REMOVAL EXPERIMENT REVEALS LIMITED EFFECTS OF A BEHAVIORALLY DOMINANT SPECIES ON ANT ASSEMBLAGES

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Abstract. Ant communities are thought to consist of a competitive hierarchy of interacting species, with an assemblage of subordinate species being structured by a dominant species. Mensurative and behavioral studies suggest a significant role for competition in structuring ant communities, although there are few experimental studies to support this contention. We examined the effect of the dominant ant *Iridomyrmex purpureus* on the ant fauna of sandstone outcrops in southeastern Australia. We conducted a mensurative survey using transect counts to compare ant assemblages at eight outcrops with, and eight without *I. purpureus*. Using cages, we then successfully excluded the dominant ant from four outcrops and compared assemblages at these exclusion sites with those at sites with and without *I. purpureus* and with procedural control sites over a period of 12 months. We conducted behavioral studies comparing *I. purpureus* with six other common species in terms of their abilities to locate, recruit to, and defend bait. While initial surveys indicated both positive and negative effects of *I. purpureus* on the activity of several subordinate species, exclusion of *I. purpureus* resulted only in changes in the abundance of other species of *Iridomyrmex*, which are behaviorally and ecologically similar to the dominant species. *Iridomyrmex purpureus* was faster at discovering bait than other species, but not always better at recruiting to the bait. It interfered with the foraging of all species tested; however, it displaced other *Iridomyrmex* from bait most often. While longer-term studies may provide more definitive results, exclusion of the dominant species over one year had strong effects only on ecologically similar species. Despite its behavioral dominance and association with several other species in the mensurative surveys, *I. purpureus* was not shown to cause any other major changes in ant community structure.

Key words: ants; behavioral experiment; community structure; competition; dominant species; Iridomyrmex purpureus; *mensurative experiment; removal experiment.*

INTRODUCTION

Field experiments examining interspecific competition show a high incidence of significant effects in a range of systems (Schoener 1983, Gurevitch et al. 1992). However, experimental evidence for competition between two species does not necessarily demonstrate that competition is an important organizing force in assemblages of coexisting species that appear to share common resources (Hairston 1981), and the importance of competition in structuring animal communities has been widely debated (e.g., Lewin 1983, Gotelli and Graves 1996, Weiher and Keddy 1999).

Competition is a dominant theme in studies of ant ecology (Hölldobler and Wilson 1990), and the association of assemblages of subordinate ants with different dominant ants has been described from a wide variety of ant communities worldwide, ranging from epigaeic to arboreal, in both natural and anthropogenically modified habitats (e.g., Room 1971, Greenslade

1976, Andersen 1984, 1986, 1997, Savolainen and Vepsäläinen 1988, 1989, Savolainen et al. 1989, Majer 1993). Different species of ants often require similar nesting and foraging conditions and are thought to interact strongly with each other to form well-structured communities (Andersen 1984, 1992, Fellers 1987, Savolainen and Vepsäläinen 1988, 1989). Direct competition and diffuse competition are thought to be important in producing ant dominance hierarchies, structured by territorial ants that are both behaviorally and ecologically dominant (Greenslade 1976, Davidson 1980). Successful exotic ant species become dominant in, and may also structure, the communities they invade (e.g., Porter and Savignano 1990, Holway 1998, Hoffmann et al. 1999, Morrison 2000), so understanding how an ant community is structured may also be important for understanding and determining resilience to invasions.

Despite calls for experimental work examining competition (Schoener 1983, Gurevitch et al. 1992), most field studies on ant communities to date have been mensurative. Without experimental data on the consequences of interference and exploitation competition in natural habitats, it is not possible to determine unequivocally whether competition plays an important

role in determining community structure. Phenomena such as ant mosaics, and other apparently structured communities, may result from simple differences in food (Blüthgen et al. 2000) or habitat preference (Djieto-Lordon and Dejean 1999), predation (Gotelli 1996), or parasitism (Feener 2000), and patterns of co-occurrence observed in such ant communities are often no greater than those expected from a random rearrangement of species among sites (Ribas and Schoereder 2002). Several recent studies have experimentally demonstrated that behavioral interactions at resources may be responsible for the displacement of native by invasive species (e.g., Holway 1999, Human and Gordon 1999, Morrison 2000). However, behavior at artificial resources may not reflect behavior at natural resources, which may be of lower quality (Kay 2002, Ribas and Schoereder 2002), and more widely dispersed. Behavioral dominance at resources needs to be shown to lead to changes at the population level if competition is to be considered important in structuring ant communities (Andersen and Patel 1994, Ribas and Schoereder 2002). Very few experimental data on the long-term population level consequences of interference and exploitation competition in a natural habitat exist.

Studies examining introductions of ant species to small islands have indicated that competition structures ant communities of low diversity (Cole 1983, Rosengren 1986), and exclusion of the meat ant *Iridomyrmex sanguineus* from enclosures for six weeks increased the success of some species at bait (Andersen and Patel 1994). The study we present here is the longest experimental removal of a dominant ant species conducted. We removed the meat ant *Iridomyrmex purpureus* from sandstone outcrops for one year in order to determine the short-term effect of this dominant species on ant assemblages in terms of abundance, diversity, and composition. We also examined behavioral interactions between the dominant species and six of the more common species in the field to determine if such interactions were consistent with effects observed in the removal study.

METHODS

Study area and system

The study was conducted between January 2000 and April 2002 on Hawkesbury sandstone outcrops with pockets of heath vegetation in the Sydney region in southeastern Australia. Outcrops in the study area are relatively undisturbed and provide a warm, open habitat. Low levels of temperature stress and disturbance provide optimal conditions for competition between ant species (Andersen 1995). The study animal, the meat ant *Iridomyrmex purpureus*, is a behaviorally and ecologically dominant ant (Greenslade 1976, Andersen and Patel 1994). In summer and autumn 2000 surveys of the study sites, 82% and 68% of ants counted in quadrats were *I. purpureus* workers (H. Gibb, *unpublished data*), which made up 84% and 82%, respectively, of

the total biomass of ants on rock substrates (Gibb and Hochuli 2003a). *Iridomyrmex purpureus* has a patchy distribution in the study area, where it is associated with disturbed and open areas (Greaves 1971), and particularly with fire trails (Gibb and Hochuli 2003a).

