

Colonisation by a dominant ant facilitated by anthropogenic disturbance: effects on ant assemblage composition, biomass and resource use

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Dominant species are thought to regulate species composition and assemblage structure. Invasion by a dominant species is thus likely to alter assemblages and anthropogenic disturbance often facilitates such invasions. In this study we examined the association of a dominant ant, *Iridomyrmex purpureus*, native to south-eastern Australia, with fire trails in national parks and its effects on ant assemblages. Association with fire trails was examined by comparing the numbers of *I. purpureus* nests on transects along fire trails with those in transects through surrounding vegetation. Ant assemblages and habitat characteristics of eight sandstone outcrops that supported colonies of *I. purpureus* were compared with those on eight that did not in summer and autumn 2000. We examined ant species richness, abundance, composition and biomass using quadrats, and resource use with *Acacia botrycephalus* seeds placed on rock and in vegetation. *I. purpureus* nests were considerably more common along fire trails than in surrounding vegetation. Sites with *I. purpureus* had similar species richness to those without, but a lower abundance and biomass of other ants and a different assemblage composition. These differences could not be attributed to any differences in measured habitat characteristics. Ecologically similar species, particularly other species of *Iridomyrmex*, were less abundant in areas with *I. purpureus*. While the biomass of other species was suppressed in areas with *I. purpureus*, the biomass of the dominant was several times that of the assemblage of other ants, a pattern shared with assemblages invaded by exotic species. In areas with *I. purpureus*, seeds were removed more rapidly from rock, but not vegetation, indicating that resources on rock may be under-exploited by other species. Regulation of invaded ant assemblages by this dominant ant is thus limited to functionally similar species, and this may be due to its use of resources that are unexploited in its absence.

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Dominant species exert their influence both behaviourally and ecologically (Ribas and Schoereder 2002). An ecologically dominant species is one that dominates community biomass (Begon et al. 1996), while a behaviourally dominant species is aggressive towards other species (Hölldobler 1983). Dominant species may structure assemblages (Hölldobler and Wilson 1990), influencing communities through their domi-

nance of resources (Fox 2002) and ecosystem biomass (Power and Mills 1995). Dominant roles are often assumed by successful invaders that out-compete native species (Morrison 2000).

Dominant ants have been shown to interfere with the foraging of other ants (Mabelis 1984, Savolainen 1991, Andersen and Patel 1994) and may have marked effects on the composition of ant communities, resulting in

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different assemblages of ants regulated by different dominant species (Hölldobler and Wilson 1990). Ant mosaics consisting of mutually exclusive territories of dominant ants and associated sub-dominant ants (Room 1971, Leston 1973, Floren and Linsenmair 2000) are thought to result from this process, and dominance hierarchies have been described from ant communities worldwide (Greenslade 1978, Mabelis 1984, Savolainen and Vepsäläinen 1988, Pisarski and Vepsäläinen 1989, Andersen 1992, Cerdá et al. 1997).

Functional groups of ants, derived from such dominance hierarchies, are expected to respond predictably to different environmental conditions (Andersen 1990) and have been used extensively in Australia to examine the effects of environmental disturbances ranging from mining (Andersen 1993, Read 1996) to fire (Andersen 1991, Vanderwoude et al. 1997, Andrew et al. 2000, York 2000) and habitat fragmentation (Gibb and Hochuli 2002). However, dominant species do not always regulate ant community structure in undisturbed habitats (Floren and Linsenmair 2000) and other factors, such as temperature (Cerdá et al. 1988, 1997), successional stage (Majer and Camer-Pesci 1991), predators (e.g. antlions, Gotelli 1996) or parasitoids (e.g. phorid flies, Feener 2000), and even random distribution of species amongst sites (Ribas and Schoereder 2002) may be more important.

Invasive exotic ant species have also been found to influence the ant assemblages that they invade, thus behaving as dominant species. The Argentine ant, *Linepithema humile*, competitively displaces native species throughout its introduced range (Holway 1999); the coastal brown ant, *Pheidole megacephala*, alters community composition and reduces species richness (Hoffmann et al. 1999); and the red imported fire ant, *Solenopsis invicta*, can reduce native ant abundance and species richness by 90% and 70% respectively (Porter and Savignano 1990). Anthropogenic disturbance is often crucial in facilitating the invasion process beyond the initial introduction, and those species that are most devastating for native ant assemblages are often also the best at inhabiting human structures (McGlynn 1999). Anthropogenic alterations of the environment can facilitate competitive displacement by invasive species (Petren and Case 1998) and disturbances such as roads provide new habitats (Stiles and Jones 1998), stress or remove native species, and allow easier movement for many invasive species (Trombulak and Frissell 2000).

