

**Dominants, subordinates and subdominants: how the distribution of resources can influence the co-occurrence of ant species**

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## Abstract

Dominant competitors govern resource use in many communities, leading to predictions of local exclusion and lower species diversity where dominant species are abundant. However, subordinate and dominant species frequently co-occur. One mechanism that could facilitate resource sharing and co-occurrence of dominant and subordinate competitors is fine-scale resource dispersion. Here, we distributed 6 g of a food resource into 1, 2, 8, 32, or 64 units in small 0.40 m<sup>2</sup> areas centred on nests of the dominant ant *Monomorium sydneyense*. We tested three hypotheses. First, we hypothesized that the species richness and abundance of foraging ants would increase with increasing resource dispersion. Accordingly, species richness doubled and total ant abundance was two orders of magnitude higher in high resource dispersion treatments. Secondly, we hypothesized that increasing resource dispersion would reduce competitive interactions such as resource turnover events and lower the probability of food resources being occupied. Substantial support for this hypothesis was observed. Finally, we tested the hypothesis that the foraging time of each species would be proportional to the relative abundance of each species irrespective of resource dispersion treatments. Expected and observed foraging times were statistically similar for only the dominant ant *M. sydneyense*. The subdominant *Pheidole rugosula* increased its foraging time much more than was expected, while two subordinate ants showed no relationship between observed and expected times. Thus, while increasing resource dispersion significantly increased overall species richness, this increase in co-occurrence did not correlate with a significant increase in foraging time for the two subordinate species. Rather, changes in resource dispersion appeared to benefit only the subdominant species. Inter-site variation appeared more important for other subordinate species in determining co-occurrence and foraging time. Multiple mechanisms facilitating co-occurrence and resource sharing operate in this community, and probably in most other communities.

## Introduction

Multiple species with apparently similar niche requirements are frequently observed to co-occur in the same habitat. The stable coexistence of multiple dominant and subordinate species in a relatively homogenous habitat has been observed in communities of mouse lemurs (Dammhahn and Kappeler 2008), butterflies (Kunte 2008), plants (Jakobsson and Eriksson 2003), and many other organisms. The co-occurrence of competing species on small spatial scales is especially common in ant communities. For example, in Australia up to 100 ant species might co-occur in plots of only 0.05 ha (Andersen 1991, 1992). However, within these ant communities dominant species often tend to disproportionately govern resources. Andersen and Patel (1994) found that while only 41% of ants caught in their traps were *Iridomyrmex sanguineus*, this species controlled 74% of the food resources. Further, experimental exclusion of *I. sanguineus* doubled the number of species and the total abundance of ants at food resources (Andersen and Patel 1994). Similarly, regulation by dominant ant species of small-scale or ‘momentary’ diversity of species attending food resources has been widely observed (e.g. Savolainen and Vepsäläinen 1988, Sarty et al. 2006, Parr 2008). These results illustrate the prevalence of competition in ant communities (Hölldobler and Wilson 1990), and lead to questions regarding how so many species are able to co-occur with dominant competitors (Andersen 2008).

Numerous mechanisms are likely to contribute towards the stable co-occurrence of so many species, many of which relate to niche differentiation (Chesson 2000, Amarasekare 2003). Stabilizing mechanisms are considered essential for species coexistence. Such mechanisms include traditional resource partitioning and frequency-dependent predation, as well as mechanisms that depend on fluctuations in population abundances and environmental factors over space and time (Chesson 2000). For example, in *Daphnia* populations of a New

York lake, highly fluctuating environmental conditions were found to be essential for the persistence of a weak competitor but were not important for that of the dominant species (Cáceres 1997).

In ant communities, variation in the ability of species to detect and exploit fluctuating resources is thought to be an important mechanism for maintaining species richness, referred to as the dominance-discovery trade-off (Feener 2000). This theory posits that strong competitors are slow colonizers of food resources, and vice versa. These trade-offs are thought to be widespread in omnivorous ground-foraging ant communities (Feener 2000), and several studies have found that they appear to facilitate local coexistence in ant communities (LeBrun 2005, Adler et al. 2007). One additional and under-studied mechanism that could allow resource sharing and co-occurrence of dominant and subordinate competitors is fine-scale resource dispersion. Considerable variation occurs between species in their ability to find food and dominate resource patches in an environment (Fellers 1987), which can create spatial or temporal refuges for weaker competitors (e.g. Ives 1991). Multiple food resources occur in even very small habitat patches (e.g.  $<1 \text{ m}^2$ ; Wehner 1987), but can vary spatially and be temporally patchy in dispersion. For example, many ants utilize bird droppings as a resource, which may be highly unpredictable and fluctuate in abundance due to factors such as spatial and temporal variation in foraging by flocks of birds (e.g. Galindo-Gonzalez et al. 2000). Similar patterns of spatially and temporally fluctuating resource dispersion levels are likely to be observed in most plant, invertebrate and vertebrate communities.