We selected nine outcrops in Marramarra National Park, six in Muogamarra Nature Reserve, and one in Maroota State Forest (see Appendix A) to examine the effect of this dominant species on ant assemblages. Eight of the selected outcrops supported at least one colony of *I. purpureus*, and eight did not. Sites were superficially similar with respect to rock area and vegetation type and were spatially independent and geographically interspersed. They were centered on an *I. purpureus* nest or on a similar point at sites without *I. purpureus*, and surveys were performed on the outcrops within a 20-m radius of this point. Sites with *I. purpureus* had between one and two *I. purpureus* nests of >1.5 m diameter within the 20-m study area and up to four additional nests within a 50-m radius. Nests of this size contain ~50 000 workers (Greaves and Hughes 1974), each 8 mm in length. A comparison of habitats showed that sites with *I. purpureus* had greater gravel, soil, and moss cover, and proximity to fire trails, and a different soil type from sites without *I. purpureus* (Gibb and Hochuli 2003a).

Experimental design and caging methods

Initial surveys were conducted at all sites in January and February (summer) and in March and April (autumn) of 2000. We randomly selected four of the sites with *I. purpureus* for exclusion of the dominant species, and four without to act as procedural controls. The aim of the caging, carried out in January and February 2001, was to examine the response of the ant assemblage to the exclusion of *I. purpureus*. At the four exclusion sites, all *I. purpureus* nests that had workers foraging upon an outcrop were caged. Equivalent numbers of procedural control cages were constructed in a similar way at four sites without *I. purpureus* such that there were four of each of the treatments: exclusion, *I. purpureus* control, no *I. purpureus* control, and procedural control. Surveys of the exclusion experiment were conducted one, four, eight, and 12 months after caging (i.e., in autumn, winter, spring, and summer, respectively). Cages were removed in February 2002 after the experiment had run for 12 months.

We considered our experiment long enough to account for changes in populations of individual nests because development from egg to adult worker ranges from one to four months for ants (Hölldobler and Wilson 1990). In addition, nest relocation is a widespread phenomenon among ants and permits rapid responses to changes in external conditions. Common species on the outcrops regularly form new nests or abandon old ones (e.g., in summer, *Polyrhachis ammon* abandons ~50% of nests over periods of <1 mo [Gibb and Hochuli 2003b]), and Hughes (1990) found that mean nest entrance turnover for ants in open woodland on

Hawkesbury sandstone bedrock proved to be between one and three months for all genera tested. However, as the experiment encompassed only one reproductive season, we cannot be sure that it provided adequate time for colonies established by alate queens to reach a detectable size. In interpreting our results, we have also considered that resource availability and the suitability of conditions for establishing new nests may also vary between years.

Nests selected for exclusion were those on the outcrop, or those from which workers foraged on the study outcrop, or were likely to expand their foraging range to the outcrop after caging of the resident colony. In practice, nests up to 50 m from the outcrop were caged, such that up to six nests were caged on or around the exclusion outcrops. Cages consisted of a frame covered with 2-mm wide aluminum fly mesh (Mitre 10, Australia, Pty Ltd) and were constructed over nests of *I. purpureus* (see Appendix B). The frame was constructed using four opposed cane poles ~80 cm in length in a rectangle of chicken wire mesh (~80 × 120 cm) and formed into a flattened four-sided pyramid. A trench 15 cm deep was dug around the nest mound 10 cm from its edge and the frame was placed on top of the mound. Fly mesh was placed over the frame and buried to 15 cm at least 10 cm from the edge of each nest mound. At the time of caging, many ants were outside the cage due to their aggressive reaction to our apparent attack of the nest. Some set up satellite nests outside the main nest and these nests were also caged or injected with cyfluthrin (Bayer Australia Limited; active ingredient 0.4 g/ kg cyfluthrin), such that numbers of workers outside the cage decreased substantially over time. Ants in cages were supplied with a small container of water and were fed honey weekly and tuna monthly. Many colonies became covered with algae and/or mold, possibly because the fly mesh collected dew and shaded the nest, and all colonies appeared to suffer a gradual decrease in worker numbers, with the populations of a few nests dying out by the end of the experiment.

Sites without *I. purpureus* were used as procedural controls as there were too few suitable undisturbed sites with *I. purpureus* to allow adequate replication. The procedural control was used to determine whether the caging or insecticide treatments affected the ant assemblage relative to that of an untreated site without *I. purpureus*. Numbers of cages and cyfluthrin treatment at procedural control and exclusion sites were similar.

Surveys were performed only on days with minimal cloud and no rain and sites were visited in a haphazard order. In the initial surveys one site was surveyed each day, and in the exclusion and post-exclusion surveys two sites were surveyed each day. For post-exclusion surveys, sites were paired on the basis of proximity to one another to reduce travel time, and pairs were a mix of treatments such that no two treatment types were paired with each other more than twice. Temperatures

were obtained from the Mangrove Mountain weather station, 20–30 km from the study sites in the initial surveys. For the remainder of the study, temperatures were monitored using three Thermochrons (iButton, Dallas Semiconductor, Dallas, Texas, USA) taped in the shade under branches of trees or shrubs at each of the study sites.

For the initial surveys, we predicted that levels of ant activity observed at sites with *I. purpureus* would be different from those observed at sites without *I. purpureus*. After removal of *I. purpureus* from the assemblage we predicted that ant activity at exclusion and *I. purpureus* sites would differ in ways that were consistent with the initial surveys. We also predicted that there would be no differences in ant activity between exclusion sites and sites without *I. purpureus* or between sites without *I. purpureus* and procedural control sites. These three planned comparisons were used for all analyses in the removal experiment.

Effect of Iridomyrmex purpureus *on ant activity*

We used activity as a surrogate for population size, as activity should be affected consistently across treatments by factors such as temperature and humidity. Activity surveys were performed using transects as this method was more likely than quadrats or pitfall traps to detect common larger species, such as those belonging to the genera *Polyrhachis* and *Camponotus*, which were of particular interest due to their similar size to *I. purpureus*. Those species that do not compete directly with *I. purpureus* for natural resources were expected to be affected by its exclusion through indirect or diffuse competition. In the initial surveys at each site, the ends of eight transects, each 10 m long, and passing through minimal vegetation, were marked with chalk on the rock surface. Transects were walked for 5 min and the presence or absence of larger species and easily recognized smaller genera of ants (<3 mm) within 2 m either side of each transect was recorded. Two transect surveys were performed each hour on the hour from 0900 to 1200.

