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Response of an open-forest ant community to invasion by the introduced ant, *Pheidole megacephala*

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Abstract The introduced tramp ant, *Pheidole megacephala*, is a well-known pest of urban areas and coastal dune ecosystems in eastern Australia. Until recently, establishment and spread of *P. megacephala* colonies has been regarded as likely only in disturbed areas. Here we describe the extent of an established colony of *P. megacephala* in a long undisturbed open forest near Maryborough in southeast Queensland and compare ant community structure with those of nearby uninfested sites. Tuna baiting revealed three distinct zones: (i) a zone totally dominated by *P. megacephala* (at least 10 ha) where few other ant ant species were detected; (ii) a zone where *P. megacephala* was absent and many other ant species were found; and (iii) a zone where opportunists (species of *Ochetellus* and *Paratrechina*) competed with *P. megacephala* at baits. Pitfall trapping over a 9-month period resulted in 12 species being recorded at the infested site, compared with a mean of 25 species recorded at adjoining uninfested forest. Over 94% of ants recorded in pitfalls at the infested site were *P. megacephala*. Most notably, *P. megacephala* had completely displaced dominant Dolichoderines (species of *Iridomyrmex*), subordinate Camponotini (species of *Camponotus*, *Opisthopsis* and *Polyrhachis*) and other species of *Pheidole* which are common at forest sites.

Key words: big-headed ant, biodiversity, biological invasion, disturbance, forest management, *Pheidole megacephala*.

INTRODUCTION

There is increasing awareness and concern about the potential loss of biodiversity resulting from forest management practices in Australia (Forest Use Working Group 1991; Commonwealth of Australia 1992a; Commonwealth of Australia 1992b). Loss of forest biodiversity may be caused by activities such as harvesting of timber products, prescribed burning practices and cattle production (Beattie *et al.* 1993). These are accepted management practices in *Corymbia variegata* (spotted gum) dominated forests of southeast Queensland. However, some elements of invertebrate biodiversity in these forests may also be under threat from the introduced tramp ant *Pheidole megacephala* (Fabricius).

Throughout the world, introductions of exotic ant species have been responsible for declines in diversity and abundance of native ant species as well as of other arthropods. The introduction and spread of *Solenopsis invicta* (the fire ant) has severely impacted on invertebrate biodiversity in southern USA. At a field station in central Texas, for example, the spread of *S. invicta* has been responsible for a reduction in native ant diversity of 70% and of native ant abundance by 90% (Porter & Savignano 1990). The diversity of other arthropods was also reduced by 35%.

On the island of Madeira, the introduction and subsequent spread of *P. megacephala* in the mid-nineteenth century, resulted in the extermination of a large fraction of the native ant fauna (Haskins & Haskins 1988). *Pheidole megacephala* was in turn completely displaced by *Linepithema humile* (the Argentine ant) about a century later (Haskins & Haskins 1965). Bermuda has a similar history of initial invasion by *P. megacephala* followed by *L. humile*, resulting in a mosaic of the two species (Lieberburg & Kranz 1975) and a severe reduction of indigenous ant diversity (Haskins & Haskins 1988). In Hawaii, *P. megacephala* has become entrenched at lower altitudes (Wilson & Taylor 1967) while *L. humile* dominates at altitudes >600 m a.s.l. (Reimer *et al.* 1990). Invasion by *P. megacephala* in particular has been associated with large reductions in ant diversity as well as of other arthropods, especially beetles (Reimer *et al.* 1990).

Pheidole megacephala (the big-headed ant), is native to southern Africa (Haskins & Haskins 1965; Wilson & Taylor 1967) and has been present in Australia for at least 100 years (Tryon 1912). It has become established along the eastern coastline of Australia (Nikitin 1979) as well as in urban areas of Darwin (Hoffmann 1998) and Perth (Majer 1994). It shares many known traits of tramp ant species including polygyny,

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dispersal through budding without a nuptial flight and uni-coloniality associated with a high level of inter-specific aggression (Jourdan 1997). Establishment of an independent colony requires an inseminated queen and at least 10 minor workers (Chang 1985). Almost always, such colonies are dispersed by anthropogenic vectors such as activities associated with human commerce (Wilson & Taylor 1967).

