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## Impact of an introduced ant on native rain forest invertebrates: *Pheidole megacephala* in monsoonal Australia

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**Abstract** *Pheidole megacephala* is an exotic ant species that has severely affected native invertebrate biodiversity throughout the tropics. Its impacts have been documented extensively in relatively depauperate invertebrate communities, but not in species-rich habitats such as tropical rain forests. Here we describe the local distribution of *P. megacephala* and its impacts on native invertebrate assemblages in and around a rain forest patch at Howard Springs, in Australia's monsoonal tropics. *P. megacephala* was found to be confined to a single area of approximately 25 ha, with its distribution centered on drainage lines and the rain forest. Significant but weak correlations were found between its abundance and vegetative canopy cover (positive) and distance from the rain forest (negative). In the most heavily infested area within the rain forest, the abundance of *P. megacephala* was 37–110 times that of total native ant abundance found within uninfested plots, as measured by pitfall traps. The abundance and richness of native ants and other invertebrates were significantly reduced in litter samples, pitfall catches and foliage beats where *P. megacephala* was present, inversely relative to the abundance of *P. megacephala*. Only two individuals of a single native ant species were found within the most infested plot, with native ant richness being reduced to

about half in the least infested plot. The most persistent functional groups of native ants in infested plots were Cryptic species, which forage primarily within soil and leaf litter, and Opportunists, which exhibit highly generalised foraging behaviour. The highest abundance of *P. megacephala* corresponded with a 42–85% decrease in the abundance of other native invertebrates. Insect larvae were totally absent from foliage beats collected at the most heavily infested plot. *P. megacephala* was found overall to be expanding its range, averaging 12 m range expansion in the dry season and contracting 7 m in the wet season. It is able to spread into surrounding savanna habitats by occupying relatively sheltered microsites, such as beneath logs and at the bases of trees. However, it is unlikely to attain high population densities in open savanna habitats because of its relative intolerance of desiccation, and the prevalence of behaviourally dominant native ant species. Howard Springs is currently the only rain forest patch in monsoonal Australia known to be infested by *P. megacephala*, but clearly this ant is a serious potential threat to the region's rain forest invertebrate fauna.

**Key words** Ants · Biodiversity · Competition · Invasion · Monsoonal Australia

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### Introduction

Ecosystem invasion by exotic species represents a major threat to biodiversity (Williamson 1997). Introduced ants are notorious pests of human settlement throughout the world, but some species are capable of invading surrounding areas, where they seriously affect both native biodiversity and agricultural production (Vander Meer et al. 1990; Williams 1994; Jourdan 1997). The imported fire ant *Solenopsis invicta*, for example, has decimated the native ant fauna in infested areas of the southeastern United States, reducing native ant abundance by 90% and species richness by 70%, and has had a serious impact on other ground-active invertebrates

(Porter and Savignano 1990). The Argentine ant *Linepithema humile* (formerly *Iridomyrmex humilis*) has displaced native ants in Cape fynbos shrublands of South Africa, disrupting ant-plant mutualisms and threatening many rare, endemic native plants (Bond and Slingsby 1984).

One of the most threatening exotic ant species is *Pheidole megacephala*. It has achieved a pantropical distribution (Wilson and Taylor 1967), where its ability to displace native ant species (Haskins and Haskins 1965; Lieberburg et al. 1975; Majer 1985; Heterick 1997), and to interfere with agricultural production (Bach 1991; Jahn and Beardsley 1994), is well documented. Since its introduction into North Queensland about a century ago (Tryon 1912), its range within Australia has expanded to include sub-tropical southern Queensland (Majer 1985; Heterick 1997), warm-temperate coastal New South Wales (Nikitin 1979; Fox and Fox 1982), the mediterranean Perth region of Western Australia (Majer 1994), and the Darwin region of the Top End of the Northern Territory in monsoonal northwestern Australia (Reichel and Andersen 1996).

Most studies of the ecological impacts of *P. megacephala* have been conducted in relatively depauperate communities, such as on oceanic islands (Haskins and Haskins 1965; Lieberburg et al. 1975) and in agroecosystems (Bach 1991; Jahn and Beardsley 1994). There have been few studies in species-rich habitats such as tropical rain forests. Furthermore, most relevant studies have been conducted in humid climates (which *P. megacephala* favours), and little is known of the impact of *P. megacephala* in the seasonally dry tropics.

In the Northern Territory, *P. megacephala* has infested a patch of rain forest at Howard Springs, 35 km east of Darwin (Reichel and Andersen 1996). Throughout Australia's monsoonal tropics, rain forest occurs as small (typically 1–10 ha), isolated patches embedded in a vast savanna landscape, and is usually associated with areas of permanent moisture or sheltered topography (McKenzie et al. 1991; Russell-Smith 1991). Virtually all reptile and mammal species occurring in these rain forest patches are habitat generalists with wide distributions (Menkhorst and Woinarski 1992; Gambold and Woinarski 1993), and only a few of the birds can be considered rain forest specialists (Woinarski 1993). The rain forest ant fauna, however, is of considerable biogeographic interest (Andersen 1992b; Reichel and Andersen 1996). More than a quarter of all ant species occurring in Northern Territory rain forests can be considered rain forest specialists, most of which are otherwise restricted to the humid rain forests of northern Queensland and New Guinea, and some represent the only Australian occurrences of South-East Asian species (Reichel and Andersen 1996).

