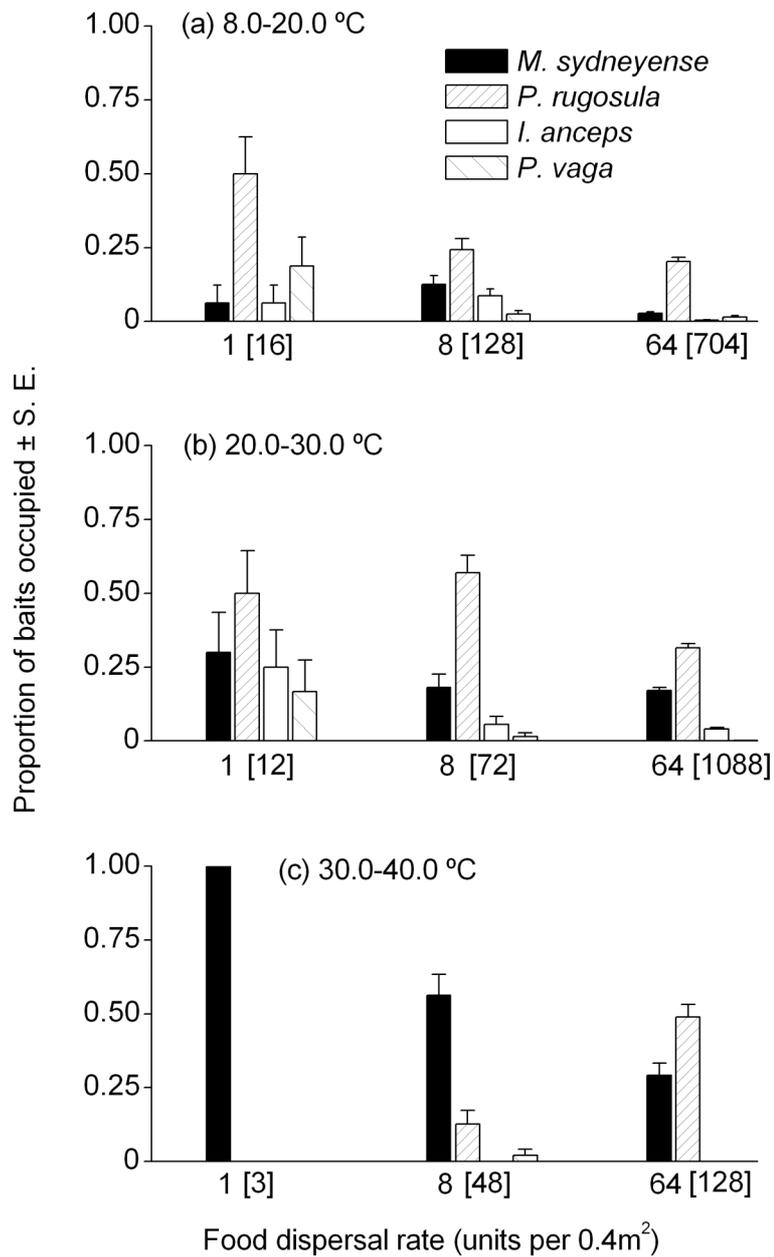


Figure 2. Proportion (\pm S.E.; n varies, depending on recorded temperature, and is shown in square brackets) of baits occupied by the four most abundant species at different temperatures and spatial dispersal rates. All trials have been combined for the three ranges of temperatures recorded during the study.

Discussion

Food dispersion, temperature, and site effects all influenced the utilization of food by different ant species. It seems likely that these factors are all major contributors to the coexistence of species within the ant community. It appeared that there was a hierarchy of influencing factors whereby site provided a base abundance for each species. Temperature further affected the presence or absence of ants, which in turn appeared to influence their ability to secure resources. Results of our study show that many small resources support a greater species diversity than the same amount of resource in one large clump. At the highest dispersion rate, the probability of a food item being occupied declined for the dominant species, allowing vacant resources for subordinate species. Previous studies have found that coexistence can be achieved with resources being dispersed over wide spatial scales (>10 m) (e.g. Levings and Traniello 1981; Albrecht and Gotelli 2001; Thomas and Holway 2005), but our study demonstrates that resource dispersion even at a fine spatial scale (<0.5 m) allows subordinate species to gain access to resources. A dispersed distribution of resources at such a relatively small spatial scale is likely to be a major mechanism allowing for species coexistence in a wide variety of communities.