The above characteristics have made *P. megacephala* a serious pest of the tropics and subtropics (Lieberburg & Kranz 1975). In Australia, it has only been recorded in urban areas and coastal dune ecosystems disturbed by human impacts and associated with a depauperate indigenous ant fauna (Majer 1985). *Pheidole megacephala* was not thought to be capable of colonising undisturbed sites with a diverse invertebrate fauna (Greenslade 1972). However, once colonies are established in disturbed areas they may spread into nearby undisturbed vegetation (Heterick 1997), especially in the absence of *Iridomyrmex* spp. (Hoffmann & Hohenhaus 1998).

In August 1998, we identified an established *P. megacephala* colony within St Mary State Forest near Maryborough in southeast Queensland (25°35'S, 152°20'E). There were no obvious signs of recent disturbance at the site except for the presence of a log extraction track and there had been no harvesting of timber there for at least 30 years. St Mary State Forest is typical of the dry sclerophyllous vegetation of the region, dominated by *Corymbia variegata* (spotted gum), *Eucalyptus siderophloia* (grey ironbark) and *Eucalyptus fibrosa* (red ironbark), and covers approximately 12 000 ha. Here we describe the extent of this ant colony and its apparent effect on the original ant community.

METHODS

Ant community structure

Ant species richness and abundance were determined by pitfall trapping at the infested site and compared

Table 1. Relative abundance of ant functional groups, ant species richness and ant abundance at uninfested plots and the plot infested by *Pheidole megacephala* as determined by pitfall trapping at St Mary State Forest, Queensland

	Functional groups (% relative abundance)									Species	Species
	DD	SC	CCS	HCS	TCS	C	OPP	GM	SP	abundance	richness
Uninfested sites	44.62	3.09	4.75	8.63	0.11	2.16	16.95	19.62	0.08	155.85	35.33
SE	2.42	0.45	0.66	0.96	0.06	0.37	1.87	1.87	0.08	11.13	0.93
Infested site	0***	3^NS	0^NS	0^NS	1^NS	2^NS	15^NS	83***	0	185^NS	12**

DD, Dominant Dolichoderines; SC, Subordinate Camponotini; CCS, Cold Climate Specialists; HCS, Hot Climate Specialists; TCS, Tropical Climate Specialists; C, Cryptic Species; OPP, Opportunists; GM, Generalised Myrmicines; SP, Specialist Predators. $*P < 0.05$, $**P < 0.01$, $***P < 0.001$, NS, not significant.