Rain forest ants are, therefore, a significant component of biodiversity in the Northern Territory, and their displacement by *P. megacephala* would represent a serious conservation threat. *P. megacephala* is known to have been present at Howard Springs for at least

15 years (A.N. Andersen, unpublished work), but nothing is known of its ecological impact. Here we investigate its distribution, environmental relationships, and impacts on invertebrate biodiversity at Howard Springs. Our aims are to: (1) document its local distribution and environmental relationships; (2) assess its impacts on native ants and other invertebrates; and (3) determine its rate of spread.

## Methods

### Study area

The study was conducted around Howard Springs Nature Park and Howard Springs Hunting Reserve, approximately 35 km east of Darwin in Australia's Northern Territory. The Nature Park covers 283 ha and contains a spring-fed, permanent, artificial pool surrounded by rain forest. The Hunting Reserve of 1605 ha adjoins the northern boundary of the Nature Park.

The regional climate is highly seasonal, with 90% of the approximately 1500 mm annual rainfall falling between November and March (wet season), with June to September (dry season) being virtually rainless (Taylor and Tulloch 1985). Mean daily temperatures vary from 25 to 33°C during the wet season and 17 to 30°C during the dry season. Mean relative humidity ranges from 72 to 83% in the wet season and 32 to 62% in the dry season (Bureau of Meteorology).

A permanent pool at Howard Springs was constructed about 50 years ago, and much of its northern end is surrounded by lawns. Fire has been excluded from most of the Nature Park for over a decade and the resulting vegetation appears more dense with greater mid-storey development than surrounding areas, which is typical of long-term fire exclusion (Andersen 1996). It is not known exactly how or when *P. megacephala* arrived at the Park.

### Sampling

#### Distribution

The local distribution of *P. megacephala* was determined from observations at 317 stations arranged in 67 transects, initiated from the rain forest boundary. Transects were spaced by 40 m, and extended into the surrounding vegetation until *P. megacephala* was no longer present, and within the rain forest to the creek line. Transects on opposite sides of the creek were treated separately. Sample stations along transects were 10 m apart, with closer intervals on vegetation boundaries and on the limit of *P. megacephala* distribution.

The abundance of *P. megacephala* and native ants was determined at four tuna baits, each 1 table-spoon (15 ml) in size, located at the corners of a 1 m × 1 m quadrat, at each baiting station. All ants present were counted after 30 min. The abundance of *P. megacephala* at baits often exceeded 500 individuals so counts were scored as abundance classes (Andersen 1992a): 1, 1 ant; 2, 2–5 ants; 3, 6–20 ants; 4, 21–50 ants; 5, 51–100 ants; 6, 101–200 ants; 7, 201–500 ants; and 8, > 500 ants. Therefore, the sum of all four baits at each station gave a station abundance value between 0 and 32. Baiting was conducted during the coolest parts of the day, between 0600 and 1000 hours, and 1600 and 1900 hours.

Measurements of projective foliage cover, a key determinant of microscale variation in temperature and humidity, were taken using a hand-held spherical densitometer at each station. Readings were taken in north, east, south and west orientations and averaged. Abundance scores of *P. megacephala* were correlated with average projective foliage cover, as well as with distance away from the rain forest boundary (stations outside the rain forest only).

To determine if the infestation consisted of one or multiple colonies, ten collections of ten ants were made around the extremities of the population's distribution and relocated to opposing ends. The collected ants were released and observed for 2 min to see if any aggressive interactions occurred with local foragers. If not, the ants were considered to belong to the same colony.

### Impacts

Studies of *P. megacephala* impacts on native invertebrates (arthropods > 1 mm) were restricted to the rain forest. The native fauna of the infested area prior to invasion is not known, so three plots (U1–3) were selected from nearby uninfested areas to serve as controls, to compare with three plots with *P. megacephala* present (I1–3).

Three sampling techniques were used: pitfall traps (collecting epigeic taxa); foliage beats (arboreal taxa); and litter samples (cryptobiotic taxa). All three methods were used to collect ants, but other invertebrates were only sufficiently abundant for statistical analysis in the last two. Pitfall traps were small (42 mm internal diameter) plastic containers, three-quarters filled with 70% ethanol as a preservative. Twenty traps were established at each plot, arranged in two parallel transects of ten traps, with 2 m spacing between traps and 20 m between transects, and operated for 48 h in May 1996. Ten foliage samples were collected by placing a 2 m × 2 m white sheet on the ground and beating the foliage above ten times. Ten litter samples of approximately 2 l of surface soil and litter were collected and placed in Tullgren funnels for a week to extract the invertebrates.

Ants were sorted to species level, and species abundances in each traps were scored according to the nine point scale described previously. Due to the poor state of taxonomy of Australian ants, species that could not be named were assigned number codes following those already published (e.g. Andersen 1991a, 1991b, 1992a) or letter codes that apply to this study only. A full collection of voucher specimens is held at the CSIRO Tropical Ecosystems Research Centre in Darwin. Ants were also classified into continental-scale functional groups in relation to environmental stress and disturbance, as has commonly been done in studies of Australian ant communities (Andersen 1995). The functional groups are: dominant Dolichoderinae; subordinate Camponotini; climate specialists; cryptic species; opportunists; generalised Myrmicinae; and specialised predators. Other invertebrates were sorted to ordinal level only.