In mesic regions of southern Australia, habitat disturbance is thought to cause a breakdown in dominance by ants of the genus *Iridomyrmex* (Andersen 1990). However, the habitat change resulting from disturbance may also be to their benefit, as thermally favourable habitats can result from disturbances such as land-clearing (Greaves 1971) and fire (Vanderwoude et al. 1997) and a succession of dominant species of

Iridomyrmex has been found to replace preceding species in heathland regenerating after sand-mining (Fox and Fox 1982).

In this study, we investigate the association of a dominant ant, the meat ant, *Iridomyrmex purpureus*, with an anthropogenic disturbance, and consequent effects of this species on ant assemblages on rock outcrops in national parks in south-eastern Australia. We predicted that substantially more *I. purpureus* nests would be found along fire trails than in nearby vegetation of similar topography and soils. At sites with *I. purpureus*, we predicted that: 1) species richness, abundance and biomass of other ants would be lower; 2) the composition of other species of ants would be different, with ecologically similar ants being affected most; and 3) food resources would be collected more rapidly both on rock and in vegetation than at sites without *I. purpureus*.

Methods

Study area and species

The study was conducted on Hawkesbury sandstone outcrops with pockets of heath vegetation in the Sydney region in south-eastern Australia. Rock outcrops are high stress, low productivity habitats (Larson 2001) and loose surface rocks and crevices have unique thermal characteristics that influence temperature-dependent and physiological processes in ectotherms (Huey et al. 1989). Hawkesbury sandstone supports a unique flora (Carolin and Tindale 1994) and surface rocks on outcrops shelter a diverse and abundant invertebrate fauna (Goldsbrough et al. 2003). The climate in the Sydney region is temperate and temperature readings for the dates of the survey were obtained from the Bureau of Meteorology for Mangrove Mountain, which is 20 to 30 km from the study sites.

Study sites were in national parks 40 to 50 km northwest of the Sydney Central Business District (33°52'00" S, 151°12'30" E, Fig. 1). We selected a total of 16 relatively undisturbed outcrops; nine in Marramara National Park, six in Muogamarra Nature Reserve, and one in Maroota State Forest. Eight of these sandstone outcrops supported *I. purpureus*, and eight did not. Sites were spatially independent and were selected to be superficially similar in terms of vegetation structure and rock area and such that the treatments '*I. purpureus*' and 'no *I. purpureus*' were geographically interspersed. Each site covered an area of 20 m radius and was centred on a nest of *I. purpureus* or an open sunny area that appeared similar to sites in which *I. purpureus* was found to nest.

Ants belonging to the *I. purpureus* species group, otherwise known as meat ants (Shattuck 1993), are considered to be ecologically dominant (Greenslade

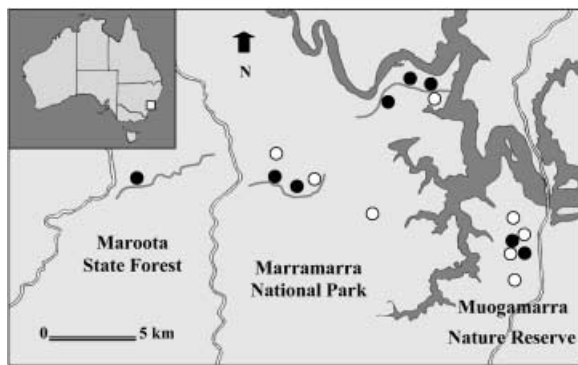


Fig. 1. Map of the study area showing sites with (●), and without (○) *I. purpureus*, and location in Australia (□). Major roads are shown in white and three of the surveyed fire trails are shown in grey. The other surveyed fire trails were in Kuring-gai Chase National Park to the east.

1976, Andersen and Patel 1994). *I. purpureus* is a diurnal ant of medium size (8 mm) and feeds mainly on arthropods and honeydew exuded by hemipteran insects associated with eucalypts (Ettershank and Ettershank 1982). It constructs large, long-lived nests, forages in large numbers, and is highly aggressive and territorial (Shattuck 1993). *I. purpureus* is common and widespread in south-eastern Australia (Shattuck 1993), however it is restricted to well-drained sunny habitats such as outcrops and ridges in heath and low woodland and is associated with clearing for roads, railways and agriculture (Greaves 1971). While *Iridomyrmex* is more successful in open habitats (Andersen 1990), there is no evidence that *I. purpureus* is an early successional species. Incipient colonies take over six years to reach maturity and shading caused by plant growth is a likely cause of mortality (Greaves and Hughes 1974). Meat ants occur in arid, semi-arid or seasonally arid environments (Greenslade and Halliday 1982), and *I. purpureus* may be on the climatic limit of its range in the more humid coastal areas.