In this study we focus on fluctuation in resource dispersion and the results of this dispersion for resource sharing and local co-occurrence of ants. A previous presence-absence analysis in our study system indicated that dispersing resources may increase species richness (Stringer et al. 2007). Here we hypothesized that a spatially divided or dispersed, but constant total amount, of resources would reduce the effect of competition and promote patterns of co-

occurrence. Specifically, we tested three hypotheses: (i) that the species richness and abundance of foraging ants will increase with increasing resource dispersion, (ii) that increasing resource dispersion would reduce competitive interactions such as resource turnover events and lower the probability of food resources being occupied, and finally (iii) that the foraging time of each species would be proportional to the relative abundance of each species irrespective of resource dispersion treatments. In all these experiments we maintained a constant total amount of food resource, but partitioned or dispersed this resource into between one and 64 units. It is recognized that there are a paucity of studies that simultaneously examine multiple hypotheses or mechanisms for co-occurrence or coexistence (Amarasekare 2003). Our study incorporated fluctuation that may be regular (as in temperature cycles over one day) and more random (e.g. the degree of resource dispersion). In our statistical approach we ranked the importance of the various factors for maximizing species co-occurrence and abundance.

## **Methods**

### **Study site and experimental design**

The study was undertaken at Sulphur Point, Tauranga, New Zealand (37°39'S, 176°11 'E). This area experiences a sub-tropical climate with warm, humid summers and mild winters. The average daytime (8 am until 5 pm) temperature at 5 cm above the soil surface and average humidity over the period of work at our study sites was 18.9°C and 70.7% RH in December, and 16.3°C and 69.9% RH in October. The experiments were conducted in a 70 × 40 m flat grassed area, which was mown approximately once a week. Ten *Monomorium sydneyense* colonies were located along the edge of the grassed area where it came into contact with an asphalt road. Each nest became a study site for the remainder of this work.

Colonies were separated by at least 10 m and did not interact with one another. All trials were started after 8 am and were finished by 6 pm on each day of study, thereby providing a range of temperatures for ant interactions. Replicate experiments were conducted in October (~ the southern hemisphere spring) and December (~ the southern hemisphere early summer) 2004. Some of the data analysed here were also used in Stringer et al. (2007), wherein we only analysed species presence/ absence on the resource after 2 hours (ignoring results presented herein on the species-specific foraging times and species turnover at resources). Similarly, some of the pitfall data used here were also presented in Stringer and Lester (2008).

The food used in our experiments was smooth, sugared peanut butter. This food was found to be a preferred food type that was highly attractive to the majority of ants, and retained its moisture and attractiveness for extended periods (Stringer and Lester 2007). Food items were placed in semicircles with radii of 50 cm (total area  $\sim 0.40 \text{ m}^2$ ) from the edge of the asphalt centred on each of the ten *M. sydneyense* colonies. Approximately 6 g of peanut butter was divided at five different rates, into 1, 2, 8, 32, or 64 equally sized items. A dispersion rate of '1' meant that all 6 g of the peanut butter was clumped in one spot within the 50-cm semicircle, whereas a rate of '64' meant that the 6 g of peanut butter was haphazardly dispersed into 64 locations within the semicircle. All the food fragments were uniquely identified by placing miniature numbered flags through the centre of the food so that the abundance of each ant species at each individual food fragment could be recorded over time. For each food item, counts were made every 10 min for the entire 2-h period. Soil surface temperature was recorded using an electronic thermometer with a probe that was placed under the grass next to the trial site. 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. Six to 10 replicate runs of this experiment were undertaken in both

October and December 2004, with variation between the numbers of replicates being due to inclement weather conditions.

### **Resource dispersion effects on richness and abundance**

To test the hypothesis that the species richness and abundance of ant species will increase with increasing resource dispersion, we used Generalized Estimating Equations (GEE; Liang and Zeger 1986). The GEE analysis was implemented in R (R Development Core Team 2009) using the `geeglm()` function from the `geepack` package. We used an autoregressive working correlation structure to model counts of species (richness) with a repeated-measures Poisson framework, and to model transformed counts,  $\log(1 + \text{count})$ , of total other ants as Gaussian repeated measures. The autoregressive working correlation structure is a standard approach for several observations recorded sequentially through time but all within a relatively short period (Hardin and Hilbe 2003). The explanatory variables for both responses were: resource dispersion (1, 2, 8, 32 or 64 resource treatments),  $\log(1 + \text{counts of } M. \text{sydneyense} \text{ at each recording time})$ , time (in 10-min intervals over the 2-h period), site, month (October or December), soil surface temperature, and the interaction between  $\log(1 + M. \text{sydneyense} \text{ counts})$  and resource dispersion. AIC and other likelihood-based analyses are not possible in GEE analysis. Instead, our approach to model selection (in particular, covariate selection) used the changes in the sum of squared residuals to compare different models (Hardin and Hilbe 2003). We viewed histograms and box plots of residuals to check for appropriateness of fitted models and lack of outlying residuals. We examined interaction terms other than the interaction between  $\log(1 + M. \text{sydneyense} \text{ counts})$  and resource dispersion, but these other interactions did not improve model fit.

### **Resource occupation rates & turnover of ant species**

An individual food resource was considered occupied (and scored 1) if four or more ants of the same species were present on the food at one or more observation times within the 2-h period of the experiment. A score of 0 was assigned if fewer than four ants were observed on each resource. The data were modelled with a logistic regression, to test the hypothesis that resource occupation was dependent on resource dispersion (1, 2, 8, 32 or 64 resource treatments) and month (October or December).