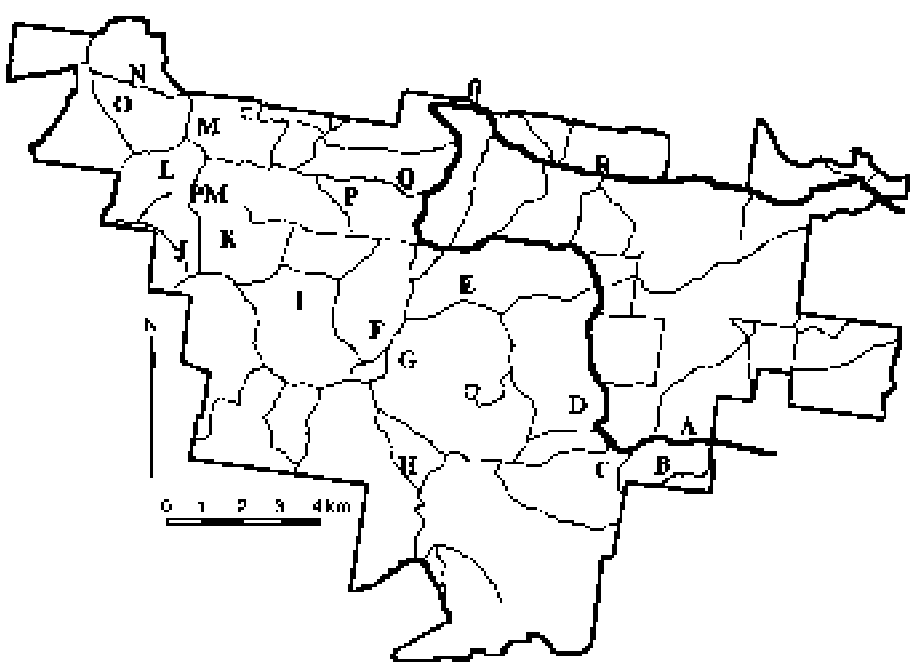

Fig. 1. Map of St Mary State Forest, Queensland, showing location of uninfested plots (A–R) and plot infested by *Pheidole megacephala* (PM).

with ant species richness and abundance obtained in the same manner from 18 nearby uninfested sites (Fig. 1). Nine pitfall traps, consisting of 18 mm internal diameter test tubes inserted into permanent polyvinyl chloride (PVC) sleeves (Majer 1978), were established at each site. Pitfall traps were opened for 4 days at each site in March, August and November 1997. Pitfall trapping is an accepted systematic means of comparing epigeal ant faunas at a number of sites, although it may under-sample cryptic and arboreal species (Andersen 1991). Few taxa could be confidently resolved to species level; instead, ants were sorted to numbered morphospecies using a verified reference collection established from other studies in the region (see Vanderwoude *et al.* 1997b). Abundances for each species in a pitfall trap were square-root transformed in order to normalize data for statistical analysis (Southwood 1978). The transformed abundances of the pitfall trap data were then summed to produce a single measure for each site. As temporal effects were not a focus of this analysis, the data from the three samples were also summed.

Ant specimens were allocated to functional groups according to their competitive interactions and habitat requirements (Andersen 1990). A functional group profile was prepared from the mean relative abundances of ants from nearby uninfested sites and this was compared with the *P. megacephala* site. An agglomerative dendogram was produced from a Bray–Curtis similarity matrix, using the unweighted pair group mean average (UPGMA) method in order to determine the degree of similarity between the uninfested sites and the *P. megacephala* site. Species richness, abundance, the relative abundance of functional groups and the number of functional groups at the infested site were

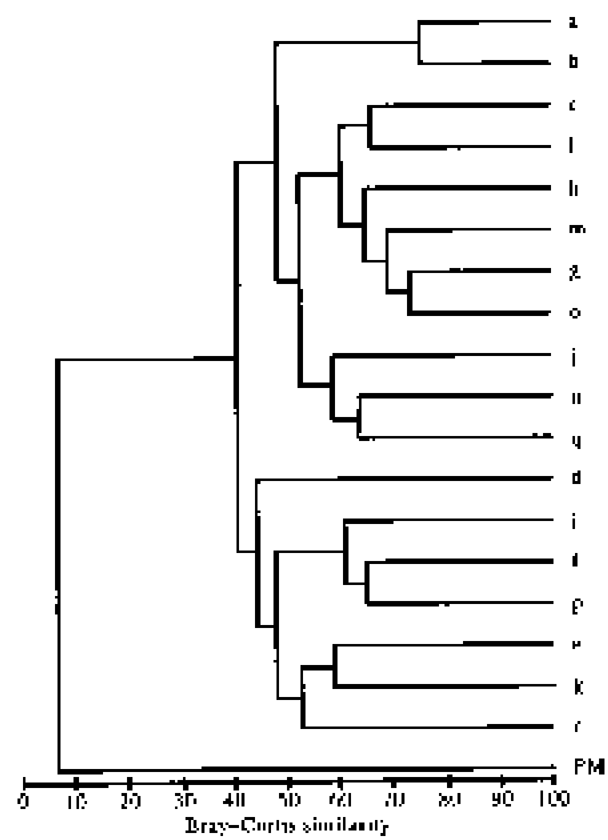

Fig. 2. Agglomerative dendogram showing the similarity of ant communities at the uninfested (a–r) plots and the plot infested with *Pheidole megacephala* (PM) at St Mary State Forest, Queensland.