Comparison of habitat characteristics of areas with and without *I. purpureus*

Characteristics of the sites that might predispose them to colonisation by *I. purpureus* were investigated in August 2000. 'Overstorey cover' and 'understorey cover' were estimated visually as a percentage of sky obscured by leaves. 'Rock cover', 'soil, gravel and moss cover' and 'vegetation cover' were estimated as a percentage of the area. We recorded the approximate distance to the nearest fire trail and the number of eucalypts (host trees for hemipteran insects) within an area of 10 m radius of the nest. We used t-tests to compare distance to the nearest dirt track, and arcsine transformed percentages of 'overstorey cover', 'under-

storey cover', 'rock cover', 'soil, gravel and moss cover' and 'vegetation cover' between sites with and without *I. purpureus*. Samples of the most common understorey plants were collected for identification in the laboratory and composition (presence/absence) at sites with and without *I. purpureus* was compared using analysis of similarities (ANOSIM, Clarke and Gorley 2001). For this test we used the Bray-Curtis similarity measure, which is not affected by joint absences (Field et al. 1982).

Three soil samples were taken from the top 5 to 10 cm of soil at each site as most soils on outcrops were shallow and deeper samples could not be obtained at many sites. Soil samples were analysed with respect to chemical properties, including pH and conductivity, as well as organic matter content and texture. Conductivity, which correlates strongly with salinity, grain size and texture, was measured using a conductometer (Metrohm Herisau, Switzerland), and pH was measured with a Micro 2 pH/ion meter (EDT Instruments, ACTIVON, NSW) using 10 g of each soil sample. Loss of organic matter on ignition was measured using 10 to 15 g of pre-weighed oven-dried sample heated to 430 °C for 24 hours. Soil texture was determined using the wet sieving technique. Percentages of sand, silt, clay and organic matter in each sample were calculated and an analysis of variance (ANOVA) was performed on the arcsine transformed data, and on untransformed conductivity and pH data.

Effects of *I. purpureus* on composition and biomass of ant assemblages

We compared ant assemblages on outcrops with and without *I. purpureus* to determine if there was an effect of the presence of this species on the abundance, species richness, biomass, or composition of other ant species. Ant assemblages were examined on 16 fine days in January and February (summer), and in March and April (autumn), 2000. Sites with and without *I. purpureus* were visited in a haphazard order on alternate days and there were no differences in mean temperatures on days of survey at sites with or without *I. purpureus* (summer: $t_{(14)} = -1.809$, $p = 0.092$; autumn: $t_{(14)} = -1.283$, $p = 0.220$) or between the surveys (*I. purpureus*: $t_{(14)} = 0.166$, $p = 0.870$; no *I. purpureus*: $t_{(14)} = 0.898$, $p = 0.385$). Species richness, abundance, composition and biomass were examined through observations of ants passing through quadrats. In open habitats with minimal leaf litter and ground vegetation, such as sandstone outcrops, quadrats can be used to provide an estimate of the relative abundance of simultaneously active species (Andersen 1991). Temporal differences inherent in quadrat based surveys can be minimized by repeated sampling.

Pilot studies showed the most efficient quadrat size for the study to be 1 m² and time of observation to be 3 min. The corners of 30 quadrats of 1 m² were marked out in chalk on each outcrop within 20 m of the *I. purpureus* nest or equivalent point before each survey was commenced. Surveys of ant assemblages were conducted between 9 am and 12 pm and 10 quadrats were observed each hour, each for 3 minutes. We recorded the abundance, identity and caste of each species passing through the quadrat. Initially all species were collected for identification in the laboratory. Once we were familiar with the ant fauna only small species were collected. When trails passed through a quadrat, we counted the number of ants of that species entering and leaving one side of the quadrat in 30 seconds and multiplied it by six to estimate the number passing through in 3 minutes, thus allowing the observer to keep track of other species.

We compared abundance of ants other than *I. purpureus*, species richness and abundance of species occurring at 50% or more of sites with and without *I. purpureus*, using ANOVA with survey as a repeated measure (Crowder and Hand 1990). No species of *Iridomyrmex*, other than *I. purpureus*, occurred at 50% of the sites, so 'other *Iridomyrmex*' (a group consisting of all *Iridomyrmex* species except *I. purpureus*) was used in the analysis instead. We used sequential Bonferroni corrections for multiple comparisons (Rice 1989) to determine the significance of each p-value such that α was set at 0.05. To exclude the possibility that environmental variation, unrelated to the presence of *I. purpureus*, was responsible for differences in the abundance of species, we tested for correlations of counts of 'other *Iridomyrmex*' and *Dolichoderus doriae* with those habitat variables that showed differences between sites with and without *I. purpureus*. We used the Pearson product-moment test (Sokal and Rohlf 1995) to test for correlations.