For the purpose of the turnover analysis, when four or more workers were foraging on an individual resource item it was considered occupied. A turnover event was defined as when a species occupying an individual bait resource was displaced and the bait was subsequently occupied by a second species. Turnovers were scored on an individual bait basis (i.e. for each of the 64 baits in the 64 bait treatment). A score of 1 was assigned if one or more turnover events occurred on an individual resource during the 2-h period of observation. A score of 0 was assigned if no turnover events occurred. We used logistic regression to model the probability of a turnover event as being dependent on resource dispersion (1, 2, 8, 32 or 64 resource treatments) and month (October or December).

### **Ant foraging time and relative abundance**

Our design provided counts of ant numbers at each food resource every 10 min for the entire 2-h period for each replicate. We obtained an estimate of the total observed foraging time spent by each species on the food resources, by summing those counts and multiplying by 10. To obtain an estimate for the expected foraging time by each species at each sampling period, we estimated the relative density of each ant species using pitfall traps. Seven pitfall traps were placed within the area used for the above baiting experiments. Each trap was filled one-third with 30% ethylene glycol and 70% water, plus 2–3 drops of dishwashing detergent to



break surface tension. Traps were left in place for 96 h, then collected and brought back to the laboratory for counting and identification. The proportion of each species in the total ant abundance was derived using the abundance data from the pitfall traps. These proportions were then multiplied by the total ant foraging time observed at each site to give the expected foraging time for each species.

The abundance data were used in an ANCOVA to test the hypothesis that the observed foraging time of each species was proportional to the relative abundance of each species, with the four most common ant species analyzed separately. Observed values of zero were removed from the dataset prior to analysis, since we have already published presence or absence modelling for a subset of these data (Stringer et al. 2007). Thus we followed the approach of Fletcher et al. (2005), and here we focus solely on the observed occurrences. The fixed factors in the model were month (October or December), resource dispersion (1, 2, 8, 32 or 64 bait treatments), and sampling site. The covariate in the model was the expected foraging time. Data were Box-Cox power transformed prior to analysis, with the power for each species estimated separately by maximum likelihood (Box and Cox 1964). The use of a Box-Cox transformation was an extension of the simple log transform used by Fletcher et al. (2005), and was implemented in R (R Development Core Team 2009) using the `boxcox()` function from the MASS package. We note here that, in all four species, the Box-Cox transform was necessary, rather than taking logs, since the confidence intervals for each estimated power did not include zero. The ANCOVA allowed us to determine whether expected foraging time had any impact on observed foraging time (i.e., a significant F-statistic). To test whether there was a one-to-one relationship between observed and expected foraging duration, we used a two-tailed t-test on the difference between unity and the estimated coefficient from the ANCOVA.

## Results

The ant species observed during our study were (in order of most to least observed over the entire study): *Pheidole rugosula* Forel; *M. sydneyense* Forel; *Paratrechina vaga* (Forel); an undescribed *Iridomyrmex* sp.; *Monomorium antarcticum* (F. Smith); *Monomorium antipodum* Forel; *Tetramorium grassii* Emery; *Tetramorium bicarinatum* (Nylander), and *Cardiocondyla minutior* Forel. All but *M. antarcticum* are exotic species to New Zealand.

### Resource dispersion effects on richness and abundance

We observed substantial support for our hypothesis that the species richness and abundance of ant species will increase with increasing resource dispersion or partitioning of the 6 g of food.

In trials with a single food resource, *M. sydneyense* quickly found and dominated this food item. Periodically, we observed a time lag in this dominant ant finding and recruiting large numbers of ants to the resource, which allowed other ant species opportunity to feed.

However, there was only ever a maximum of three ant species observed on the food item over the 2-h period of observation. When *M. sydneyense* densities were high, other ant species were completely excluded (Fig. 1). In trials with the maximum partitioning of the 6 g of food into 64 resources, a maximum richness of six species was observed, but only in situations when *M. sydneyense* densities were low. The relationship between *M. sydneyense* abundance and the abundance of other ants was weaker in trials with high resource abundances.

*Monomorium sydneyense* recruited more workers when the 6 g of food was widely dispersed (i.e. in trials with 8 – 64 resources in the 50-cm radius semicircle), but did not recruit to all resources leaving many available for other ant species. This high abundance of available resources was associated with an increase in species richness and abundance of other ants (Fig. 1).

The GEE analysis supported these observations, showing a significant positive effect of resource dispersion on both species richness and the total abundance of other ants (Table 1). As the numbers of *M. sydneyense* increased, we observed a significant increase in species richness but a significant decrease in the total abundance of other ant species. However, the significant resource density  $\times$  *M. sydneyense* abundance interaction terms (Table 1;  $p \leq 0.033$ ) indicated that the effect of *M. sydneyense* on both species richness and abundance changed with increasing resource density. For species richness, the significant negative interaction indicated that as resource dispersion increased and thus other species were able to access the food, the ability of *M. sydneyense* to control all those food resources was reduced. We believe the size of the positive *M. sydneyense* main effect is due to the almost complete domination by *M. sydneyense* of single food resources. Similarly, for total abundance of other ants, the significant positive interaction indicated that as resource dispersion levels increased, the abundance of other ants was not constrained as much by *M. sydneyense* as when only a single food resource was present. The significant site factor in the GEE analysis indicated that several of our sites showed different patterns from our reference Site A (Table 1). Although it is difficult to specifically state the cause of this significant site effect, it is likely to be related to spatial variation in the dispersion and size of ant colonies between sites. Increasing temperature had a significant negative effect on the total abundance of other ants ( $p < 0.001$ ), but had no overall effect on ant species richness. There was no difference in response of species richness or the total abundance of other ants between months of our study, indicating consistency of our results across time (Table 1).