After exclusion, the transect surveys were performed slightly differently to maximize efficiency in the field. Surveys were conducted between 0800 and 1200 hours, with winter surveys starting at 0930, and summer surveys starting at 0800 in order to avoid periods of low ant activity at low and high temperatures. We used 10 transects, marked as in the initial survey; however each was 8 m in length, and we walked along them for 3 min and recorded ant abundance, rather than presence/absence. For highly abundant species that formed trails, we made an estimate of the number of individuals passing within 2 m of the transect. Surveys took 40 min and transects were surveyed twice, alternating between a pair of sites to minimize temporal confounding.

Samples of ants at each site were taken, classified to genus and morphospecies, and identified to species level by experts (D. Smith and A. N. Andersen), if

possible. We compared the abundance of all ants, ants other than *I. purpureus*, and species occurring at 50% or more of sites, as well as species richness between treatments using repeated-measures ANOVA (SYSTAT 9, SPSS 1998). The group "other *Iridomyrmex*," which accounted for individual workers of all species of *Iridomyrmex* other than *I. purpureus*, was used for all analyses as no single species of *Iridomyrmex* was found at 50% of sites. While this effectively lumped some species that might compete with one another (see Fox et al. 1985), the diversity and variability of this group was too high to examine species individually. *Iridomyrmex* and behaviorally similar dolichoderine ants are classified as belonging to the "Dominant Dolichoderinae," a guild of behaviorally and ecologically dominant ants in Australia (Andersen 1990). This guild consists of active, aggressive, and abundant ants that are able to monopolize resources. As a group, they are predicted to have an impact upon groups of behaviorally different ants, including the behaviorally submissive Camponotinae and poorly competitive opportunistic taxa, such as the disturbance-associated *Rhytidoponera* (Andersen 1990). We describe these taxa as "subordinate," following functional group conventions. We tested the effect of exclusion on the total number of *Iridomyrmex* to determine if removal of *I. purpureus* resulted in replacement by a complex of ecologically similar species. This also allowed us to examine whether changes in the total number of dominant *Iridomyrmex* resulted in changes in the abundance of behaviorally subordinate taxa.

We compared presence/absence counts on the eight transects at each site for the treatments "*I. purpureus*" and "no *I. purpureus*" for the initial surveys, and after exclusion, we examined effects on the abundance of the same taxa for the three planned comparisons of treatments. Data were fourth root transformed for each transect when necessary to meet the assumption of homogeneity of variances. When *P* values for two-factor interactions were less than or close to 0.05, we used simple effects tests (Keppel 1982) to test for the effect of each factor on each level of the other factor. We used the original $MS_{residual}$ for these tests as they were considered part of the original analysis (Keppel 1982, Quinn and Keough 2002). We tested to ensure that power for the exclusion surveys, with four rather than the original eight replicates of each treatment, was adequate to detect differences between treatment types using the effect size determined in the initial surveys (as recommended by Fairweather 1991). Corrections for multiple comparisons (Rice 1989) were considered too conservative in the context of this study.

The composition of ant assemblages at sites with and without *I. purpureus* in the initial surveys, and for the three relevant pairs of experimental treatments, was compared using Analysis of Similarities (ANOSIM) on the PRIMER software package (Clarke and Gorley 2001) on presence/absence transformed data. *Irido-*
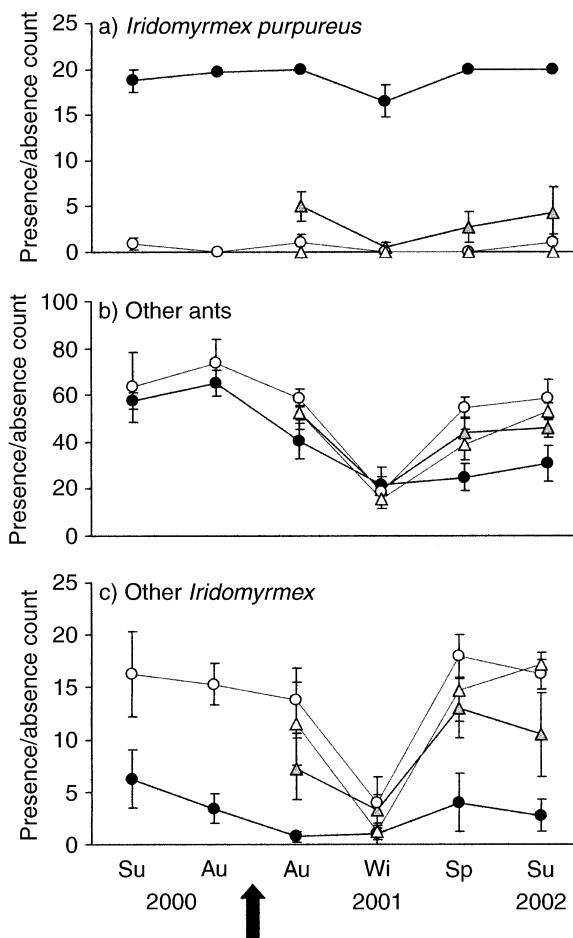

FIG. 1. Mean (±1 SE) presence/absence count per treatment (N = 4 sites) of (a) *I. purpureus*, (b) other ants, and (c) other *Iridomyrmex* at sites with and without *I. purpureus* before and during the exclusion experiment. Symbols indicate sites with *I. purpureus* (solid circles), sites without *I. purpureus* (open circles), exclusion sites (gray triangles), and procedural control sites (open triangles). Corrections have been made for different numbers of transects used in initial and exclusion surveys. For "other ants," counts per transect could be greater than 1 because the counts of different species were added together. Arrow represents commencement of exclusion experiment and sampling times are abbreviated as Su (summer), Au (autumn), Wi (winter), and Sp (spring).

myrmex purpureus was excluded from the data set for these analyses and we used the Bray-Curtis similarity measure as it is not affected by joint absences (Field et al. 1982).

Abilities of common species to discover, recruit to, and defend resources

Behavioral experiments were conducted in October–November 2001 and March–April 2002 at sites close to those that had been used in the exclusion experiment. The aim of these experiments was to compare the intrinsic abilities of *Iridomyrmex purpureus* and six of the most common ant species to discover, recruit to,

TABLE 1. *P* values for planned repeated-measures ANOVA on the presence/absence count of common species in the treatments ''*Iridomyrmex purpureus*'' and ''no *Iridomyrmex purpureus*'' before exclusion; and fourth-root-transformed abundance in the treatments ''exclusion'' and ''*I. purpureus*'' after exclusion.