We compared ant assemblages at sites with and without *I. purpureus* using ANOSIM, with *I. purpureus* excluded from the data set. We used the Bray-Curtis similarity measure and five thousand permutations of the data. Ant abundance was fourth-root transformed to reduce the weighting of abundant species whilst preserving relative abundance information (Clarke 1993). Similarity percentages (SIMPER) analysis (Clarke and Gorley 2001) was also performed to determine which species contributed most when significant differences occurred.

Biomass was calculated using the power model from Gowing and Recher (1984) length-weight equations for the Formicidae. Ant length was measured for five prostrate specimens of each species as the distance between the tips of the mandibles and gaster. For polymorphic ants, biomass estimates were calculated for the different castes and a mean of a range of castes was taken for species that were continuously polymorphic. The

biomass of each species was then multiplied by its abundance per quadrat to determine the total biomass of ants. ANOVA, with survey as the repeated measure for each site, was used to compare the biomass of ants at sites with and without *I. purpureus*, both including and excluding *I. purpureus* from the data set. Data for total biomass were log₁₀ transformed and no significant interactions occurred.

Effects on resource use in two habitats

The effect of the presence of *I. purpureus* on seed removal by ant assemblages on rock and in vegetation was compared using seeds of *Acacia botrycephalus* at four sandstone outcrops with, and four without, *I. purpureus*. *A. botrycephalus* is a common plant in the Sydney region and its seeds are thus a natural food resource appropriate to this study. Myrmecochorous plants are 'unexpectedly numerous' in Australia, particularly in dry heath and sclerophyll vegetation (Berg 1975). Between 9 and 40% of all species in 0.1 ha plots in the nearby Kuring-gai Chase National Park, which is also set on Hawkesbury sandstone, were found to be adapted for ant dispersal (Rice and Westoby 1981). Seeds of *A. botrycephalus* are approximately 5 mm long with an elaiosome, which is lipid-rich and attractive to ants (Berg 1975). While not all ants collect seeds with elaiosomes, ants from at least ten ant genera present in the study area have previously been shown to remove seeds (Berg 1975). Non-fumigated seeds with intact elaiosomes were obtained from a commercial nursery. Seeds were contained within petri dishes with lids that protected them from predation by vertebrates. Three evenly spaced holes, each approximately 1 cm wide, were cut in the sides of each petri dish and 20 seeds of *A. botrycephalus* were placed inside. Eight petri dishes were placed in vegetation patches, and eight on rock at each site. All petri dishes were examined periodically for 6 hours, by which time most were empty. Numbers of seeds remaining and ants or arthropods present in, entering, or carrying seeds away from the tray were recorded at 15, 30, 60, 120, 240 and 360 min. Placement of seed trays commenced at 9:15 am on fine days and was staggered over 10 minutes, the time taken to sequentially count all seeds and ants in the 16 trays dispersed throughout the area.

We tested the effects of substrate type and the presence of *I. purpureus* using ANOVA at the time at which more than 50% of seeds had been removed from all sites. An average value for the number of seeds remaining in the eight seed trays at each site was used in the analysis, such that site was the replicate unit. Simple effects tests (Keppel 1982) were used to separate effects when interactions occurred. We used a t-test assuming unequal variances to compare the abundance of *I. purpureus* at seed trays on rock and in vegetation and

Table 1. Correlations (R-values and significance) a) amongst soil characteristics; and b) between soil characteristics and counts of those species that showed significant differences between sites with and without *I. purpureus*.

	Fire trail distance	Conductivity	% OM	% Sand	% Silt
a) Soil characteristic					
Conductivity	0.409				
% OM	0.171	0.013			
% Sand	0.219	0.259	-0.685**		
% Silt	-0.224	-0.232	0.725**	-0.982***	
b) Species					
<i>Dolichoderus doriae</i>	0.272	0.336	0.251	-0.163	0.193
'Other <i>Iridomyrmex</i> '	0.573*	0.288	0.408	-0.151	0.179

OM = Organic matter, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

ANOVA to determine the effects of substrate type and the presence of *I. purpureus* on the abundance of *R. metallica* (the only other ant common enough at seed trays to examine), and all ants other than *I. purpureus*, at seed trays. Only significant interactions are reported.