To gain an estimate of the relative importance of each of the explanatory variables for predicting species richness in our GEE analysis, we re-ran the model excluding each significant ( $p < 0.05$ ) variable in turn. For variables involved in the resource dispersion  $\times$  *M. sydneyense* interaction, removal of each main effect was accompanied by removal of the

interaction term. The relative size in the change of the unexplained sum-of-squares in the reduced model compared with the full model enabled a ranking of the importance of the predictors to be determined. Site was the most important explanatory variable, followed by resource dispersion (including its interaction with *M. sydneyense*) and finally, numbers of *M. sydneyense* (including the interaction term with resource dispersion).

Similarly, we also ranked the relative importance of each of the significant ( $p < 0.05$ ) explanatory variables for predicting the total abundance of other ants. Site was again the most important predictor, followed by resource dispersion (including its interaction with *M. sydneyense*), temperature, time and finally, numbers of *M. sydneyense* (including the interaction with resource dispersion).

### **Resource occupation rates & turnover of ant species**

We found support for the hypothesis that increasing resource dispersion would reduce competitive interactions such as resource turnover events and lower the probability of food resources being occupied. The maximum turnover rate was observed in December at a resource dispersion of 1, when 30% of the occupied baits were first secured by one species that was then usurped by another (Fig. 2i). The rate of turnover declined to 5% for the highest levels of resource dispersion in December. Accordingly, the logistic regression model indicated a significant decrease in the proportion of turnover events that occurred with increasing resource dispersion ( $\beta \pm SE = -0.011 \pm 0.005$ ;  $z = -1.978$ ;  $p = 0.048$ ). Patterns of species turnover in October were similar (Fig. 2i). This model also indicated significant differences between months in the turnover dynamics, with October having fewer turnover events than December ( $\beta \pm SE = -0.995 \pm 0.296$ ;  $z = -3.358$ ;  $p < 0.001$ ). The most common species turnover events were between the most abundant ants, *M. sydneyense* and *Ph. rugosula*. Turnover events between these two species accounted for 42 (74%) of the total 57

observed in the entire study. *Monomorium sydneyense* more frequently replaced *Ph. rugosula* (86%, n=36) than vice-versa. *Paratrechina vaga* was replaced by *M. sydneyense* on three occasions, by *Ph. rugosula* on three occasions, and twice by *Iridomyrmex* sp. Thus *M. sydneyense* appeared to be the dominant species, with *Ph. rugosula* as the subdominant species.

The probability of an individual food item being occupied by any ant species also declined in treatments of increasing resource dispersion (Fig. 2ii). When the 6 g of food was increasingly divided into smaller separated resources, the probability of each individual resource being occupied by ants declined significantly ( $\beta \pm \text{SE} = -0.018 \pm 0.002$ ;  $z = -7.266$ ;  $p < 0.001$ ). The logistic regression analysis also indicated that significantly fewer resources were occupied in October than in December ( $\beta \pm \text{SE} = -0.459 \pm 0.095$ ;  $z = -4.862$ ;  $p < 0.001$ ). During December and October the occupation rates at a dispersion level of 1 or 2 baits was always greater than 83%, which at the level of 64 resources declined to  $53 \pm 16\%$  (mean  $\pm$  standard error) and  $38 \pm 16\%$  for December and October, respectively. This difference in resource occupation at high food partitioning appeared to be responsible for the significant effect of month in the logistic regression analysis.

### **Ant foraging time and relative abundance**

Increasing the dispersion of food resources substantially increased the observed foraging time for *Ph. rugosula* and *M. sydneyense*, but less so for the subordinate species *Iridomyrmex* sp. and *Pa. vaga* (Fig. 3).

The observed foraging time for *M. sydneyense* was not significantly different from our expected values. The coefficient on expected foraging minutes was  $1.014 \pm 0.228$  (estimate  $\pm$  SE), which was significantly greater than zero ( $P < 0.001$ ) but not different from unity ( $P = 0.952$ ) (Fig. 4). In addition to the significant effect of expected foraging time, the explanatory

variables of month and site were also significant in explaining variation of observed foraging time by *M. sydneyense* in the ANCOVA (Table 2;  $P \leq 0.014$ ). Of all the other ant species we examined, the subdominant species *Ph. rugosula* appeared to benefit most from the increasing resource dispersion (Figs. 3 and 4). The foraging time observed for *Ph. rugosula* increased with expected foraging minutes at a rate of  $2.073 \pm 0.184$ , which was significantly greater than unity ( $P < 0.001$ ). All the other explanatory variables in the ANCOVA model for *Ph. rugosula* were significant (Table 2;  $P \leq 0.026$ ).

Perhaps as a result of the substantial increase in foraging time by both *Ph. rugosula* and *M. sydneyense* associated with increasing food dispersion, the change in observed foraging time by the subordinate ant species *Pa. vaga* and *Iridomyrmex* sp. was much reduced (Fig. 3). In fact, in the ANCOVA models, there were no significant changes in observed foraging time with expected foraging time for either species ( $P \geq 0.372$ ). For both subordinate species, ‘site’ was a significant variable for explaining observed foraging minutes, while resource dispersion was significant only in the analysis of *Iridomyrmex* sp. (Table 2).