A) ANOVA

	Taxon†							
	Ca (62.5)		Dd§ (50)		Ix (100)		Pa (100)	
Source of variation	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Before exclusion								
I. purpureus vs. no *I. purpureus*								
Treatment$_{1,28}$	0.54	0.474	**8.17**	**0.013**‖	**13.1**	**0.003**‖	**7.75**	**0.015**¶
Survey$_{1,28}$	0.48	0.501	0.57	0.463	0.53	0.477	2.92	0.109
Survey × Treatment$_{1,28}$	0.48	0.501	1.12	0.308	0.22	0.649	0.32	0.578
After exclusion								
I. purpureus vs. *exclusion*								
Treatment$_{1,6}$	0.18	0.671	⋯	⋯	5.64	0.055‖	0.00	0.962
Survey$_{3,18}$	1.06	0.389‡	⋯	⋯	**7.57**	**0.002**	3.13	0.052
Survey × Treatment$_{3,18}$	0.51	0.678‡	⋯	⋯	2.95	0.060	0.51	0.683

B) Abundance (mean ± 1 SE)

	Taxon			
Site type	Ca	Dd	Ix	Pa
Exclusion	4.3 ± 3.9	0.0 ± 0.0	183 ± 108	11.3 ± 4.6
I. purpureus	3.3 ± 3.3	0.0 ± 0.0	13.3 ± 7.9	11.5 ± 4.5
No. *I. purpureus*	16.8 ± 16.4	6.8 ± 4.4	365 ± 132	4.8 ± 2.3
Procedural control	8.8 ± 6.9	8.8 ± 5.6	369 ± 162	9.0 ± 4.8

Notes: Significant *F* and *P* values are shown in bold. Abundance of taxa (mean ± 1 SE) in each treatment in the final post-exclusion survey is shown in part B. Surveys commenced before exclusion in January and March 2000; and after exclusion in March, June, and October 2001, and in January 2002. Species abbreviations: Ca = *Camponotus aeneopilosus*; Dd = *Dolichoderus doriae*; Ix = other *Iridomyrmex*; Pa = *Polyrhachis ammon*; Pr = *Polyrhachis rowlandi*; SR = Species richness; O = Ants other than *I. purpureus*.

† Numbers in parentheses give percentage of sites in which taxon is present.

‡ June exclusion data were not used due to excessive zeros (df = 2, 12).

§ Analysis could not be performed for any season during the exclusion experiment due to excessive zeros.

‖ Fewer numbers of the species in the presence of *I. purpureus*.

¶ Greater numbers of the species in the presence of *I. purpureus*.

and defend a bait. Honey was placed on a card on a sandstone surface 30 cm from eight nests of *Monomorium* (*leae* spp. group), nine nests of *Camponotus aeneopilosus*, and ten nests of each of *I. purpureus*, other *Iridomyrmex* (*bicknelli* spp. group), *Ochetellus glaber*, *Polyrhachis ammon*, and *Rhytidoponera metallica*. All ants of non-target species approaching within 30 cm of the bait card were removed from the area using a sticky tape. Target species were allowed up to 30 min to discover the bait, and a further 30 min to recruit to it. We recorded the time at which the first, fifth, tenth, twentieth, and thirtieth ants of the target species arrived. We allowed other species to approach the bait after 30 ants had arrived, or, if recruitment was slow or nonexistent, 30 min after discovery of the bait. The first five interactions between the target species and other species were recorded. We did not record interactions involving the same individuals that followed on immediately from previously recorded interactions. We recorded the species that initiated each interaction and classified the interaction as ''aggression'' or ''encounter.'' Aggressive interactions involved obvious biting, lunging, or some form of chemical aggression made obvious through gaster raising by the target or non-target species. Encounters were re-

corded when two species came into contact and either avoided one another or did not engage in any obvious aggression. We recorded the composition of ants at the bait 30 min after the target species was exposed to interactions with other species. Outcomes for each trial where bait had been discovered were recorded as one of the following: ''abandoned,'' indicating that the species had left the bait despite a lack of interactions with other species; ''retained,'' where the species retained possession of the bait; or ''displaced'' when the target species was displaced by another species. When the target species did not discover the bait, no interactions could be recorded so *n* was often <10 for outcomes.

Rates of discovery of bait and recruitment abilities of the target species were compared with those of *I. purpureus* using a Mann-Whitney *U* test on ranked time to discovery and number of times 30 ants were recruited. Proportions of trials involving each class of interaction or outcome are only presented visually as they were not independent of discovery and recruitment ability and multiple interactions were recorded per trial.

RESULTS

Effect of Iridomyrmex purpureus *on ant activity*

In the initial surveys, *Iridomyrmex purpureus* occurred in 95–100% of transects within 20 m of a nest (Fig. 1a).

TABLE 1. Extended.

Taxon†							
Pr (100)		Rm (100)		SR		O	
F	P	F	P	F	P	F	P
6.24	**0.026¶**	2.77	0.118	0.68	0.423	1.21	0.351
18.1	**0.001**	1.17	0.299	0.23	0.639	1.16	0.302
3.94	0.067	0.01	0.944	0.38	0.548	0.85	0.494
0.05	0.831	0.34	0.581	3.95	0.094	5.39	0.059‖
2.50	0.092	**3.47**	**0.038**	**7.29**	**0.002**	**10.2**	**0.000**
0.06	0.982	0.57	0.642	0.57	0.643	2.82	0.068

Taxon			
Pr	Rm	SR	O
6.3 ± 1.7	20.3 ± 6.8	10.3 ± 0.9	464 ± 212
8.0 ± 1.4	16.8 ± 5.0	8.8 ± 1.5	59.3 ± 9.2
3.5 ± 1.6	26.5 ± 8.5	12.5 ± 0.9	707 ± 284
6.0 ± 2.7	12.3 ± 1.4	9.5 ± 0.5	439 ± 162

Six other "large" species (>3 mm) occurred at 50% or more of the sites (Table 1) out of a total of 56 observed species. Initial surveys showed that the presence/absence counts of *Polyrhachis ammon* and *P. rowlandi* were greater, while those of the dolichoderine ants *Dolichoderus doriae*, and "other *Iridomyrmex*" (Fig. 1c), were lower at sites with *I. purpureus* (Table 1). Quadrat surveys, which were conducted at the same time, accounted for all ants, regardless of size, but detected differences only for other *Iridomyrmex* and *D. doriae*, indicating that *I. purpureus* did not affect the abundance of any small ant species (Gibb and Hochuli 2003a).