Association of *I. purpureus* with fire trails

We examined the association of *I. purpureus* with six fire trails: 2 in Marramarra National Park, 1 in Maroota State Forest and 3 in Kuring-gai Chase National Park between April 2001 and May 2002 (Fig. 1). Kuring-gai Chase is a national park set on Hawkesbury sandstone immediately south-east of Muogamarra Nature Reserve. Fire trails are dirt roads that provide access for service vehicles. Those used in this study are present in aerial photos from 1947, indicating that they have been present for greater than 50 years, and the trail through Maroota State Forest was created in the 1840s (Andrews et al. 1990). For the fire trail surveys, a starting point in low woodland or heath close to the end of the trail was chosen and an observer walked 1 km along the trail, counting nests of *I. purpureus* along the 3 m-wide trail, and up to 1.5 m from its edge. We also searched for nests in surrounding vegetation, commencing the search at greater than 20 m from the track and close to the point at which a fire trail survey was started. A 1-km transect through vegetation was measured using a Global Positioning System (GPS 12, Garmin, Kansas) and we searched for nests within 3 m either side of our path. Vegetation transects were slightly biased towards more open areas such as ridgetops, grassy areas and rock outcrops, as these areas were easier to traverse than thick scrub. This bias would have increased the chance that nests were found relative to a more randomly selected route. Meat ant nests are conspicuous due to their large size – most are larger than 1 m in diameter and occur in relatively unshaded areas, so all nests within 3 m of the vegetation transect were expected to be seen by the observer. We used a chi-square test (Siegel 1956) to determine if the number of nests found along fire trails was greater than expected relative to in vegetation.

Results

Comparison of habitat characteristics of areas with and without *I. purpureus*

Sites with *I. purpureus* were closer to fire trails ($t_{(14)} = -2.40$, $p = 0.031$) and contained a higher percentage of 'soil, gravel and moss cover' than sites without *I. purpureus* ($t_{(14)} = 2.40$, $p = 0.031$), however there were no differences for any other habitat characteristics ($p > 0.3$). There were no differences in the composition of dominant vegetation between sites with and without *I. purpureus* (ANOSIM: Global $R = 0.480$, $p = 0.960$).

There were no differences in soil pH ($F_{(1,14)} = 0.450$, $p = 0.513$) or clay content ($F_{(1,14)} = 2.323$, $p = 0.137$) between sites with and without *I. purpureus*, however conductivity was greater at sites without *I. purpureus* ($F_{(1,14)} = 5.389$, $p = 0.036$). Sand, silt and organic matter content were correlated with one-another (Table 1a) and sand content ($F_{(1,14)} = 5.614$, $p = 0.024$) was greater at sites with *I. purpureus*, while silt ($F_{(1,14)} = 5.073$, $p = 0.031$) and organic matter ($F_{(1,14)} = 8.143$, $p = 0.008$) content were greatest at sites without.

Effects of *I. purpureus* on composition and biomass of ant assemblages

There was no difference in species richness between sites that supported *I. purpureus* and those that did not. Abundance of other ant species, however, was greater at sites without *I. purpureus* (Table 2). Of the 12 species occurring at 50% or more of the sites, only 2 (other than *I. purpureus*) showed significant differences after sequential Bonferroni corrections (Rice 1989, Table 2). These were the dolichoderine ants, *Dolichoderus doriae* and 'other *Iridomyrmex*', both of which had significantly lower counts at sites with *I. purpureus*. There were no significant effects of survey or the interaction between survey and presence of *I. purpureus* so only results for the effect of *I. purpureus* are presented. Neither of the species found to differ in abundance between sites with and without *I. purpureus* showed any correlation with the habitat factors that also differed,

Table 2. Mean \pm se and analyses for ant abundance, species richness, and count of ant species occurring at 50% or more of the sites. Analyses are repeated measures ANOVA, and χ^2 for data where variances were non-homogeneous. No interactions or survey effects occurred. p values that were significant after sequential Bonferroni corrections (Rice 1989) are in bold type.