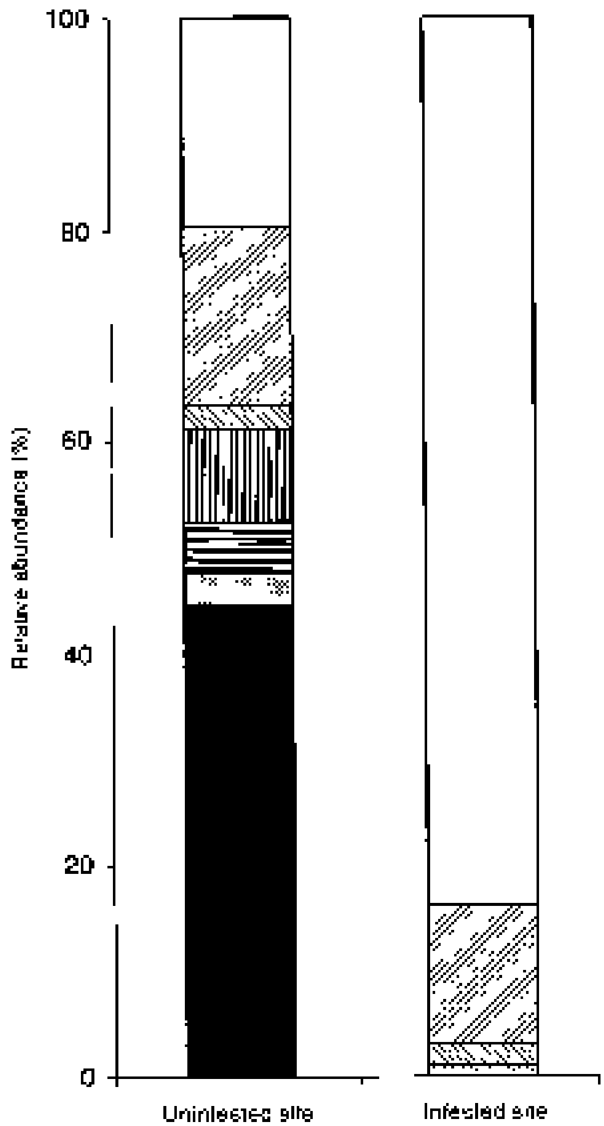

Fig. 3. Functional group profile the plot infested with *Pheidole megacephala* compared with profile of adjoining plots in uninfested forest at St Mary State Forest, Queensland. DD, Dominant Dolichoderines (■); SC, Subordinate Camponotini (□); CCS, Cold Climate Specialists (▤); HCS, Hot Climate Specialists (▥); TCS, Tropical Climate Specialists (▧); C, Cryptic Species (▨); OPP, Opportunists (▨); GM, Generalised Myrmicines (□); SP, Specialist Predators (▧).

compared with the same parameters from 18 uninfested sites using one-way analysis of variance (ANOVA).

The spatial extent of the colony was assessed using tuna baits in November 1998. At each bait site, litter was brushed away and about 10 g of tuna was placed on the ground during the warmest part of the day between 11.00 and 14.00 hours. Baits were inspected 1 h later. Initially, baits were spaced at 10-m intervals along two intersecting transects. It quickly became apparent that the colony was too large to be assessed in this fashion and baits were spaced at 25-m intervals along east–west transects and also at point locations. Abundance and identities of all ants within 10 cm of baits were recorded. Abundance for each ant species observed at a bait was scored as follows: 1 = 1 ant; 2 = 2–5 ants; 3 = 6–20 ants; 4 = 21–50 ants; 5 = >50 ants. Three observations where the total number of ant individuals observed at a bait was less than 10 were not included in the results.