After one month of exclusion, cages proved effective at reducing the count of *I. purpureus* by 75% (Fig. 1a), and its abundance by 99.5%, and this reduction was maintained throughout the 12 months of the experiment. The power of the analysis to detect differences for species that had shown a significant association with the presence of *I. purpureus* in initial surveys remained high (>0.8, the conventionally accepted level [Cohen 1988]), except for *P. ammon* in autumn. Exclusion surveys revealed that the presence of *I. purpureus* affected only the abundance of "other ants" and "other *Iridomyrmex*" (Table 1), and that effects were significant only in some seasons. Other ants were more abundant at exclusion sites than at *I. purpureus* sites in spring ($F_{1,18} = 10.78$, $P = 0.004$) and summer ($F_{1,18} = 11.18$, $P = 0.004$), but not autumn ($F_{1,18} = 3.75$, $P = 0.069$) or winter ($F_{1,18} = 0.06$, $P = 0.807$; Fig. 1b). Other *Iridomyrmex* were more abundant at exclusion sites than sites with *I. purpureus* in autumn ($F_{1,18} = 8.11$, $P = 0.011$), spring ($F_{1,18} = 20.34$, $P < 0.001$), and summer ($F_{1,18} = 17.42$, $P = 0.001$), but not winter ($F_{1,18} =$

0.52, $P = 0.479$; Fig. 1c). Exclusion of *I. purpureus* did not result in total replacement by other *Iridomyrmex*, as sites with *I. purpureus* had significantly more total *Iridomyrmex* than exclusion sites ($F_{1,6} = 70.76$, $P < 0.001$). Total numbers of *Iridomyrmex* at exclusion sites were between 2% (in winter) and 15% (in spring) of the numbers at sites with *I. purpureus*.

Planned comparisons between exclusion sites and no *I. purpureus* sites showed that *Dolichoderus doriae* remained less abundant at exclusion sites than at no *I. purpureus* sites ($F_{1,6} = 11.21$, $P = 0.015$), even after one year of *I. purpureus* exclusion. Other *Iridomyrmex* showed a similar pattern ($F_{1,6} = 5.12$, $P = 0.064$). Planned comparisons between ant abundances at no *I. purpureus* sites and procedural control sites revealed no effect of the caging treatment on abundance for any of the taxa examined ($F_{1,6} < 6.0$, $P > 0.05$).

Initial surveys showed a difference in the composition of ant assemblages that was significant in both summer (Global $R = 0.309$, $P < 0.01$) and autumn (Global $R = 0.367$, $P < 0.01$). After exclusion, however, there were no differences in assemblages between exclusion sites and *I. purpureus* sites in any season for any of the planned comparisons ($0.422 >$ Global $R > -0.349$, $P > 0.05$).

Abilities of common species to discover, recruit to, and defend resources

Iridomyrmex purpureus was faster at locating bait than all other ant taxa (Fig. 2a), discovering all bait within 5 min of placement. Most ant taxa discovered the majority of their bait within 5 min, and *Polyrhachis ammon* and *Monomorium* (*leae* spp. group) did not
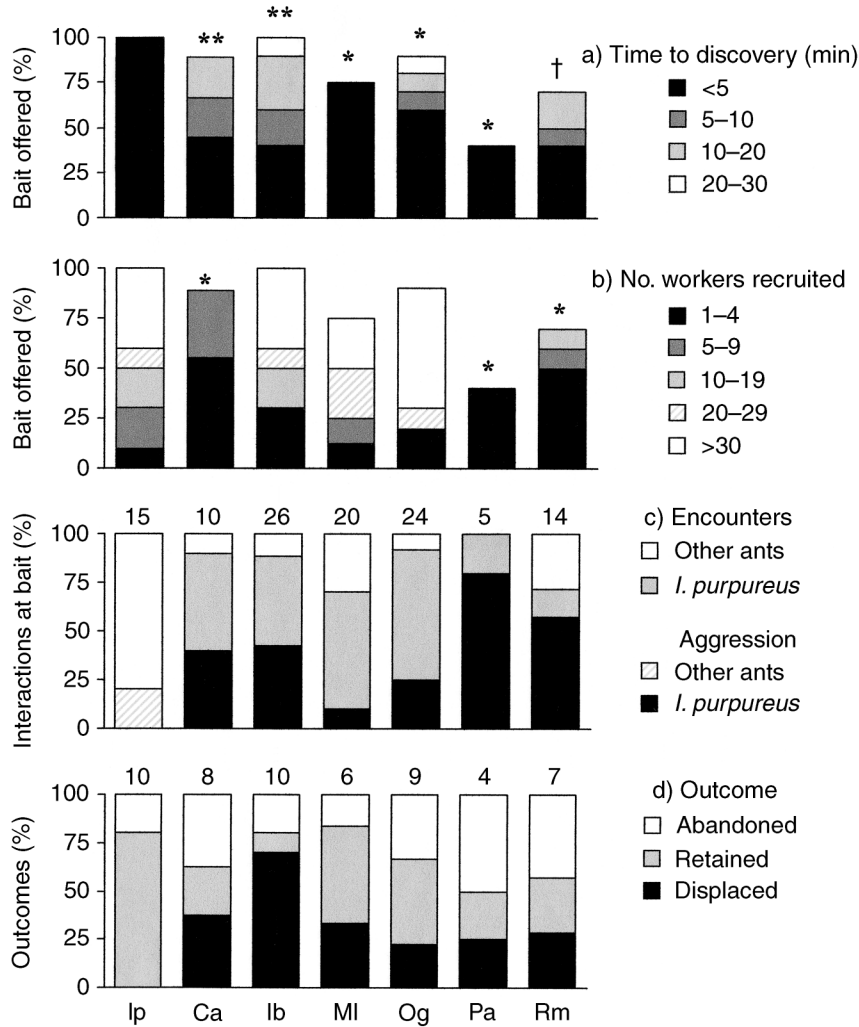
FIG. 2. Responses to bait by seven common ant taxa as percentages of protected bait offered: (a) time to discovery, (b) maximum number of workers recruited, and (c) types of interactions; and (d) outcome as percentages of bait discovered. For (a) and (b), symbols indicate statistically significant pairwise comparisons (*I. purpureus* vs. each other species of ant) using the Mann-Whitney *U* test: † $P < 0.10$, * $P < 0.05$, ** $P < 0.01$. Ip = *Iridomyrmex purpureus*, Ca = *Camponotus aeneopilosus*, Ib = *Iridomyrmex* (*bicknelli* spp. group), Ml = *Monomorium* (*leae* spp. group), Og = *Ochetellus glaber*, Pa = *Polyrhachis ammon*, Rm = *Rhytidoponera metallica*. For (a) and (b), $N = 10$ for all taxa, except for *Monomorium* where $N = 8$, and *C. aeneopilosus* where $N = 9$. For (c) and (d), *N* is given above bars.