The abundance of *P. megacephala* in the three infested plots in foliage beats and litter samples was compared using one-way ANOVAs. Abundance in pitfall traps was analysed by a Kruskal-Wallis ANOVA because of lack of homogeneity. Analyses of native ant and other invertebrate abundance and richness were performed using two-way ANOVAs with plots nested as infested or uninfested.

### Rate of spread

Unlike most ants, *P. megacephala* does not have a nuptial flight, with dispersal occurring by the migration of a queen and a small group of workers to generally within about 1 m of the parent colony (Hölldobler and Wilson 1990). On a local scale, this dispersal method limits the rate of spread of *P. megacephala* and provides the opportunity for detailed measurement of spread.

Four sites were selected to investigate the rate of spread of *P. megacephala*. Two were located in vegetation along the creek line, one in evergreen monsoonal rain forest (RF) and the other in riparian vegetation (RV). The others were in surrounding, drier vegetation types of semi-evergreen dry vine-thicket (VT) and open shrubland (OS).

Parallel pairs of transects were used at each site, with the transects spaced 20 m apart in VT and OS, and on either side of the creek in RF and RV. Transects were positioned so that their

mid-points represented the initial limit of the distribution of *P. megacephala*. Sample stations were established every 2 m along transects, with an initial ten stations per transect. The length of each transect, and hence the number of stations, was increased where required depending on changes in *P. megacephala* distribution.

The abundance of *P. megacephala* and native ant species was quantified at each station using four tuna baits (as described previously) and one pitfall trap per station. Baiting was performed 24 h after pitfall trap removal to minimise disturbance, which might artificially increase ant abundance (Greenslade 1973). Baits were also removed after sampling so as not to aid the spread of *P. megacephala*. Transects were sampled once a month from April to August 1996 (dry season) using both collection methods, and then for tuna baits only from December 1996 to April 1997 (wet season) and August to September 1997 (dry season).

The second transects of RF and RV, in July and August 1996, respectively, were excluded from analysis because *P. megacephala* increased its range around (instead of along) them, giving a misleading measure of spread. Flooding prevented sampling at both RV transects and transect 1 of RF during the late wet season and they were removed from analysis during these times.

## Results

### Distribution

*P. megacephala* was found to occupy approximately 25 ha, predominantly along drainage lines. Greatest abundance occurred within rain forest and decreased into drier vegetation types. Three abundance levels of *P. megacephala* can be recognised in the rain forest (Fig. 1), being greatest at the southern end (I1), and differing significantly (Kruskal Wallis ANOVA,  $H = 42.21$ ,  $df = 2$ ,  $P < 0.001$  for pitfall traps; one-way ANOVA,  $F = 28.4$ ,  $F = 60.7$ ,  $df = 2$ ,  $19$ ,  $P < 0.001$  for foliage beats and litter samples respectively). Plot differences in abundance were particularly pronounced in pitfall traps, with the average number of individuals per trap at I1 exceeding 1100, compared to less than 100 for the two less-infested plots. This abundance at I1 corresponded to a 37- to 110 fold increase compared with total native ant abundance in pitfall traps at uninfested plots. The abundance of *P. megacephala* had a significant, but relatively weak, positive relationship with canopy cover ( $r^2 = 0.17$ ,  $P < 0.001$ ) and a significant but weak negative relationship with distance from the rain forest edge ( $r^2 = 0.08$ ,  $P < 0.001$ ). No aggressive interactions were observed between transported and local workers.

### Impacts on native ants

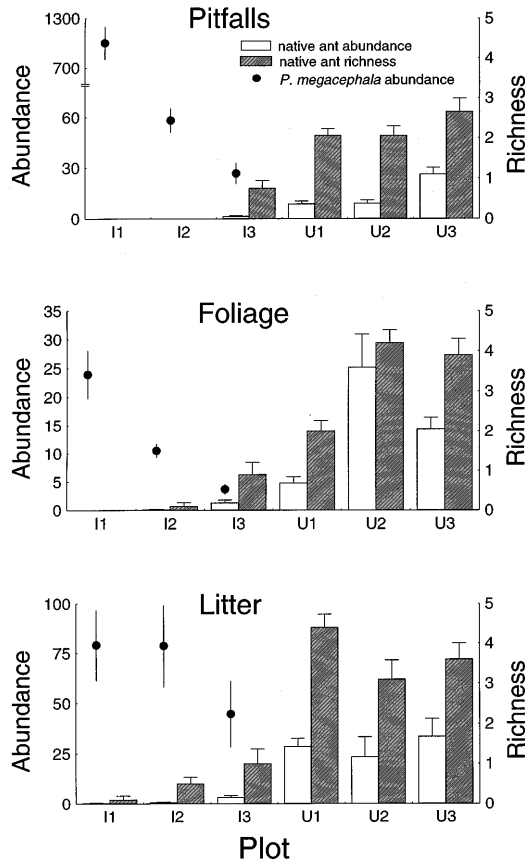
A total of 149 ant species from 40 genera were recorded during the study. Eight other introduced species, *Monomorium destructor*, *M. floricola*, *M. pharaonis*, *Tapinoma melanocephalum*, *Paratrechina longicornis*, *Solenopsis geminata*, *Tetramorium bicarinatum* and *T. simillimum* were recorded in addition to *P. megacephala*. None of these additional introduced species were found co-occurring with *P. megacephala*. Of the native species, the richest genera were *Pheidole* (16 spe-

cies), *Polyrhachis* (16), *Monomorium* (11), *Iridomyrmex* (10), *Rhytidoponera* (8), and *Meranoplus* (5).