Other site characteristics

Basal area and the number of trees per hectare were measured by establishing three 0.05-ha subplots at each site where the pitfall traps were located and measuring all stems >10 cm diameter at breast height over bark (d.b.h.o.b.). Shrub cover was calculated using the line intercept method by measuring the overhang of shrubs <10 cm d.b.h.o.b. along transects that bisected each 0.05-ha plot. Grass cover and the amount of bare ground were estimated using 1-m^2 quadrats placed over each pitfall. Grass cover and bare ground in each quadrat were scored using a modified Domin scale as follows: 1 = a single occurrence; 2 = two occurrences; 3 = scattered (≤5% cover); 4 = 6–15% cover; 5 = 16–25% cover; 6 = 26–33% cover; 7 = 34–50% cover; 8 = 51–75% cover, 9 = 76–99% cover and 10 = 100% cover. A cover index was obtained by summing the score for each quadrat. Soils were described from 10-cm-diameter auger samples.

RESULTS

Pitfall trapping

Over all sites, 84 species or morphospecies were collected. Over 94% of the ants collected in pitfall traps at the infested site were *P. megacephala*. A total of 12 ant species from four functional groups were recorded at the infested site, compared with a mean of 25 species from seven functional groups at the uninfested sites. Species richness ($F = 10.76$, $P < 0.01$), the relative abundance of Dominant Dolichoderines ($F = 17.86$, $P < 0.001$) and the number of functional groups recorded ($F = 19.00$, $P < 0.001$) were significantly lower at the infested site; and the relative abundance of Generalised Myrmicines (comprised mostly of *P. megacephala*) was significantly higher ($F = 61.37$, $P < 0.001$) (Table 1). Ant abundance at the infested site was not significantly different to that at the uninfested sites. An agglomerative dendogram showing the relationship between infested and uninfested sites (Fig. 2) shows that the uninfested sites had a similarity to each other of >40%, while the *P. megacephala* site had a Bray–Curtis similarity to all other sites of less than 10%. The functional group profile of uninfested sites is compared with the *P. megacephala* site in Fig. 3.

Table 2. Number of ant species and percentage relative abundance of Opportunists, *Pheidole megacephala* and other ant species recorded at tuna baits in the *P. megacephala* zone, the intermediate zone and uninfested forest at St Mary State Forest, Queensland

Zone	n	No. of species	*P. megacephala*	Opportunists	Others
P. megacephala only	76	1	100	0	0
Intermediate zone	43	12	58	30	12
No *P. megacephala*	28	20	0	42	58

Table 3. Estimated basal area, stocking, per cent shrub cover, grass cover index and bare ground index at the plot infested with *Pheidole megacephala* and 18 uninfested sites at St Mary State Forest, Queensland

	Basal area (m^2/ha)	Stocking (stems/ha)	Shrub cover (%)	Grass cover index	Bare ground index
Uninfested sites	11.48	237.00	30.94	46.39	32.4
SE	0.89	21.04	4.81	3.07	2.15
Infested site	17.26^{NS}	186.67^{NS}	20.65^{NS}	48.00^{NS}	31.00^{NS}

*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$. NS, not significant.

Tuna baiting

Baiting revealed three distinct zones (Table 2, Fig. 4). An area of at least 10 ha was completely dominated by *P. megacephala*, as shown by the large numbers of *P. megacephala* workers recorded at baits in less than 1 h. In this zone, an abundance score of 5 (>50 ants) was recorded at 86% of baits and an abundance score of 4 (21–50 ants) was recorded at 14% of baits. The second zone was characterized by the complete absence of *P. megacephala*. In this zone a variety of species was observed at baits. Species turnover was high, with different ant species often dominating at adjacent baits. In an area between the *P. megacephala* colony and the uninfested areas of the forest, and also at small areas within the colony boundary, were intermediate zones where *P. megacephala* and Opportunists competed for the same resources. Opportunist ant species such as *Ochetellus* (*glaber*, and sp. B), *Paratrechina* (*minutum* gp., *vaga* gp. and *obscura* gp.) and *Rhytidoponera 'metallica'* were observed feeding at the same baits as *P. megacephala*.