discover bait after this time period, possibly indicating a limited foraging range or direction of travel from their nests. Planned comparisons revealed that *I. purpureus* discovered bait significantly faster than almost all other species (Fig. 2a).

Comparison of numbers of workers from different ant species recruited to bait revealed marked differences in recruitment ability (Fig. 2b). While both species of *Iridomyrmex*, *Monomorium* (*leae* spp. group), and *Ochetellus glaber* were all observed to recruit at least 30 ants on several occasions, the three remaining species recruited only weakly, if at all. We observed a maximum of 13 workers of *Rhytidoponera metallica*, seven of *Camponotus aeneopilosus*, and four of *Po-*

lyrhachis ammon at protected bait. Comparison of recruitment abilities of *I. purpureus* and other taxa (Fig. 2b) revealed that *I. purpureus* recruited 30 workers significantly more often than *C. aeneopilosus*, *P. ammon*, and *R. metallica*, but no differently from *I.* (*bicknelli* spp. group), *Monomorium* (*leae* spp. group), or *O. glaber*. Recruitment patterns were particularly similar between the two *Iridomyrmex* taxa.

Iridomyrmex purpureus attempted to access bait occupied by other ants and interacted with them more often than other species, possibly because it was both more abundant, and more active (Fig. 2c). Between 22% and 80% of interactions involved aggression from *I. purpureus*, with *P. ammon* apparently suffering the

highest proportion of aggressive interactions, although only five interactions were observed for this species. Fights with *I. purpureus* sometimes led to the deaths of other ants, but never of *I. purpureus*.

Displacement of a target species from its bait was due to *I. purpureus* in all cases but one, where a smaller *Iridomyrmex* species displaced *C. aeneopilosus*. All target species suffered displacement by *I. purpureus*, ranging from 22% of outcomes for *O. glaber*, to 70% for *Iridomyrmex* (*bicknelli* spp. group; Fig. 2d). In contrast, *I. purpureus* was never displaced from its bait and retained 80% of bait discovered, a far higher proportion than any other species. Abandonment of bait not prompted by interactions with other species was also common, ranging from 17% of bait discovered for *Monomorium* (*leae* spp. group) to 50% for *P. ammon*. *Iridomyrmex* (*bicknelli* spp. group) abandoned less bait than all other species except *I. purpureus*, so may have come into greater contact with the dominant species by remaining at bait longer, and in larger numbers.

DISCUSSION

Removal of an ecologically dominant ant, *Iridomyrmex purpureus*, from rock outcrops showed that it influences the structure of ant communities in this habitat. We found that *I. purpureus* displaced other species from bait through aggressive behaviors, and that sites with *I. purpureus* supported a different ant fauna from those without. However, over one year, our removal experiment revealed effects of *I. purpureus* only on other *Iridomyrmex*. Our data thus support the contention that current competition plays a limited role in structuring ant communities in these habitats.

We approached the question of how a dominant species affects a community from several perspectives and found that conclusions drawn from our mensurative, behavioral, and removal experiments differed. Our initial surveys provided support for the theory that both direct and indirect competition are important in structuring ant communities. Patterns observed in the mensurative study could be construed as being the result of a direct negative effect of *I. purpureus* on other *Iridomyrmex* and *Dolichoderus doriae*. Increases in the abundance of *Polyrhachis ammon* and *P. rowlandi* could then be interpreted as the result of reduced effects of competition from these species. Findings from our behavioral experiments supported the contention that other species are displaced from resources by *I. purpureus* and are thus likely to be less abundant in its presence. While experimental removal of *I. purpureus* revealed evidence of direct competition, it did not provide evidence of indirect or diffuse competition. Effects on activity were apparent only for the behaviorally and ecologically similar "other *Iridomyrmex*" group, which was dominant in the absence of *I. purpureus*, with effects on "other ants" driven by this taxon. Similarly, concurrent resource use surveys showed that the impact of *I. purpureus* exclusion on resource use by other ants was significant only for other *Iridomyrmex*, and that other groups had low success at bait (Gibb 2003). These findings support the contention that competition is important within the guild of dominant ants (the Dominant Dolichoderinae), and are consistent with evidence that invasive ants have strongest effects on ecologically similar species (Holway et al. 2002). The long-term impact of *I. purpureus* on behaviorally dissimilar species is less clear.

Functional redundancy is thought to occur between behaviorally similar species within levels of an ant dominance hierarchy (Savolainen and Vepsäläinen 1988, 1989, Andersen 1990), such that "subordinate" species may appear to show no effect of removal of a dominant ant because they are always displaced from rich resources by dominant ants of one species or another. This hypothesis is supported by the behavior of both *I. purpureus* and other species of *Iridomyrmex*, which attack and displace several subordinate species from bait (H. Gibb, *personal observation*). Sites with *I. purpureus* had a much greater total abundance of dominant ants than exclusion sites because replacement by other species of *Iridomyrmex* was only partial. However, the depauperate community of dominant ants at exclusion sites did not result in a greater abundance of any of the common subordinate species in this experiment. It is possible that "other *Iridomyrmex*" had a suppressing effect on the group of subordinate species equivalent to that of *I. purpureus*, although it seems unlikely, due to their small size and low numbers relative to *I. purpureus*. Experimental manipulation of the entire assemblage of dominant ants is necessary to directly determine their role as a functional group in structuring ant communities.