Not all ant species responded in a similar manner to variation in food dispersion and temperature. Differences in the thermal tolerances of ants is thought to be an additional force driving resource acquisition rates, thus promoting ant coexistence (Cerdá et al. 1997; Retana and Cerdá 2000). Each of the species responded differently to increasing temperature. Our statistical model predicted that as temperature increased, the probability of bait occupation increased for both *M. sydneyense* and *I. anceps* (though at a higher rate for *M. sydneyense*), but remained constant for *P. rugosula*, and declined for *P. vaga*. This result suggests that there is a change in the dominant ant species due to differences in foraging intensity because of differences in soil surface temperatures. Our results are in line with similar studies that have indicated temperature to be a strong force acting on food utilization rates (Thomas & Holway 2005; Cerdá et al. 1997; Fellers 1989). That *M. sydneyense* had the highest rate of increase of bait occupation with increasing temperature from cool to warm (decreasing thermal stress) is typical for ecologically dominant ant species (Andersen 1995). Only at the warmer trials was *M. sydneyense* dominant and occupying all the individual large resource clumps, when *P. rugosula* shifted its foraging toward unoccupied smaller resource items (Figure 2). Thus, it is likely that the influence of dominant species on subordinate foraging

success is overstated in other studies which do not account for small scale variation in the spatial distribution of food resources.

Our result that an increasing dispersion of a constant amount of food resources may promote coexistence is consistent with the resource concentration hypothesis, which states that species diversity is inversely proportional to spatial food concentration (Root 1973). An increase in the spread of a resource increases the probability of a part of it being found by any organism (Cain et al. 1985). Different ant species have different foraging strategies. Some species recruit a large number of foragers to discovered food resources and others forage singly (Andersen 1995; Wilson 1971). Within our study the probability of any ant species occupying a food item declined with an increasing dispersion of food, but most dramatically for *P. vaga*. Little is known about the foraging behaviour of *P. vaga*, however, this species had a low abundance within the study sites. It is likely that *P. vaga* was numerically limited in how it could respond to any change in the number of resources in any one environment. With higher numbers it may have been able to recruit to more baits, as was apparent for some of the other species. An alternative hypothesis may be that *P. vaga* may not be as strongly attracted to the food that we used. Differing food preferences is thought to be another mechanism for species coexistence in ant communities (Ribas et al. 2003; Sanders and Gordon 2003).

A further mechanism promoting species coexistence between competing organisms is the spatial variation of species abundance between sites (Palmer 2003; Morrison 2000). This is especially the case for ant communities, in which interspecific competition is important and numerical dominance enables resource acquisition (Palmer 2003). Our data demonstrated considerable differences between sites and species in ant abundance, and in their utilization rates of food. Differences in ant abundance between sites may be driven by a variety of biotic and abiotic factors including nest availability (Hölldobler and Wilson 1990), microhabitat variation (Palmer 2003), differences in vegetation (Ribas et al. 2003), and other food resources (Sanders and Gordon 2003). The presence of existing nests of competing species also influences species abundance (Ryti and Case 1992). Whatever the mechanism for differences in ant abundance between sites, variation in the density of different species clearly influenced resource acquisition. Differences in the abundance of different ant species between sites must also aid species coexistence in this area. Thus there are within and between site factors that contribute to the acquisition of food and coexistence.

Perhaps the key result for this paper is that factors such as temperature and resource dispersion are important in coexistence patterns at small spatial scales, because different species respond differently to each of these factors. However, the experiment was somewhat artificial as we experimentally added resources at what may have been unnaturally high densities. A key area for future research is with spatial and temporal variability in the natural, fine-scale resource distributions within individual patches. The conclusions from this study are likely to be broadly relevant to a variety of systems wherein multiple resources and competing species occur within individual patches.

Acknowledgements We thank Shirley Pledger for additional statistical advice. Funding was provided by Victoria University of Wellington, the Entomological Society of New Zealand, and Biosecurity New Zealand. All experimental work complied with the current regulations and laws of New Zealand.

References

- Agresti A (2002) *Categorical data analysis*, 2nd edn. Wiley, New York.
- Albrecht M, Gotelli NJ (2001) Spatial and temporal niche partitioning in grassland ants. *Oecologia* 126: 134-141.
- Andersen AN (1995) A classification of Australian ant communities, based on functional groups which parallel plant life-forms in relation to stress and disturbance. *J Biogeog* 22: 15-29.
- Bestelmeyer BT (2000) The trade-off between thermal tolerance and behavioural dominance in a subtropical South American ant community. *J Anim Ecol* 69: 998-1009.
- Cain ML, Eccleston J, Kareiva PM (1985) The influence of food plant dispersion on caterpillar searching success. *Ecol Entomol* 10:1-7.
- Cerdá X, Retana J, Cros S (1997) Thermal disruption of transitive hierarchies in Mediterranean ant communities. *J Anim Ecol* 66: 363-374.
- Cerdá X, Retana J, Manzandeda A (1998) The role of competition by dominants and temperature in the foraging of subordinate species in Mediterranean ant communities. *Oecologia* 117: 404-412.