Native ant abundance and richness were consistently higher in uninfested plots compared with infested plots (Fig. 1; Table 1). Within infested plots, native ant abundance and richness were negatively correlated with *P. megacephala* abundance (Table 2), except for species richness in litter samples.

Given that plots I1 and I3 were the most and least infested plots respectively, and that *P. megacephala* is

currently spreading in a northerly direction (see section on Rate of spread), it is most likely that plots I1–3 represent successional stages of invasion from oldest to most recent respectively. Assuming this, patterns of displacement of the native ant fauna following invasion are evident. At low levels of infestation (I3), all functional groups of native species remain present, although highly reduced in species richness (Fig. 2). The first



**Fig. 1** Mean (+SE) *Pheidole megacephala* abundance and native ant abundance and richness per sample within the rain forest as found by 20 pitfall traps, 10 foliage beats and 10 litter samples at infested (I1–3) and uninfested plots (U1–3)

**Table 1** Results of two-way ANOVAs of native ant abundance and richness between three infested and three uninfested plots within the rain forest as determined by different collection methods (data in Figs. 4, 5). *L* and *Q* indicate  $\log_{10}(x + 1)$  and quadratic root transformations, respectively; *df* = 1, 4

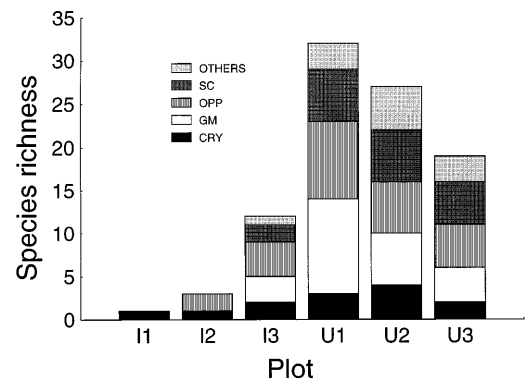
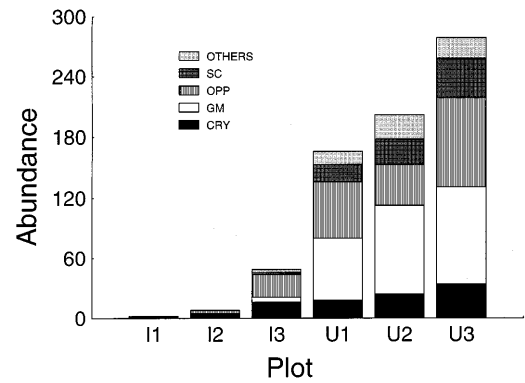
Variable	Collection method	<i>F</i>
Abundance	Pitfall traps (L)	1057.93***
Abundance	Foliage beats (L)	262.15***
Abundance	Litter (L)	167.07***
Richness	Pitfall traps (Q)	389.82***
Richness	Foliage beats	184.94***
Richness	Litter	132.94***

\*\*\**P* < 0.001

**Table 2** Results of analyses of correlations between *Pheidole megacephala* abundance and native ant abundance and richness as determined by different collection methods within three infested plots in the rain forest. *L* and *Q* indicate  $\log_{10}(x + 1)$  and quadratic root transformations respectively for native ant variables (*left*) and *P. megacephala* abundance (*right*); – indicates that raw data were used

Native ants variable	Transformations	Collection method	<i>r</i>
Abundance	Q, L	Pitfall traps	–0.419***
Abundance	L, Q	Foliage beats	–0.671***
Abundance	Q, Q	Litter	–0.375*
Richness	L, L	Pitfall traps	–0.425***
Richness	L, L	Foliage beats	–0.788***
Richness	–, Q	Litter	–0.344

\**P* < 0.05, \*\*\**P* < 0.001

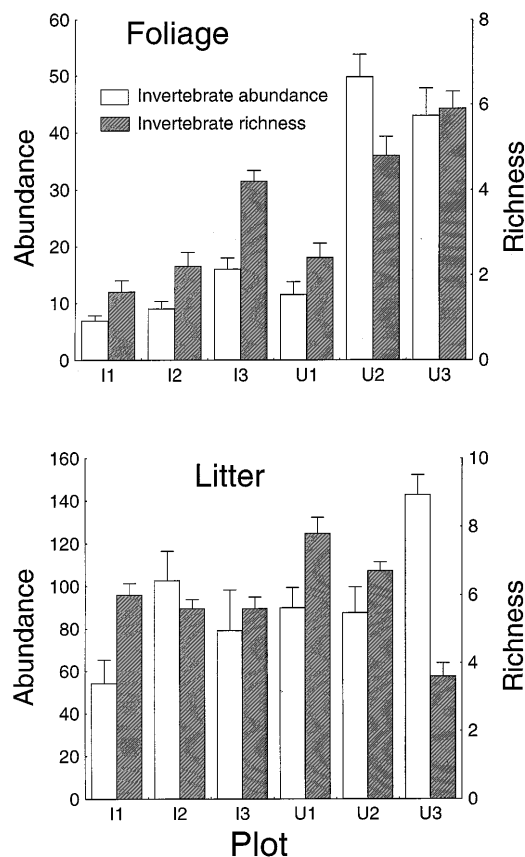


**Fig. 2** Functional group composition of native ant abundance and richness at infested (I1–3) and uninfested plots (U1–3) within rain forest (legend codes: *CRY* Cryptic species, *GM* Generalised Myrmicinae, *OPP* Opportunists, *SC* Subordinate Camponotini, *OTHERS* all remaining functional groups combined)

species to be excluded were the submissive and large Subordinate Camponotini (species of *Camponotus*, *Polyrhachis*, and *Calomyrmex*), and Generalised Myrmicinae, especially native *Pheidole* species. The former nest in rotting logs and other natural cavities, which are the preferred nest sites of *P. megacephala*. As *P. megacephala* abundance increases, only Cryptic species (such as *Hypoponera* spp.) and small Opportunists (species of *Tapinoma* and *Cardiocondyla*) are able to persist in low numbers, such that only eight individuals of three species were found in I2. Only two individuals of the Cryptic species *Hypoponera* sp. D were found persisting in I1.