Variable/species	% sites	<i>I.p.</i> (mean \pm se)	No <i>I.p.</i> (mean \pm se)	$F_{(1,14)}$ (p)
Abundance of other ants ¹		97.2 \pm 13.1	145.7 \pm 12.6	7.07 (0.019)
Species richness		14.5 \pm 1.8	15.8 \pm 1.2	0.32 (0.584)
<i>Camponotus aeneopilosus</i>	56	3.3 \pm 1.5	5.1 \pm 1.9	0.59 (0.457)
<i>Meranoplus B</i>	56	1.5 \pm 0.8	3.6 \pm 1.1	2.30 (0.152)
<i>Ochetellus glaber</i>	75	3.6 \pm 1.1	4.8 \pm 1.1	0.52 (0.484)
Other <i>Iridomyrmex</i>	94	8.7 \pm 2.7	20.3 \pm 3.0	14.4 (0.002)
<i>Pheidole B</i>	50	1.8 \pm 0.8	1.9 \pm 1.0	0.01 (0.925)
<i>Polyrhachis ammon</i>	100	12.5 \pm 2.1	8.9 \pm 1.8	1.73 (0.209)
<i>Rhytidoponera metallica</i>	100	22.9 \pm 2.9	18.9 \pm 3.5	0.76 (0.397)
<i>Technomyrmex albipes</i>	63	3.8 \pm 1.7	1.1 \pm 0.6	2.05 (0.174)
<i>Tetramorium fuscipes</i>	50	6.6 \pm 3.2	3.0 \pm 1.6	1.02 (0.330)
				$\chi^2_{(1)}$
<i>Dolichoderus doriae</i>	50	0.0 \pm 0.0	5.5 \pm 1.2	12.9 (<0.001)
<i>Iridomyrmex purpureus</i>	56	47.0 \pm 3.4	0.1 \pm 0.1	12.3 (<0.001)
<i>Polyrhachis rowlandi</i>	94	6.5 \pm 2.1	2.0 \pm 0.5	5.02 (0.025)

¹4th root transformed at quadrat level.

except 'other *Iridomyrmex*', the count of which was positively correlated with distance from the closest fire trail (Table 1b).

Ant assemblages at sites with *I. purpureus* were significantly different from those at sites without in summer (Global R = 0.241, p = 0.013), and not quite so in autumn (Global R = 0.150, p = 0.070). SIMPER revealed that other *Iridomyrmex* (21%) contributed most to this difference in summer, followed by *Rhytidoponera metallica* (12%), *Tetramorium fuscipes* (6%), and *Polyrhachis ammon* (6%). Of these taxa, only 'other *Iridomyrmex*' was more common at sites without *I. purpureus*.

Where it was present, *I. purpureus* represented 83.9 \pm 6.0% (mean \pm se) and 81.8 \pm 3.7% of the ant biomass in summer and autumn surveys respectively, resulting in a significantly higher total biomass of ants at sites with *I. purpureus* ($F_{(1,14)} = 31.50$, p < 0.001) (Fig. 2) and during summer ($F_{(1,14)} = 5.73$, p = 0.031). However, the total biomass of ants other than *I. purpureus* at sites with *I. purpureus* was significantly lower ($F_{(1,14)} = 8.45$, p =

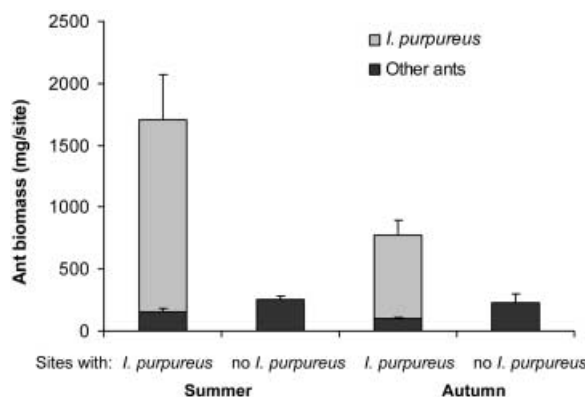


Fig. 2. Mean \pm se of biomass of ants at sites with and without *I. purpureus* during summer and autumn surveys.

0.011) and there were no differences between surveys ($F_{(1,14)} = 0.82$, p = 0.381).

Effects on resource use in two habitats

We analysed data for the seed removal experiment at 240 minutes after commencement, by which time 57% of the seeds had been removed from the petri dishes. Significantly more seeds were removed at sites with *I. purpureus* than those without, and from vegetation than rock (Fig. 3, Table 3). Removal of seeds from rock at sites without *I. purpureus* was substantially slower than from all other treatments, although the interaction between substrate and presence of *I. purpureus* was not significant.

Of the species observed at trays, individuals of *I. purpureus*, *Rhytidoponera metallica*, species of *Camponotus* and 'other *Iridomyrmex*' were all observed to carry seeds away, while smaller species of *Pheidole*, *Monomorium*, *Tetramorium*, *Meranoplus* and *Anonychomyrma* tended to chew on the seeds in situ. *Iridomyrmex purpureus* was found more often on rock than vegetation substrates ($t_{(1)} = 3.07$; p = 0.022). *R. metallica* was found significantly more often on the trays in vegetation ($F_{(1,1)} = 5.731$, p = 0.034) but showed no effect of the presence of *I. purpureus* ($F_{(1,1)} = 0.500$, p = 0.493). Other ants showed no effects of substrate ($F_{(1,1)} = 0.098$, p = 0.760) or the presence of *I. purpureus* ($F_{(1,1)} = 0.004$, p = 0.951).