Access to persistent honeydew resources is thought to be essential for behavioral and ecological dominance within an ant community (Way 1958, Room 1975), and competitive abilities may limit the species able to access such resources (Buckley 1987). Our behavioral experiments support the contention that *I. purpureus* is behaviorally dominant; resource use experiments indicate that other *Iridomyrmex* are less successful at honey bait in the presence of *I. purpureus* (Gibb 2003); and field observations (H. Gibb, *personal observation*) indicate that other species of *Iridomyrmex* are the predominant tenders of homopterans at most sites from which *I. purpureus* is absent. All honeydew sources detected within 20 m of a nest of *I. purpureus* were tended by *I. purpureus* and it is likely that displacement of smaller species of *Iridomyrmex* from this resource is the major cause of their reduced abundance in the presence of *I. purpureus*.

Displacement from resources by a behaviorally dominant species may eventually lead to population-level changes (Andersen and Patel 1994), however interactions between species may differ between natural and artificial resources. Ants may forage more intensively at experimental bait than natural food sources, as it is

usually richer (Davidson 1997, Ribas and Schoereder 2002). Aggression and monopolization of resources also becomes more profitable with increasing predictability and spatial clustering (Pimm 1978, Grant and Guha 1993, Goldberg et al. 2001), and large artificial bait will thus attract behaviorally dominant taxa, such as *Iridomyrmex*. In contrast, ''subordinate'' species such as *Polyrhachis ammon* and *P. rowlandi*, which were not affected by the presence of *I. purpureus*, rely mainly on flower nectar, extra-floral nectarines, and bird feces (H. Gibb, *personal observation*), and these are widely dispersed, ephemeral resources that are difficult to monopolize.

Patterns of species co-occurrence may be driven by contemporary factors other than competition, such as habitat preference (e.g., for open or disturbed habitats [Andersen 1991, Punttila et al. 1996, Stiles and Jones 1998, Gibb and Hochuli 2003*a*]), or interactions with species in other trophic levels (Gotelli 1996, Feener 2000). Differences in food and habitat preferences may evolve as a consequence of competition; however they may also result from other past processes, such as geographic separation, genetic drift, and past resource availability. Manipulative experiments are of great value in disentangling the roles of contemporary processes in determining community structure and there is a dearth of such studies on ants. However, they are of more limited value in determining the importance of past processes. Longer-term manipulative studies investigating the temporal dynamics of interactions may partially address this constraint.

Our findings suggest that the short-term effects of a dominant species on an ant community may be more limited than predicted from associations of ant species apparent in our mensurative survey, and the behavioral dominance of *Iridomyrmex purpureus* at resources. Partitioning of resources in terms of quality, habitat, dispersal, and predictability may be important in allowing the coexistence of so many different, yet superficially similar, species in ant communities, and may represent the ''ghost of competition past'' (Connell 1980). However, within the timeframe of this study, impacts of the behaviorally dominant species were manifested only through species similarly dependent on monopolizing large and predictable resources.

LITERATURE CITED

Andersen, A. N. 1984. Community organization of ants in the Victorian Mallee. Victorian Naturalist **101**:248–251.

Andersen, A. N. 1986. Patterns of ant community organization in mesic southeastern Australia. Australian Journal of Ecology **11**:87–98.

Andersen, A. N. 1990. The use of ant communities to evaluate change in Australian terrestrial ecosystems: a review and a recipe. Proceedings of the Ecological Society of Australia **16**:347–357.

Andersen, A. N. 1991. Responses of ground-foraging ant communities to three experimental fire regimes in a Savanna forest of tropical Australia. Biotropica **23**:575–585.

Andersen, A. N. 1992. Regulation of ''momentary'' diversity by dominant species in exceptionally rich ant communities of the Australian seasonal tropics. American Naturalist **140**: 401–420.

Andersen, A. N. 1995. A classification of Australian ant communities, based on functional groups which parallel plant life-forms in relation to stress and disturbance. Journal of Biogeography **22**:15–29.

Andersen, A. N. 1997. Using ants as bioindicators: multiscale issues in ant community ecology. Conservation Ecology **1**(1):8. [Online, URL: <http://www.consecol.org/vol1/iss1/art8>.]

Andersen, A. N., and A. D. Patel. 1994. Meat ants as dominant members of Australian ant communities: an experimental test of their influence on the foraging success and forager abundance of other species. Oecologia **98**:15–24.

Blüthgen, N., M. Verhaagh, W. Goitía, K. Jaffé, W. Morawetz, and W. Barthlott. 2000. How plants shape the ant community in the Amazonian rainforest canopy: the key role of extrafloral nectaries and homopteran honeydew. Oecologia **125**:229–240.

Buckley, R. C. 1987. Ant–plant–homopteran interactions. Advances in Ecological Research **16**:53–85.

Clarke, K. R., and K. R. Gorley. 2001. PRIMER. Version 5. PRIMER-E, Plymouth, UK.

Cohen, J. 1988. Statistical power analysis for the behavioral sciences. Lawrence Erlbaum Associates, Hillsdale, New Jersey, USA.

Cole, B. J. 1983. Assembly of mangrove ant communities: patterns of geographical distribution. Journal of Animal Ecology **52**:339–347.

Connell, J. H. 1980. Diversity and the coevolution of competitors, or the ghost of competition past. Oikos **35**:131–138.

Davidson, D. W. 1980. Some consequences of diffuse competition in a desert ant community. American Naturalist **116**:92–105.

Davidson, D. W. 1997. The role of resource imbalances in the evolutionary ecology of tropical arboreal ants. Biological Journal of the Linnaean Society **61**:153–181.

Djieto-Lordon, C., and A. Dejean. 1999. Tropical arboreal ant mosaics: innate attraction and imprinting determine nest site selection in dominant ants. Behavioural Ecology and Sociobiology **45**:219–225.

Fairweather, P. G. 1991. Statistical power and design requirements for environmental monitoring. Australian Journal of Marine and Freshwater Research **42**:555–567.

Feener, D. H. 2000. Is the assembly of ant communities mediated by parasitoids? Oikos **90**:79–88.

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

Field, J. G., K. R. Clarke, and R. M. Warwick. 1982. A practical strategy for analysing multispecies distribution patterns. Marine Ecology Progress Series **8**:37–52.

Fox, B. J., M. D. Fox, and E. Archer. 1985. Experimental confirmation of competition between two dominant species of *Iridomyrmex* (Hymenoptera: Formicidae). Australian Journal of Ecology **10**:105–110.