### Impacts on other invertebrates

The abundance and ordinal richness of other invertebrates were highly variable at uninfested plots, but were both significantly higher than at infested plots (Fig. 3; Table 3), except for richness in litter samples. Likewise, invertebrate abundance was negatively correlated with *P. megacephala* abundance for both collection methods, but richness only correlated significantly in foliage samples (Table 4). Invertebrate taxa varied in their



**Fig. 3** Mean (+SE) of non-ant invertebrate abundance and ordinal richness within rain forest as found by 10 foliage beats and 10 litter samples at infested (I1–3) and uninfested plots (U1–3)

sensitivity to *P. megacephala*. Spiders collected in foliage beats, for example, were significantly reduced in abundance but remained present in all plots. Pseudoscorpions and insect larvae, on the other hand, were absent in the two most infested plots.

### Rate of spread

Changes in the distribution of *P. megacephala* were observed on all transects, with all but one (transect 2 of OS) showing a net expansion of range over the term of the study (Fig. 4). There was a clear trend of expansion of range during the dry season and reduction during the wet (Fig. 5). Mean overall range expansion over the two dry season periods was 9.2 m and 15.4 m respectively, with a mean reduction of 7 m occurring during the wet season. Mean overall range expansion between April 1996 and September 1997 was 22.4 m. The two closed-canopy vegetation types RF and VT had the greatest overall range expansions of 42 m (transect 1 in RF), 34 and 24 m (transects 1 and 2 respectively in VT).

**Table 3** Results of two-way ANOVAs of non-ant invertebrate abundance and richness, and abundance of specific groups between three infested and three uninfested plots within the rain forest as determined by different collection methods. Significance of transformation equation is from Cochran's test of homogeneity. *L* indicates  $\log_{10}(x + 1)$  transformation; *df* = 1, 4

Variable	Collection method	<i>F</i>
Abundance (L)	Foliage beats	80.35***
Abundance	Litter	7.15**
Richness	Foliage beats	36.29***
Richness	Litter	1.09
Spider abundance (L)	Foliage beats	58.28***
Pseudoscorpion abundance (L)	Litter	19.08***
Larvae abundance	Foliage beats	14***
Larvae abundance	Litter	33.26***

\*\**P* < 0.01, \*\*\**P* < 0.001

**Table 4** Results of correlation analyses between *P. megacephala* abundance and non-ant macro-invertebrate abundance and richness as determined by different collection methods within three infested plots within the rain forest. *P. megacephala* abundance was the independent variable and variables listed are dependent. *L* and *Q* indicate  $\log_{10}(x + 1)$  and quadratic root transformations respectively for native ant variables (*left*) and *P. megacephala* abundance (*right*); – indicates that raw data were used

Native ants variable	Transformation	Collection method	<i>R</i>
Abundance	Q, L	Foliage beats	–0.633***
Abundance	Q, Q	Litter	–0.431*
Richness	–, –	Foliage beats	–0.568***
Richness	Q, Q	Litter	–0.76
Larvae abundance	L, Q	Foliage beats	–0.415***
Larvae abundance	L, Q	Litter	–0.369**
Spider abundance	Q, L	Foliage beats	–0.602***