Association of *I. purpureus* with fire trails

I. purpureus nests were more common along fire trails than in surrounding vegetation ($\chi^2_{(1)} = 14.67$, p < 0.001, Fig. 4).

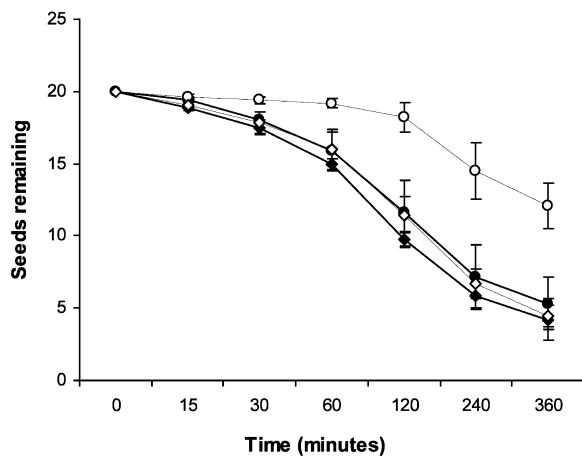


Fig. 3. Mean \pm se of *Acacia botrycephalus* seeds remaining over the period of the resource use experiment at sites with *I. purpureus*: on rock (●) and in vegetation (◆); and at sites without *I. purpureus*: on rock (○) and in vegetation (◇).

Discussion

We have shown that *Iridomyrmex purpureus* is associated with fire trails in the study area and it follows that anthropogenic disturbance has altered its distribution. The association of sites with *I. purpureus* with fire trails implies that habitat characteristics and, in turn, other ant species, may also be affected by proximity to fire trails, however there is little evidence that this is the case. Roads are known to influence soil chemistry, as well as the surrounding physical environment (Trombulak and Frissell 2000), however in this study there was no correlation between distance to fire trail and any of the habitat or soil variables and no correlation of habitat or soil variables with ant abundances. While the abundance of other species of *Iridomyrmex* was negatively correlated with distance to fire trail, this group requires warm, open habitats (Andersen 1990), such as those found on fire trails, so this relationship is most likely to be due to interactions with *I. purpureus*. Increased conductivity, organic matter and soil cover at sites with *I. purpureus* may be the result of mound-building by *I. purpureus* as the soil around large, long-lived ant nests has increased nutrient levels relative to unoccupied sites (Gentry and Stiritz 1972, Beattie and Culver 1983).

Table 3. Analysis of variance of the number of *Acacia botrycephalus* seeds remaining on different substrates at sites with and without *I. purpureus* after 240 minutes

Source	df	Sum of squares	F ratio	P-value
<i>I. purpureus</i>	1	66.5	6.31	0.027
Substrate	1	82.7	7.84	0.016
Substrate \times <i>I. purpureus</i>	1	42.7	4.05	0.067
Error	112	126.5		



Fig. 4. Mean \pm se of abundance of *I. purpureus* nests along fire trails and in surrounding vegetation. $N = 6 \times 1$ km transects along fire trails in Marramorra National Park, Maroota State Forest and Kuring-gai Chase National Park.

Iridomyrmex purpureus requires open areas with trees (Greaves 1971), a habitat likely to have been limited in the study area before European colonisation as there is no evidence of previous annual burning of the Sydney sandstone vegetation by Aboriginal people (Benson and Howell 1990, Benson and Redpath 1997). Fire trails provide a suitable open habitat for *I. purpureus* and may benefit this species through increased access to sunny nest sites. A relatively high nest temperature allows a high rate of worker production and may be a requirement for dominance of an ant community (Room 1971). Fire trails also provide an ideal route for colony expansion as *I. purpureus* colonies are founded most effectively through budding (Greaves and Hughes 1974). They remove barriers to movement into a new area and allow *I. purpureus*, and potentially more harmful species such as the recently introduced red imported fire ant, *Solenopsis invicta* (Stiles and Jones 1998), to penetrate protected habitats far from large-scale anthropogenic disturbances.