## Discussion

We observed considerable support for our first hypothesis that the species richness and abundance of foraging ants will increase with increasing dispersion of a constant amount of resources. In low resource dispersion treatments, the dominant species quickly controlled resources. Yet while the dominant species increased its abundance in high resource dispersion treatments, it did not control all resources, leaving opportunities for subordinate competitors. Parr (2008) similarly found that dominant ants appear to control local species richness. Our results here support our earlier work based on presence-absence analysis of species at resources, which ignored temporal variation in abundance and foraging patterns (Stringer et

al. 2007). Temporal variation was clearly important even in treatments when the food resources were distributed into two or eight items, as under these conditions subordinate ant species had opportunity to forage prior to being usurped by the dominant *M. sydneyense*. Our results are in accordance with the dominance-discovery trade-off theory (Feener 2000), though we demonstrate how discovery and dominance can be modified with resource dispersion.

Perhaps the clearest evidence for reduced competition in treatments of high resource dispersion is from the turnover analysis. Significantly fewer turnover events were observed in high resource dispersion than in low resource dispersion treatments, in support of the second hypothesis of this study. The maximum turnover rate was observed in December at a resource dispersion of one, when 30% of the occupied baits were first secured by one species that was then usurped by another. The most common usurper was the dominant *M. sydneyense*. Ants in the genus *Monomorium* have potent venom that repels other ants, providing them with a competitive advantage over many ant species (Adams and Traniello 1981; Andersen et al. 1991; Holway 1999). Upon being approached while feeding, *M. sydneyense* exuded droplets of venom, which appeared to trigger avoidance behaviour in other ant species. In her study of interference competition, Fellers (1987) observed an approximately equal number of overt aggressive and avoidance behaviours. Avoidance or escape behaviour is similarly considered to be a major category of competitive behavioural interactions, such as with salamanders (Deitloff et al. 2008). Avoidance behaviours are likely to be difficult to quantify precisely in many systems, and as a consequence in our study we believe our estimated levels of aggression and competitive interactions between ants are under-represented.

Our third and final hypothesis was that the foraging time of each species would be proportional to the relative abundance of each species irrespective of resource dispersion treatments. This hypothesis was formulated around the idea that if increasing resource

dispersion was a mechanism that could mediate the influence of competition and resource domination by *M. sydneyense*, we would expect to see fewer competitive effects with increasing resource dispersion levels. Expected and observed foraging times were statistically similar for only one of our four commonly observed species: the dominant *M. sydneyense*. In trials with high resource dispersion, the subdominant species *Ph. rugosula* increased its foraging time significantly more than was expected. The maximum rate of partitioning of food resources resulted in a 7-8 fold increase in the foraging time for *Ph. rugosula*, relative to an unpartitioned single resource. *Pheidole rugosula* was the most abundant ant observed and appeared not to be recruitment-limited. Perhaps *Ph. rugosula* may have recruits underground waiting for such resource opportunities as do ants elsewhere (Pfeiffer and Linsenmair 1998). As a likely consequence of *Ph. rugosula*'s increased resource utilization at high dispersion levels, the two other subordinate ants showed no relationship between observed and expected foraging time.

It is logical that alleviating competitive effects by the dominant species may preferentially benefit the most functionally similar subdominant competitor (Gibb and Hochuli 2004). Should the subdominant ant have a sufficient recruitment ability to be able to occupy many of the resources and repel other species, little or no change might be expected in the foraging behaviour of subordinate species.

Most species are not uniformly distributed across a landscape, including ant populations in our study area (Stinger and Lester 2008). Thus we might expect spatial variation in the effects of resource dispersion on co-occurrence patterns, as a consequence of factors including variation in the abundance of subdominant species. Indeed, we found that the most important factor enabling subordinate species to access resources was inter-site variation. This was a surprising result given our study sites were very similar, with little plant or structural habitat diversity. The most likely explanation for significant site variation was



fine-scale variation in ant abundances related to spatial variation in the nests of other ant species. Andersen (2008) hypothesized that species richness in communities is likely to be a function of propagule arrival, which is probably true for local as well as regional communities. Variation in the abundance of dominant ants can influence local species assembly and composition (Lester et al. 2009), and even competitive outcomes (Palmer 2004). Temperature can also play a role in shaping the species richness of this (Stringer et al. 2007) and other ant communities (Cerdá et al. 1998), but no such effect was observed in our analysis. Rather, the total abundance of other ant species significantly declined with temperature, perhaps due to the preference of *M. sydneyense* for higher temperatures (Stringer et al. 2007), such as we observed in December.

Multiple mechanisms facilitating co-occurrence and resource sharing operate in this community, and probably in many other communities. With increasing dispersion we observed a significant increase in overall species richness on our food resources. However, this increase in co-occurrence did not correlate with a significant increase in foraging time for the two subordinate species. Rather, the change in resource dispersion appeared to substantially benefit the subdominant species *Ph. rugosula*. Inter-site variation was more important for other subordinate species in determining co-occurrence and foraging time. Multiple ecological mechanisms allowing co-occurrence and resource sharing are likely to operate in most communities. Modifying the influence of dominant species may have little effects on co-occurrence, or may only influence a subset of species. We echo Amarasekare's (2003) suggestion that future studies should simultaneously examine multiple hypotheses or mechanisms for co-occurrence or coexistence.