\**P* < 0.05, \*\*\**P* < 0.001

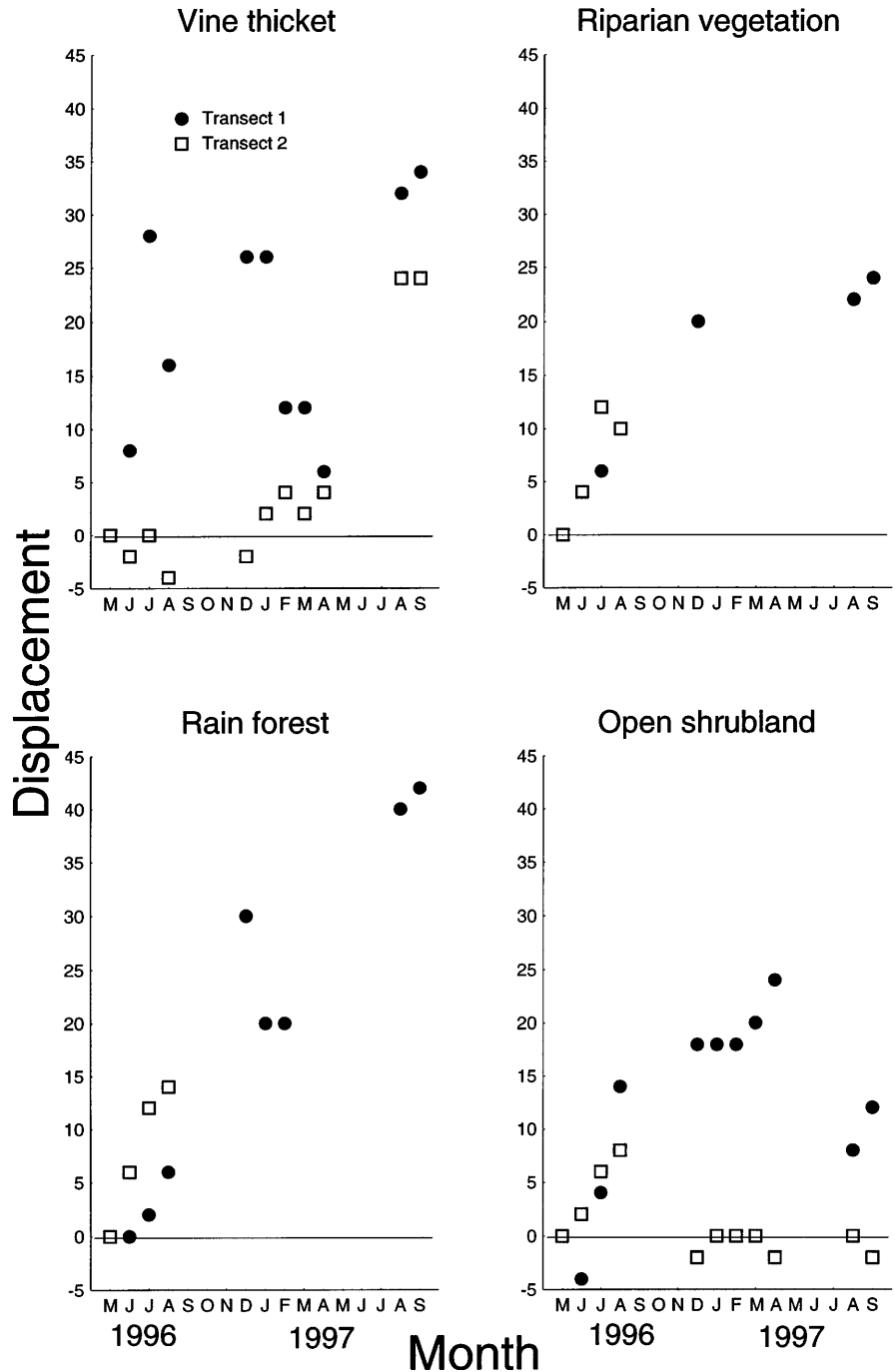
The responses of behaviourally dominant native ant species to range expansions by *P. megacephala* are illustrated in Fig. 6 for selected transects during the 1996 dry season (May–August). Epigeic *Iridomyrmex* spp. (collected in pitfall traps) and arboreal *Oecophylla smaragdina* (counted at baits) were clearly displaced as *P. megacephala* increased its range. *Papyrius* sp. at baits, on the other hand, managed to maintain its distribution, even gaining ground previously occupied by *P. megacephala*. However, the colony was ultimately eliminated in January 1997 when *P. megacephala* spread around it.

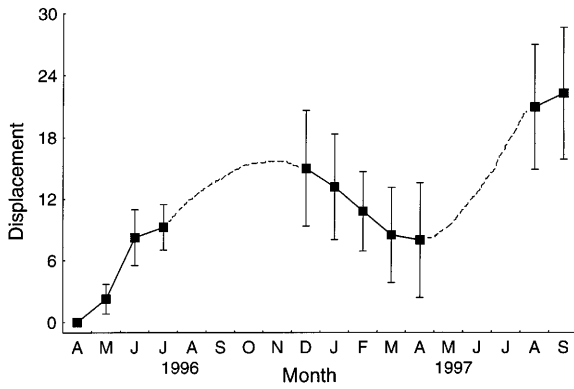
**Discussion**

Local distribution

*P. megacephala* is currently locally restricted to a single area of approximately 25 ha. The lack of aggression between workers from the extremes of this area indicates that the infestation represents a single “super-colony”. The absence of territorial boundaries of individual colonies is typical of this and other tramp species (Wilson

**Fig. 4** Change in distribution (m) of *P. megacephala* along eight permanent transects in four vegetation types, sampled between May and August 1996, December and April 1996–1997 and August to September 1997. Displacement is the change in distribution from the first sample time. Initial data point of transect 1 of each vegetation type, positioned at 0 under transect 2 data point