- Davidson DW (1998) Resource discovery versus resource domination in ants: a functional mechanism for breaking the tradeoff. *Ecol Entomol* 23: 484-490.
- de Lilse JF, Kerr IS (1963) The climate and weather of the Bay of Plenty region. New Zealand Meteorological Service Misc. Pub. 15.
- Fellers JH (1989) Daily and seasonal activity in woodland ants. *Oecologia* 78:69-76.
- Greenslade PJM (1971) Interspecific competition and frequency changes among ants in Solomon Islands coconut plantations. *J Appl Ecol* 8: 323-349.
- Greenslade PJM (1979) *A guide to the ants of South Australia*. Australian Museum, Adelaide.
- Hölldobler B, Wilson EO (1990) *The ants*. Belknap Press, Harvard University Press, Cambridge, Massachusetts.
- Horgan FG (2005) Aggregated distribution of resources creates competition refuges for rainforest dung beetles. *Ecography* 28: 603-618.
- Ives AR (1991) Aggregation and coexistence in a carrion fly community. *Ecol Monogr* 61: 75-94.
- Kaspari M, Ward PS, Yuan M (2004) Energy gradients and the geographic distribution of local ant diversity. *Oecologia* 140: 407-413.
- Kouki J, Hanski I (1995) Population aggregation facilitates coexistence of many competing carrion fly species. *Oikos* 72: 223-227.
- Lester PJ (2005) Determinants for the successful establishment of exotic ants in New Zealand. *Divers Distrib* 11: 279-288.
- Leston D (1973) The ant mosaic – tropical tree crops and the limiting of pests and diseases. *Pest Articles and New Summaries* 19: 311-341.
- Levings SC, Traniello JF (1981) Territoriality, nest dispersion, and community structure in ants. *Psyche* 88: 265-319.
- Morrison LW (2000) Mechanisms of interspecific competition among an invasive and two native fire ants. *Oikos* 90: 238-252.
- NIWA (2005) National Institute of Water and Atmospheric Research: The climate of New Zealand. www.niwa.co.nz/edu/resources/climate/overview/map_north (16/3/2005).

- Palmer TM (2003) Spatial habitat heterogeneity influences competition and coexistence in an African Acacia ant guild. *Ecology* 84:2843-2855.
- Retana J, Cerdá X (2000) Patterns of diversity and composition of Mediterranean ground ant communities tracking spatial and temporal variability in the thermal environment. *Oecologia* 123:436-444.
- Ribas CR, Schoerder JH, Pic M, Soares SM (2003) Tree heterogeneity, resource availability, and larger scale processes regulating boreal ant species richness. *Austral Ecology* 28:305-314.
- Root RB (1973) Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). *Ecological Monographs* 43:95-124.
- Ryti RT, Case TJ (1992) The role of neighborhood competition in the spacing and diversity of ant communities. *Am Nat* 139: 355-374.
- Sanders NJ, Gordon DM (2003) Resource-dependent interactions and the organization of desert ant communities. *Ecology* 84:1024-1031.
- Savolainen R, Vepsäläinen K (1988) A competition hierarchy among boreal ants: impact on resource partitioning and community structure. *Oikos* 51: 135-155.
- Stringer LD (2005) Temperature variation, resource concentration, and foraging behaviour influencing the effect of *Monomorium sydneyense* (Hymenoptera: Formicidae) on the ant community of Tauranga, New Zealand. MSc Thesis, Victoria University of Wellington, New Zealand.
- Thomas ML, Holway DA (2005) Condition-specific competition between invasive Argentine ants and Australian *Iridomyrmex*. *J Anim Ecol* 74: 532-542.
- Wehner R (1987) Spatial orientation of foraging behavior in individually searching desert ants, *Cataglyphis* (Sahara Desert) and *Ocymyrmex* (Namid Desert). In: Pasteels JM, Deneubourg J-L (eds) From individual to collective behavior in social insects. *Experimentia Supplement* 54, 15-42. Birkhäuser Verlag, Basel .
- Wilson EO (1971) *The insect societies*. Belknap Press, Harvard University Press, Cambridge, Massachusetts.