Other site characteristics

Basal area (F = 2.25), trees per hectare (F = 0.30), shrub cover (F = 0.24), grass cover (F = 0.01) and amount of bare ground (F = 0.02) at the infested site were not significantly different to those at the uninfested sites (Table 3). Soils generally exhibited a strong texture contrast between A (20–30% clay) and B (>45% clay) horizons and B horizons were either moderately or strongly acidic. One site (r) was classified as a sodosol. Nine sites, including the infested site, possessed moderately acidic B horizons and were classified as red or brown chromosols. The nine remaining sites possessed strongly acidic B horizons and were classified as grey, red or brown kurosols (Isbell 1996).

DISCUSSION

Dominant Dolichoderines (species of *Iridomyrmex*) and Subordinate Camponotini (e.g. species of *Camponotus*, *Polyrhachis* and *Opisthopsis*) control the structure and dynamics of open forest ant communities in southeast Queensland through their aggressive behaviour and monopolization of resources (Andersen 1995). When the abundance of these groups is reduced (by decreased insolation at ground level, for example), Opportunists (e.g. species of *Rhytidoponera*, *Paratrechina*, *Ochetellus* and *Tetramorium*) become dominant (Vanderwoude *et al.* 1997b).

Until now, it was thought that *P. megacephala* would not establish or persist in undisturbed environments with high ant species-richness, nor displace dominant Dolichoderines. Heterick (1997) reported the spread of *P. megacephala* from a highly disturbed lawn area into the adjoining forest edge in urban Mount Coot-tha (Brisbane, Queensland). However, Dominant Dolichoderines were still recorded in the same plots as *P. megacephala*. Hoffmann (1998) argued that *P. megacephala* did not spread into open savannah in northern Australia due to desiccation and competition with *Iridomyrmex*. However, the evidence presented here suggests strongly that *P. megacephala* have been able to spread substantially into a long-undisturbed forest and displace Dominant Dolichoderines at St Mary State Forest. At least 30% and as many as 65% of ants recorded in pitfalls at uninfested sites were Dominant Dolichoderines, and Subordinate Camponotini were recorded at 17 of the 18 uninfested sites. The complete absence of Dominant Dolichoderines at the infested site is highly atypical. *Iridomyrmex* is the dominant ant genus in open forests of southeast Queensland. Ants from this group are favoured by high insolation but are still recorded in spotted gum forest even after subcanopy closure caused by the long-term absence of fire (Vanderwoude *et al.* 1997a). Although the mechanism of invasion by *P. megacephala* into this forested site remains undetermined, it may well be

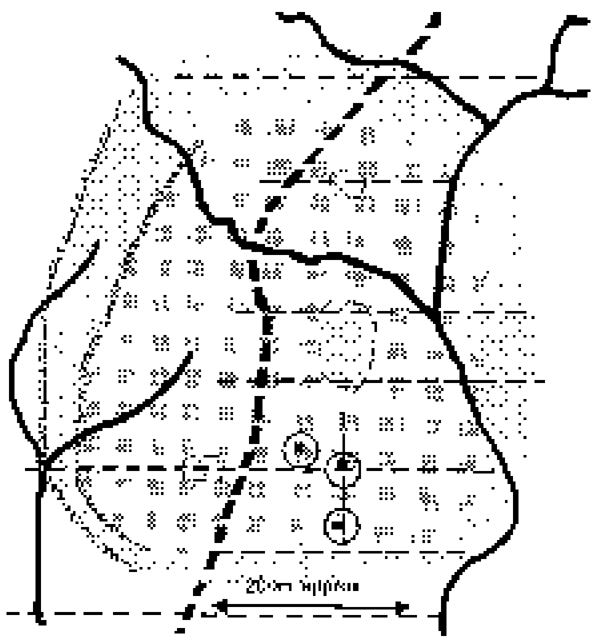

Fig. 4. Diagram of infested site at St Mary State Forest, Queensland, showing the approximate area occupied by *Pheidole megacephala* (dark shading), the intermediate zone occupied by *P. megacephala* and Opportunists (light shading), the uninfested surrounding area (unshaded), transects (dashed lines), 0.05-ha sub plots (circles), track (heavy dashed line) and gullies (heavy solid line). Zone boundaries marked with stippling are estimates.

associated with some disturbance that is now not apparent.