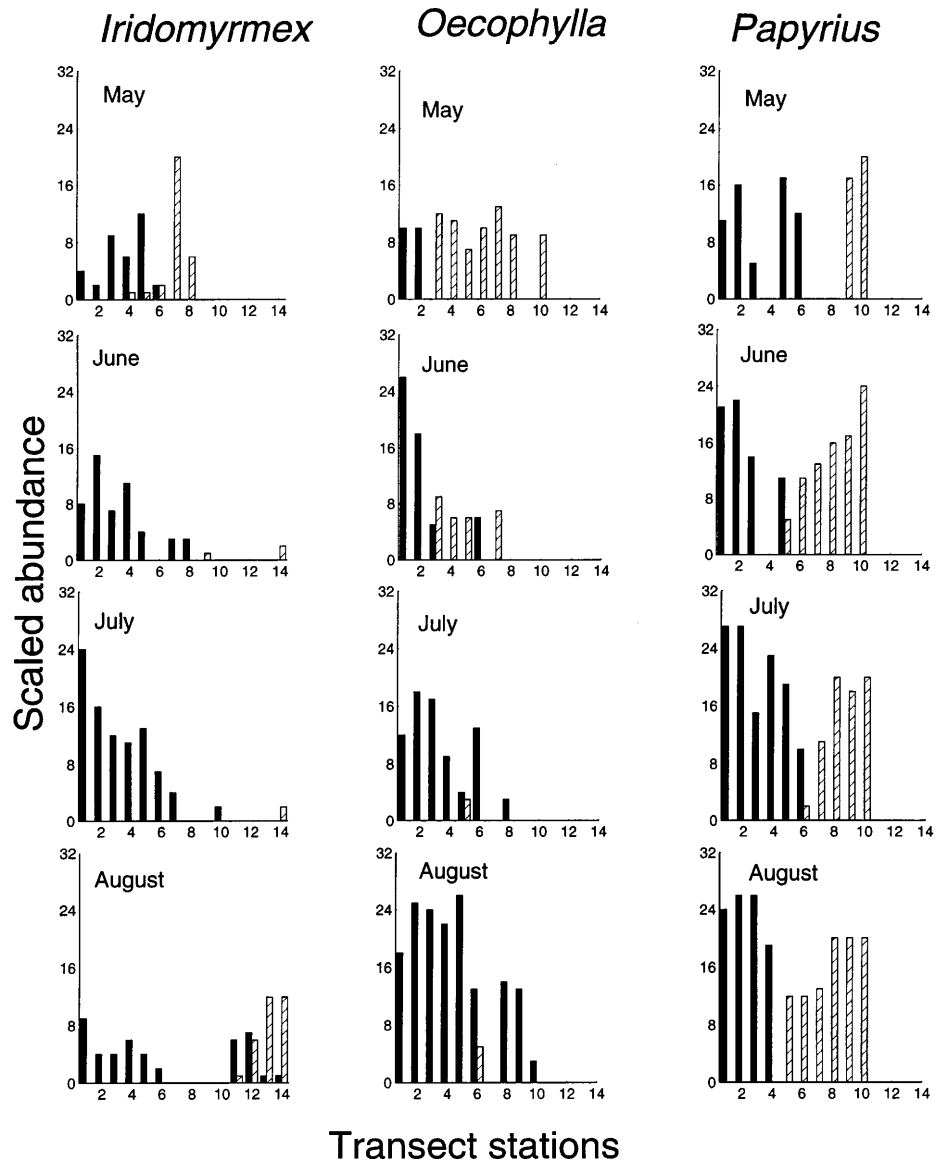
**Fig. 5** Average ( $\pm$ SE) and net displacement (m) (in relation to first sample) of *P. megacephala* along all permanent transects combined, from May 1996 to August 1997. Intermittent line between sample points represents presumed trends between sampling times

1971), and is believed to contribute to their dominance over indigenous ant faunas.

Greatest abundances of *P. megacephala* were clearly associated with drainage lines and particularly with rain forest vegetation. *P. megacephala* is known to favour shaded and moist habitats (Greenslade 1972; Majer 1994), and rain forest has greater canopy cover, and presumably higher humidity and lower ambient temperature, than other vegetation types in the region.

The abundance of *P. megacephala* declined away from the rain forest and was generally absent 200 m from its boundary, except in disturbed and irrigated areas. The tendency of *P. megacephala* to thrive in disturbed areas has been previously reported, and probably occurs because the simplified local ant fauna is less able to resist invasion (Greenslade 1972; Fox and Fox 1982; Majer 1985, 1994). *P. megacephala* was present on bare,

**Fig. 6** Responses of behaviourally dominant native ant taxa, *Iridomyrmex* spp. collected in pitfall traps, *Oecophylla smaragdina* and *Papyrius* sp. (shaded bars), both counted at baits, to changes in local distribution of *P. megacephala* (filled bars). Transect stations are spaced 2 m apart



Transect stations

fully insolated ground in these disturbed areas, but only foraged in these places during the cool parts of the day (B.D. Hoffmann, personal observation).

#### Impacts on native ants and other invertebrates

The abundance of *P. megacephala* in infested areas within the rain forest was exceptionally high, representing up to a 110-fold increase in total ant abundance compared with uninfested plots. An increase in ant biomass (primarily of the invasive species) following invasion is well known (e.g. Porter and Savignano 1990), but findings here are not consistent with those found for *P. megacephala* in Queensland (Heterick 1997), where there was no real change in total ant numbers. This is probably because that study concerned dry sclerophyllous vegetation, which is not optimal *P. megacephala* habitat. Interestingly, the abundance of *P. megacephala* remains very high at the limits of its distribution within the rain forest, instead of gradually attenuating.

Abundance and richness of native ants and other invertebrates were severely reduced where *P. megacephala* was present, consistent with similar studies from elsewhere in the world. Despite the near-saturation of the environment by *P. megacephala*, one native species was able to persist as a cryptic rarity, as has also occurred elsewhere (e.g. Haskins and Haskins 1988). However, the single native species recorded at the most heavily infested plot represents a 95–97% decrease in species richness compared with uninfested plots. As a comparison, at faunistically depauperate plots undergoing mine site rehabilitation in Queensland, Majer (1985) found only a 50–80% drop in ant species richness in plots where *P. megacephala* was present. Like Heterick (1997), Majer's study was performed in open vegetation.