## Acknowledgements

Funding was provided by Fulbright New Zealand, Victoria University of Wellington, the Entomological Society of New Zealand, and Biosecurity New Zealand.

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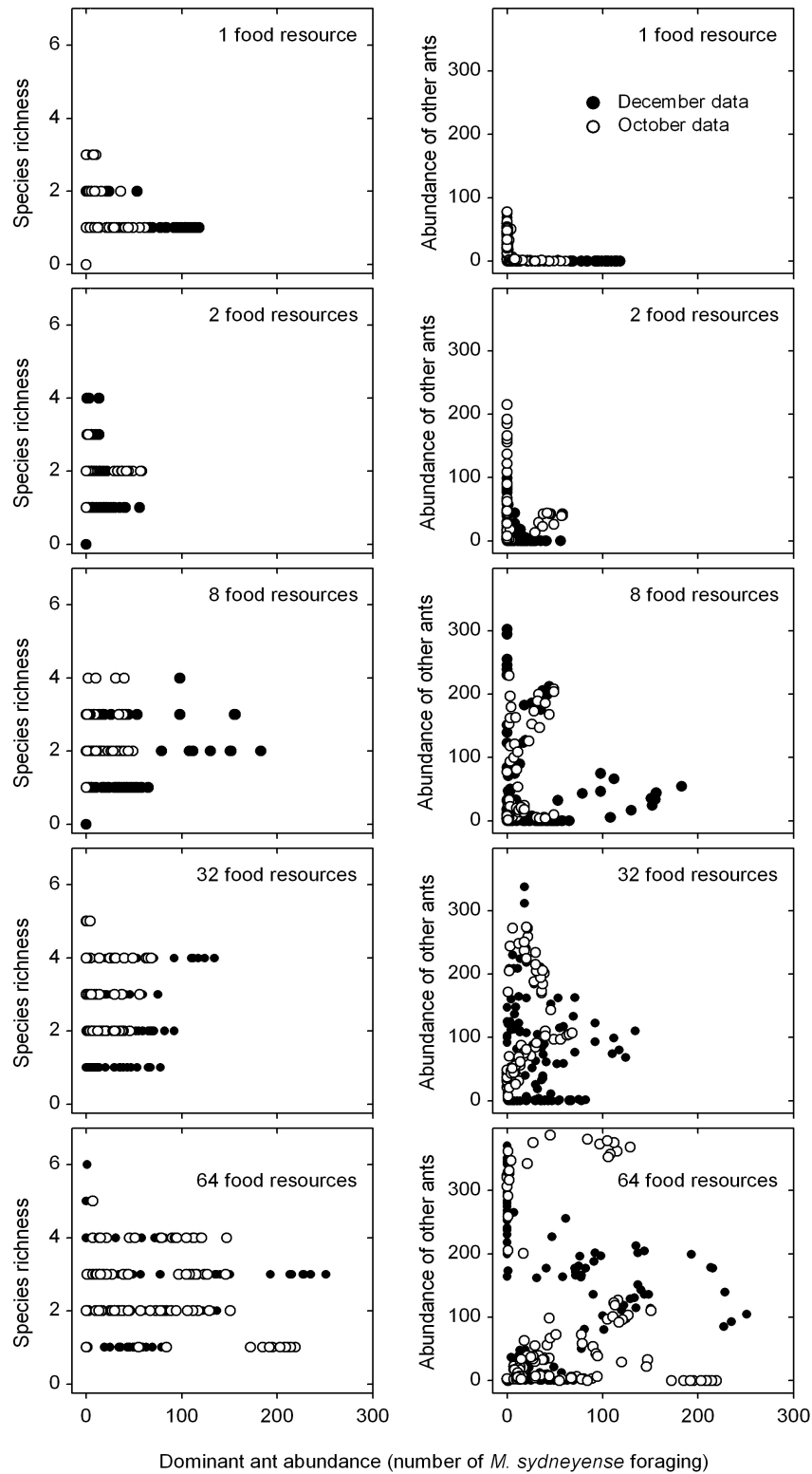
**Table 1.** Results from the GEE analysis modelling species richness and  $\log(1 + \text{total abundance of ants other than } M. \text{sydneyense})$ , each as a function of resource dispersion,  $\log(1 + \text{counts of } M. \text{sydneyense} \text{ at each recording time})$ , time (in 10-min intervals over the 2-h period), site, month, soil temperature, and the interaction between transformed *M. sydneyense* counts and resource dispersion. All ‘site’ analyses are in comparison with Site A, and the Month variable compares the responses in October with those in December.