Only Opportunists demonstrated coexistence with *P. megacephala*. Opportunists were the most abundant ants found in pitfall traps after *P. megacephala* at the infested site. At tuna baits in the intermediate zone, they were observed actively competing for resources. The absence of Dominant Dolichoderines and Subordinate Camponotini, and the reduction in abundance of indigenous Generalised Myrmicines in this zone may have provided conditions suitable for increases in abundance of Opportunist species. However, the relative abundance of Opportunists at the infested site was not significantly different from the uninfested sites and this suggests that *P. megacephala* has assumed, at least partly, the functional role of Dominant Dolichoderines and Subordinate Camponotini by controlling the abundance of Opportunists. Functional diversity was also reduced at the infested site. No Subordinate Camponotini, Cold Climate Specialists, Hot Climate Specialists, or Specialised Predators were recorded at all, suggesting that *P. megacephala* displaced them also.

No site variable we measured appeared to be correlated with the differences in ant community structure at the infested site. Basal area was high compared with that in uninfested sites and the number of trees per hectare was low, but not significantly so. In fact, these characteristics reflect the long period (>30 years) since timber was selectively harvested from this compartment. Shrub cover, grass cover and the amount of bare ground were all similar to the uninfested sites and therefore were not factors implicated in the changes we observed. This study demonstrates that *P. megacephala* invasions in open forests of southeast Queensland have the capacity to reduce forest invertebrate biodiversity dramatically by altering ant community dynamics. The complete absence of Dominant Dolichoderines, Subordinate Camponotini, Hot Climate Specialists, Cold Climate Specialists, and Specialized Predators at the infested site indicates that 'typical' ant community structure and dynamics no longer exist there. In the light of the dispersal strategy of *P. megacephala* (budding of newly inseminated queens to the parent colony), it is likely that this colony will continue to spread, further altering ant community structure.

Vectors for the introduction of *P. megacephala* to new locations are invariably anthropogenic (Hoffmann & Hohenhaus 1998). Although the means of introduction in this case is unclear, several forest management activities have the potential to result in future introductions. Among the most obvious of these activities are timber harvesting, road construction and the transport and feeding of cattle. These activities may involve the movement of machinery into forests from areas already infested by *P. megacephala*. Such machinery may harbor small *P. megacephala* colonies capable of initiating new infestations.

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REFERENCES

Andersen A. N. (1990) The use of ant communities to evaluate change in Australian terrestrial ecosystems: a review and a recipe. *Proc. Ecol. Soc. Aust.* 16, 347–57.

Andersen A. N. (1991) Sampling communities of ground foraging ants: Pitfall catches compared with quadrat counts in an Australian tropical savanna. *Aust. J. Ecol.* 16, 273–9.

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. *J. Biogeogr.* 22, 15–29.

Beattie A., Auld B., Greenslade P. *et al.* (1992) Changes in Australian terrestrial biodiversity since European settlement and into the future. In: *Australia's Renewable Resources: Sustainability and Global Change* International Geosphere-Biosphere Program Australia Planning Workshop, Bureau of Rural Resources Proceedings no. 14 (eds R. M. Gifford & M. M. Barson) pp. 189–202. Australian Government Printing Service, Canberra.

Chang V. C. S. (1985) Colony revival, and notes on rearing and life history of the big-headed ant. *Proc. Hawaii Entomol. Soc.* 25, 53–8.

Commonwealth of Australia (1992a) *National Forest Policy Statement. A New Focus for Australia's Forests.* Commonwealth of Australia, Canberra.

Commonwealth of Australia (1992b) *National Strategy for Ecologically Sustainable Development.* Commonwealth of Australia, Canberra.