Gibb, H. 2003. Factors affecting the community structure of ants and other arthropods on Hawkesbury sandstone outcrops. Dissertation. University of Sydney, Australia.

Gibb, H., and D. F. Hochuli. 2003*a*. Colonisation by a dominant ant facilitated by anthropogenic disturbance: effects on ant community composition, biomass, and resource use. Oikos, **103:**469–478.

Gibb, H., and D. F. Hochuli. 2003*b*. Nest relocation in the golden spiny ant, *Polyrhachis ammon*: environmental cues and temporal castes. Insectes Sociaux 50, *in press.*

Goldberg, J. L., J. W. A. Grant, and L. Lefebvre. 2001. Effects of the temporal predictability and spatial clumping of food on the intensity of competitive aggression in the Zenaida dove. Behavioural Ecology 12:490–495.

Gotelli, N. J. 1996. Ant community structure: effects of predatory ant lions. Ecology 77:630–638.

Gotelli, N. J., and G. R. Graves. 1996. Null models in ecology. Smithsonian Institution Press, Washington, D.C., USA.

Grant, J. W. A., and R. T. Guha. 1993. Spatial clumping of food increases its monopolization and defense by convict cichlids, *Cichlasoma nigrofasciatum*. Behavioral Ecology 4:293–296.

Greaves, T. 1971. The distribution of three forms of the meat ant *Iridomyrmex purpureus* (Hymenoptera: Formicidae) in Australia. Journal of the Australian Entomological Society 10:15–21.

Greaves, T., and R. D. Hughes. 1974. The population biology of the meat ant. Journal of the Australian Entomological Society 13:329–351.

Greenslade, P. J. M. 1976. The meat ant *Iridomyrmex purpureus* (Hymenoptera: Formicidae) as a dominant member of ant communities. Journal of the Australian Entomological Society 15:237–240.

Gurevitch, J., L. L. Morrow, A. Wallace, and J. S. Walsh. 1992. A meta-analysis of competition in field experiments. American Naturalist 140:539–572.

Hairston, N. G. 1981. An experimental test of a guild: salamander competition. Ecology 62:65–72.

Hoffmann, B. D., A. N. Andersen, and G. J. E. Hill. 1999. Impact of an introduced ant on native rain forest invertebrates: *Pheidole megacephala* in monsoonal Australia. Oecologia 120:595–604.

Hölldobler, B., and E. O. Wilson. 1990. The ants. Springer-Verlag, London, UK.

Holway, D. A. 1998. Factors governing rate of invasion: a natural experiment using Argentine ants. Oecologia 115:206–212.

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

Holway, D. A., L. Lach, A. V. Suarez, N. D. Tsutsui, and T. J. Case. 2002. The causes and consequences of ant invasions. Annual Reviews in Ecology and Systematics 33:181–233.

Hughes, L. 1990. The relocation of ant nest entrances: potential consequences for ant-dispersed seeds. Australian Journal of Ecology 16:207–214.

Human, K. G., and D. M. Gordon. 1999. Behavioural interactions of the invasive Argentine ant with native ant species. Insectes Sociaux 46:159–163.

Kay, A. 2002. Applying optimal foraging theory to assess nutrient availability ratios for ants. Ecology 83:1935–1944.

Keppel, G. 1982. Design and analysis: a researcher's handbook. Second edition. Prentice-Hall, Englewood Cliffs, New Jersey, USA.

Lewin, R. 1983. Santa Rosalia was a goat. Science 221:636–639.

Majer, J. D. 1993. Comparison of the arboreal ant mosaic in Ghana, Brazil, Papua New Guinea and Australia—its structure and influence on arthropod diversity. Pages 115–141 *in* J. L. Salle and J. D. Gauld, editors. Hymenoptera and biodiversity. CAB International, Bristol, UK.

Morrison, L. W. 2000. Mechanisms of interspecific competition among an invasive and two native fire ants. Oikos 90:238–252.

Pimm, S. L. 1978. An experimental approach to the effects of predictability on community structure. American Zoologist 18:797–808.

Porter, S. D., and D. A. Savignano. 1990. Invasion of polygyne fire ants decimates native ants and disrupts arthropod community. Ecology 71:2095–2106.

Punttila, P., Y. Haila, and H. Tukia. 1996. Ant communities in taiga clearcuts: habitat effects and species interactions. Ecography 19:16–28.

Quinn, G., and M. Keough. 2002. Experimental design and analysis for biologists. Cambridge University Press, Cambridge, UK.

Ribas, C. R., and J. H. Schoereder. 2002. Are all ant mosaics caused by competition? Oecologia 131:606–611.

Rice, W. R. 1989. Analyzing tables of statistical tests. Evolution 43:223–225.

Room, P. M. 1971. The relative distributions of ant species in Ghana's cocoa farms. Journal of Animal Ecology 40:735–751.

Room, P. M. 1975. Relative distributions of ant species in cocoa plantations in Papua New Guinea. Journal of Applied Ecology 12:47–61.

Rosengren, R. 1986. Competition and coexistence in an insular ant community—a manipulation experiment (Hymenoptera: Formicidae). Annals Zoologici Fennici 23:297–302.

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

Savolainen, R., and K. Vepsäläinen. 1989. Niche differentiation of ant species within territories of the wood ant *Formica polyctena*. Oikos 56:3–16.

Savolainen, R., K. Vepsäläinen, and H. Wuorenrinne. 1989. Ant assemblages in the taiga biome: testing the role of territorial wood ants. Oecologia 81:481–486.

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

SPSS. 1998. SYSTAT 9. SPSS, Chicago, Illinois, USA.

Stiles, J. H., and R. H. Jones. 1998. Distribution of the red imported fire ant, *Solenopsis invicta*, in road and powerline habitats. Landscape Ecology 335:335–346.

Way, M. J. 1958. The influence of other ant species on biological control of *Oecophylla longinoda* (Latr.). Proceedings X of the International Congress of Entomology 4:595–596.

Weiher, E., and P. Keddy. 1999. Ecological assembly rules: perspectives, advances, retreats. Cambridge University Press, Melbourne, Australia.

APPENDIX A

A map of the study area showing location of sites is available in ESA's Electronic Data Archive: *Ecological Archives* E085-014-A1.

APPENDIX B

A photo of one of the exclusion cages in which nests of *Iridomyrmex purpureus* were contained is available in ESA's Electronic Data Archive: *Ecological Archives* E085-014-A2.