Factor	Species Richness			Total abundance of other ants		
	Estimate (SE)	Wald	p	Estimate (SE)	Wald	p
Intercept	0.668 (0.132)	25.501	< 0.001	3.712 (0.361)	105.471	< 0.001
Resource dispersion (BD)	0.010 (0.003)	16.774	< 0.001	0.017 (0.006)	7.475	0.006
<i>M. sydneyense</i> (Ms)	0.156 (0.036)	18.615	< 0.001	-0.123 (0.047)	6.727	0.009
Time	-0.001 (0.000)	1.697	0.193	0.004 (0.001)	16.818	< 0.001
Site B	-0.125 (0.093)	1.781	0.182	-0.393 (0.352)	1.242	0.265
Site C	-0.842 (0.131)	41.237	< 0.001	-3.239 (0.453)	51.143	< 0.001
Site D	-0.117 (0.132)	0.793	0.373	-0.750 (0.441)	2.894	0.089
Site E	-0.037 (0.130)	0.079	0.778	-1.132 (0.483)	5.497	0.019
Site F	-0.383 (0.185)	4.278	0.039	-1.680 (0.568)	8.745	0.003
Site G	-0.351 (0.071)	24.619	< 0.001	0.490 (0.406)	1.459	0.227
Site H	-0.353 (0.117)	9.122	0.003	-2.129 (0.400)	28.309	< 0.001
Site I	-0.437 (0.116)	14.286	< 0.001	1.162 (0.309)	14.095	< 0.001
Site J	-1.098 (0.088)	157.377	< 0.001	-3.562 (0.446)	63.670	< 0.001
Month (October)	0.012 (0.062)	0.036	0.850	-0.187 (0.222)	0.705	0.401
Temperature	-0.007 (0.004)	3.016	0.082	-0.034 (0.010)	12.159	< 0.001
BD x Ms	-0.002 (0.001)	4.538	0.033	0.004 (0.002)	6.339	0.012

**Table 2.** ANCOVA results testing the relationship between observed and expected foraging time. The fixed factors in the model were Month (October or December), resource dispersion (6 g of peanut butter divided at five different rates into 1, 2, 8, 32, or 64 equally sized items), and sampling site. The covariate in the model was the expected foraging time, predicted from the relative abundance of each species at our study site. Data were Box-Cox transformed prior to analysis.

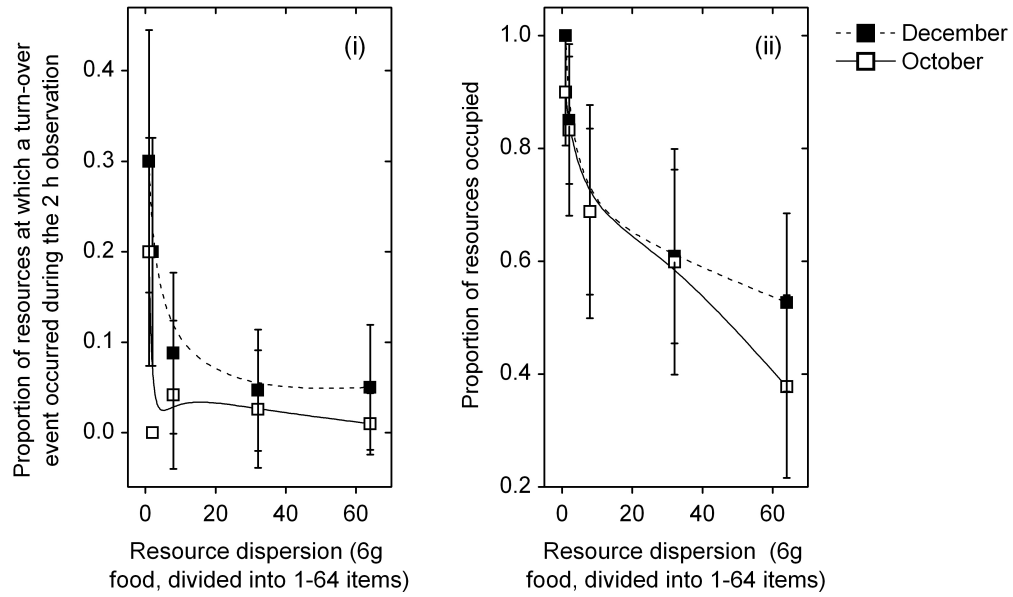
Explanatory variable <sup>§</sup>	<i>M. sydneyense</i>		<i>Ph. rugosula</i>		<i>Iridomyrmex</i> sp.		<i>Pa. vaga</i>	
	F	p	F	p	F	p	F	p
Expected abundance	45.569	<0.001	392.376	<0.001	0.832	0.372	0.599	0.444
Month	6.363	0.014	5.317	0.026	2.998	0.098	0.183	0.672
Resource dispersion	2.702	0.106	8.615	0.005	8.106	0.010	1.301	0.261
Site	4.098	<0.001	3.898	0.003	4.593	0.002	3.209	0.007

§ Numerator degrees of freedom in the F-statistics were always 1, except for ‘site’ which varied between 6 and 9 for the different species