Forest Use Working Group (1991) *Final Report – Forest Use.* Report of the Forest Use Working Group, Ecologically Sustainable Working Groups. Australian Government Printing Service, Canberra.

Greenslade P. J. M. (1972) Comparative ecology of four tropical ant species. *Insect. Soc.* 19, 195–212.

Haskins C. P. & Haskins E. F. (1965) *Pheidole megacephala* and *Iridomyrmex humilis* in Bermuda – equilibrium or slow replacement? *Ecology* 46, 736–40.

Haskins C. P. & Haskins E. F. (1988) Final observations on *Pheidole megacephala* and *Iridomyrmex humilis* in Bermuda. *Psyche* 95, 177–84.

Heterick B. (1997) The interaction between the coastal brown ant, *Pheidole megacephala* (Fabricius), and other invertebrate fauna of Mt Coot-tha (Brisbane, Australia). *Aust. J. Ecol.* 22, 218–21.

Hoffmann B. D. & Hohenhaus R. N. (1998) Big-headed ants: Tiny marauder threatens northern ecosystems. *Wildl. Aust.* Winter, 13–5.

Hoffmann B. D. (1998) The big-headed ant *Pheidole megacephala*: a new threat to monsoonal northwestern Australia. *Pac. Conserv. Biol.* 4, 250–5.

Isbell R. F. (1996) *The Australian Soil Classification.* CSIRO Publishing, Melbourne.

Jourdan H. (1997) Threats on Pacific islands: the spread of the Tramp Ant *Wasmannia auropunctata* (Hymenoptera: Formicidae). *Pac. Conserv. Biol.* 3, 61–4.

Lieberburg I. & Kranz P. M. (1975) Bermudian ants revisited: the status and interaction of *Pheidole megacephala* and *Iridomyrmex humilis*. *Ecology* 56, 473–8.

Majer J. D. (1978) An improved pitfall trap for sampling ants and other epigaeic invertebrates. *J. Aust. Entomol. Soc.* 17, 261–2.

Majer J. D. (1985) Recolonisation by ants of rehabilitated mineral sand mines on North Stradbroke Island, Queensland, with particular reference to seed removal. *Aust. J. Ecol.* 10, 31–48.

Majer J. D. (1994) Spread of argentine ants (*Linepithema humile*), with special reference to Western Australia. In: *Exotic Ants (Biology, Impact, and Control of Introduced Species)* (ed. D. F. Williams) pp. 163–73. Westview Press, Oxford.

Nikitin M. I. (1979) Geographical distribution of three species of small ants common in New South Wales. *Aust. Entomol. Mag.* 5, 101–2.

Porter S. D. & Savignano D. A. (1990) Invasion of polygyne fire ants decimates native ants and disrupts arthropod community. *Ecology* 71, 2095–106.

Reimer N., Beardsley J. W. & Jahn G. (1990) Pest ants in the Hawaiian islands. In: *Applied Myrmecology: a World Perspective* (eds R. K. Vander Meer, K. Jaffe & A. Cedeno) pp. 40–50. Westview Press, Oxford.

Southwood T. R. E. (1978) *Ecological Methods with Particular Reference to Insect Populations.* Chapman & Hall, London.

Tryon H. (1912) The naturalization of an exotic ant (*Pheidole megacephala*, Fab.). *Qld. Nat.* 9, 225–9.

Vanderwoude C., Andersen A. N. & House A. P. N. (1997a) Ant communities as bioindicators in relation to fire management of spotted gum (*Eucalyptus maculata* Hook.) forests in south-east Queensland. *Mem. Mus. Vic.* 56, 671–5.

Vanderwoude C., Andersen A. N. & House A. P. N. (1997b) Community organisation, biogeography and seasonality of ants in an open forest of south-eastern Queensland. *Aust. J. Zool.* 45, 523–37.

Wilson E. O. & Taylor R. W. (1967) The ants of Polynesia. *Pac. Insects Monogr.* 14, 1–109.