Majer and de Kock (1992), studying the rehabilitation of sand mines in South Africa, found that after 5 years *P. megacephala* abundance reached a peak of 97% of all ant abundance, but then decreased until year 13 when ant community composition was more characteristic of undisturbed forest. The infestation at Howard Springs appears to be far more persistent, and is continuing to expand.

Given the key ecological roles of ants, the massive disruption wrought by *P. megacephala* on native ant communities at Howard Springs is likely to have ecosystem-wide repercussions. In South Africa, invasion by *L. humile* has disrupted native ant-plant mutualisms, seriously threatening the local persistence of endemic Proteaceae (Bond and Slingsby 1984). We have observed what appears to be comparable vegetation change, mediated by invasion of *P. megacephala*, at Howard Springs. In uninfested areas, the native *Urena lobata* L. and the introduced *Senna obtusifolia* (L.) Irwin occur as small isolated shrubs, with obvious signs of damage by insect folivores. In contrast, plants in infested areas are considerably larger, occur in dense stands, and have little, if any, folivore damage. Both these plants have

extra-floral nectaries, and the tending of these nectaries by the exceptionally high populations of *P. megacephala* appear to have caused these plants to flourish. The invasion of these plants into the rain forest is thereby facilitated, which further increases the risk of rain forest degradation by wildfires during the dry season (Russell-Smith and Bowman 1992).

The overall abundance of other native invertebrates was 42–85% lower in the most heavily infested plot than in uninfested plots. This is comparable to the reductions wrought on non-ant arthropod abundance by *S. invicta* in the southern United States (Porter and Savignano 1990). Heterick (1997), however, found no significant difference in total invertebrate abundance in the presence of *P. megacephala* in his Queensland study. Invertebrate taxa differed in their sensitivity to *P. megacephala*, resulting in marked compositional changes in the invertebrate assemblages. These changes are likely to have important ecosystem consequences, especially for insectivorous reptiles, birds and mammals.

#### Range expansion

The infestation of *P. megacephala* was found to be expanding, most rapidly in the more closed vegetation types of rain forest and dry vine thicket. This is probably because of reduced water stress, with both habitats offering relatively more shade and a deep litter layer. A general absence of behaviourally dominant native ant species within these habitats would also facilitate local invasion by *P. megacephala*.

Outside the rain forest, the presence of extremely aggressive native ant species of *Iridomyrmex* (Andersen 1992a; Andersen and Patel 1994) are undoubtedly a factor limiting *P. megacephala*, as has been demonstrated for other invasive ants elsewhere (e.g. Way et al. 1997). The exceptional dominance of Australia's open habitats by *Iridomyrmex* appears to make them relatively immune to invasion by exotic ants, compared with structurally similar habitats elsewhere in the world (Andersen 1997). Despite this, as *P. megacephala* spread into the more open vegetation types, we witnessed its gradual displacement of *Iridomyrmex*. However, the fire exclusion policy at Howard Springs has resulted in structurally more complex and shaded savanna habitats than is typical of the region, and this severely limits *Iridomyrmex* populations (Andersen 1991a). For example, the site dominated by the northern meat ant *I. sanguineus* studied by Andersen and Patel (1994) has remained unburnt since that study, and *I. sanguineus* is now entirely absent. Neither *I. sanguineus* or any members of the *anceps* group of *Iridomyrmex*, both of which dominate ant communities of most savanna habitats in the region, were abundant at any of our study sites.

Sheltered micro-sites appear to be critical to the spread and persistence of *P. megacephala* outside shaded vegetation. This was particularly true in the open shrubland, where the occurrence of *P. megacephala* at its



limits was always associated with logs, the base of trees, or clumps of grass. Within the dry vine-thicket, *P. megacephala* was present under an entire log extending well past its apparent distribution, yet could not be found only 1 m away from the log (B. Hoffmann, personal observation). Sheltered microsites were also exploited above ground within the frass of wood-boring insects.

The temporary range contraction during the wet season is consistent with the observation of Beardsley et al. (1982) that heavy rainfall resulted in a 10-fold reduction of *P. megacephala* populations in Hawaiian pineapple fields. Water-logged soil may in fact be a factor limiting its abundance. Interestingly, though, the greatest abundance and greatest distribution of *P. megacephala* at Howard Springs is associated with the most flood-prone soils, so it is likely that the ant is primarily arboreal during the height of the wet season. This association with poorly drained soils would allow the ant to benefit from greater soil moisture longer into the dry season.

## Conclusion

*P. megacephala* is known to be a serious threat to relatively depauperate faunas in the humid tropics, and we have demonstrated that this is also true for diverse faunas in the monsoonal tropics. At Howard Springs, *P. megacephala* has had a severe impact on a species-rich invertebrate fauna. Although *P. megacephala* has a clear preference for shady, humid habitat, our results demonstrate that it is capable of spreading into open habitats. Although it is never likely to reach high population levels in these habitats, because of the relative scarcity of sheltered microsites and the prevalence of behaviourally dominant native ants, open habitats could be potentially used as dispersal routes to new, favourable habitat patches. Therefore, *P. megacephala* has an extremely large potential distribution in Australia's monsoonal tropics. The isolated distribution of *P. megacephala* at Howard Springs makes its local eradication potentially feasible using chemicals that have been developed to control other exotic ants (Hoffmann 1998). Action now may prove a profitable investment in the future of the biodiversity of monsoonal Australia.

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