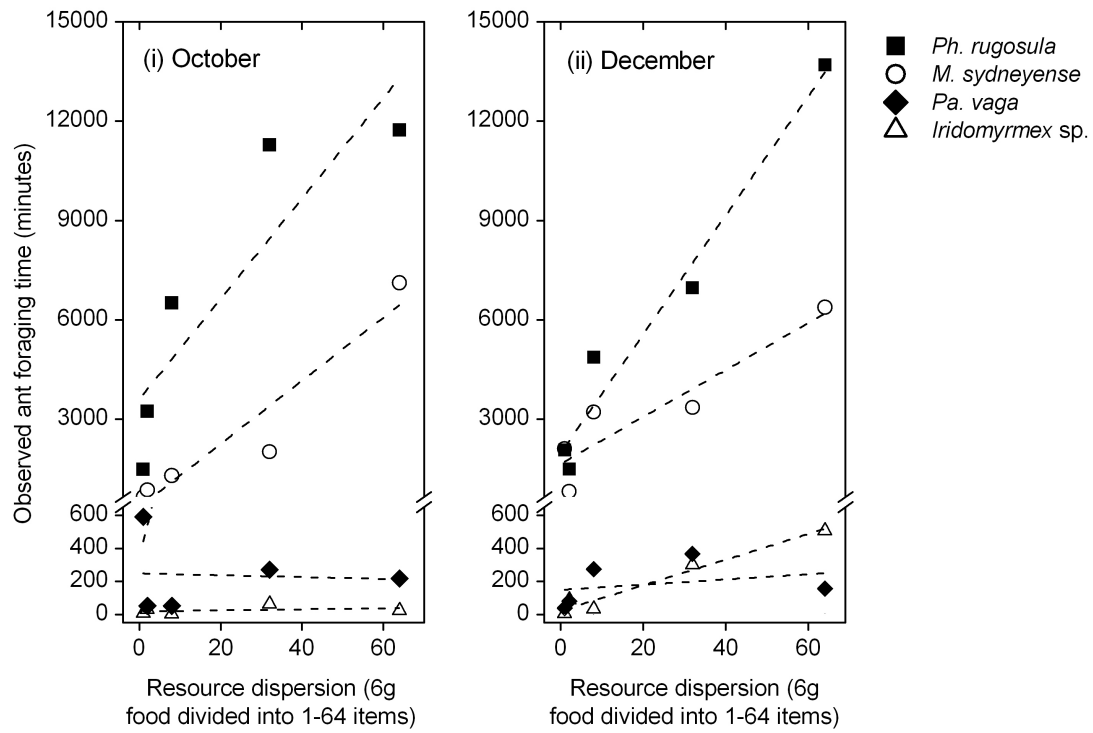


**Figure 1.** The influence of dominant ant (*M. sydneyense*) abundance on ant species richness, and on the total abundance of all other ant species. Data are shown for each resource dispersion treatment, where 6 g of food was partitioned into 1, 2, 8, 32, or 64 resources.

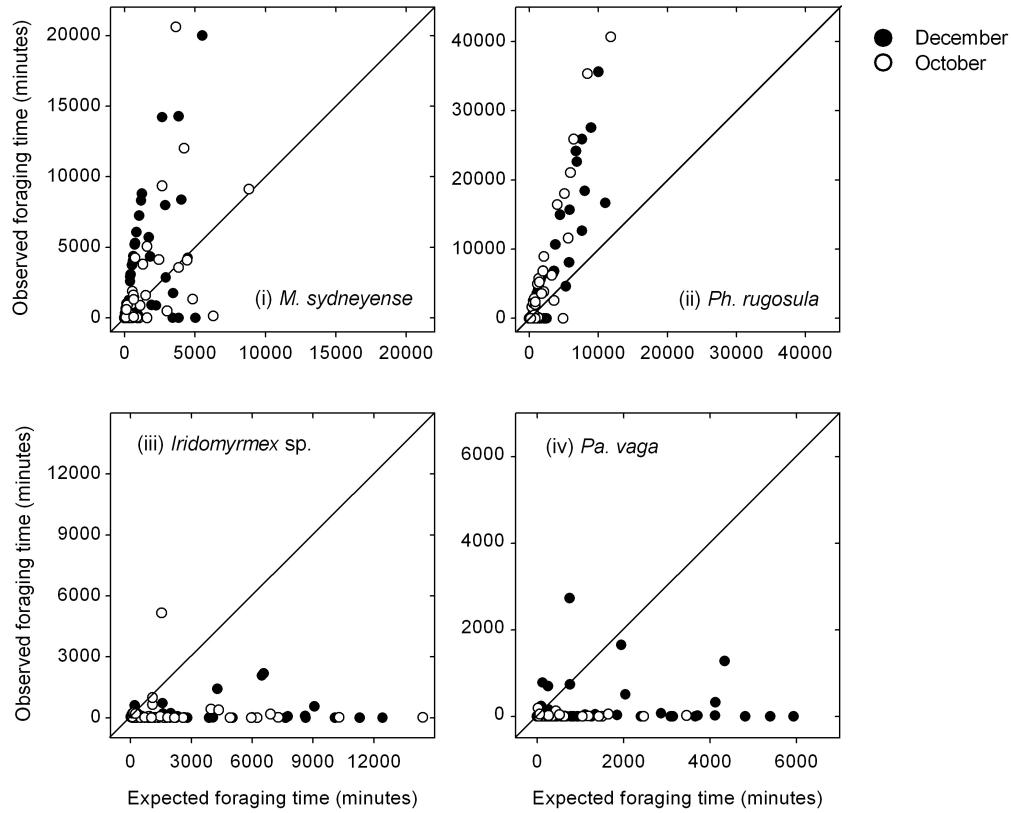




**Figure 2.** (i) The proportion of turnover events (where one species displaced another on a food item) significantly declines with increasing resource numbers, and similarly (ii) the proportion of resources occupied by ants declines with increasing resource numbers. Error bars are one standard error; fitted lines are spline curves.



**Figure 3.** Mean observed foraging time associated with increasing food dispersion, for each of the four most common ant species observed.



**Figure 4.** Expected and observed ant foraging minutes for the four most common ant species.

The expected foraging time for each species was calculated as follows. First, the proportional representation of each species in the total ant abundance was derived using the abundance data from the pitfall traps. This proportion was then multiplied by the total ant foraging time observed at each site. The solid line represents a 1:1 relationship.