We would expect the invasion of an ant assemblage by a species as dominant in biomass and aggressive as *I. purpureus* to result in considerable changes in assemblage composition, however effects appear to be limited to species with similar ecological roles. Differences in assemblages in both surveys were due mainly to a reduced abundance of the dolichoderine ants 'other *Iridomyrmex*' and *Dolichoderus doriae* at sites with *I. purpureus*. Other species of *Iridomyrmex* behave similarly to *I. purpureus*, and belong to the 'Dominant Dolichoderinae', a group of highly abundant, active,

aggressive dolichoderine ants that are able to monopolize resources (Andersen 1990). Different species of *Iridomyrmex* have been shown to replace each other as dominants following experimental removal in regenerating coastal heathland (Haering and Fox 1987). Partial coexistence of *I. purpureus* and smaller species of *Iridomyrmex* may be due to partitioning in size of scavenged items as larger ants select larger food items (Fellers 1987). Effects of the dominant ant species on other levels of the hierarchy were less clear, as *Dolichoderus doriae* was the only other species affected by the presence of *I. purpureus*. *Dolichoderus* are restricted to cooler, wetter regions of southern Australia and may be poorly equipped for encounters with aggressive species of the more arid-adapted *Iridomyrmex* (Andersen 1990).

Iridomyrmex purpureus was clearly ecologically dominant at the study sites, particularly during summer, making up over 80% of the biomass of ants. In contrast, at sites without *I. purpureus*, no single species contributed more than 26% of the ant biomass. The total biomass of ants where *I. purpureus* occurred was six and three times greater in summer and autumn, respectively. An increase in the total biomass of an ant assemblage following invasion is well known (Hoffmann et al. 1999). Invasive exotic ants have been found to exist in abundances far greater than native ants, and the change in biomass at sites invaded by *I. purpureus* is comparable to that of those invaded by *Pheidole megacephala* (Hoffmann et al. 1999) and *Solenopsis invicta* (Porter and Savignano 1990). While release from parasitoids may contribute to the extraordinary abundance of invasive ants in invaded relative to native regions (Feener 1981, 2000, Orr and Seike 1998, Morrison 1999), it is unlikely to explain the range expansion of *I. purpureus* as it is native to this area of Australia.

Our study of resource use confirms that *I. purpureus* exploits resources in some habitats more efficiently than other species – seeds on rock substrates remained unused far longer when *I. purpureus* was absent. Large workers lose water more slowly than small workers (Lighton et al. 1994), so the large body mass of *I. purpureus* may allow it to forage longer than other *Iridomyrmex* at high temperatures on exposed outcrops. While *I. purpureus* was often observed in seed trays on rock, it was seen only rarely in the more complex vegetation, where *R. metallica* was most successful. High temperatures and open habitats favour behaviours such as high activity and rapid recruitment to resources that are necessary for dominance in ant communities (Andersen 1990). Differences between rock and vegetation habitats may thus reflect larger scale patterns in the distribution of *Iridomyrmex* between arid and non-arid areas.

The success of *I. purpureus* at seed trays did not appear to be to the detriment of other species, in contrast to a previous study that found the success of

other species at baits to be reduced in the presence of meat ants (Andersen and Patel 1994). Bait size, attractiveness and predictability may be important factors in the disparity between these studies. Dispersed food resources are known to dramatically reduce interspecific competition in geckoes (Petren and Case 1998), and the rate of intraspecific aggression between doves (Goldberg et al. 2001), relative to clumped food sources, and similar effects may be found for ants. Baits used in experiments are often richer than naturally available resources, and some ant species tend to forage more intensively for such resources (Floren and Linsenmair 2000), resulting in an increased rate of agonistic interactions between species (Ribas and Schoederer 2002). Aggressive domination of persistent honeydew resources may be a prerequisite for high abundance in ant species and thus important in dominance of the ant community (Way 1958, Room 1975). Seeds with elaiosomes may be a less valuable resource, so may not favour aggressive foraging behaviours.

The human-assisted movement of *I. purpureus* into new areas may have several negative consequences for the original fauna in addition to the effects on ant assemblages discussed above. *I. purpureus* is reported to assist the invasion of non-native plants with elaiosomes through myrmecochory (Smith 1989) and transports seeds considerably further than most ant species (Buckley 1982) and thus has the potential to alter seed dispersal dynamics around fire trails. Previous studies give some indication of effects of dominant ants on non-ant fauna. High abundance of the dominant wood ant, *Formica aquilonia*, has been shown to reduce the biomass of arthropod predators (Laakso and Setälä 2000) and to interfere with the foraging of great tits, *Parus major* (Haemig 1996), and in infested areas invasive ants reduce invertebrate abundance (Hoffmann et al. 1999), and species richness (Porter and Savignano 1990), considerably. Understanding the effect of a dominant ant thus requires examination of effects on populations beyond the ant community, particularly those species that provide resources for, prey on, or are preyed upon by the dominant species. As *I. purpureus* often forms trails several hundred metres long (Greenslade 1975, Greenaway 1981), its impact on resources may also extend the edge effects of a road a considerable distance into the surrounding habitat.

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