Impacts of an incursion of African Big-headed ants, *Pheidole megacephala* (Fabricius), in urban bushland in Perth, Western Australia

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An incursion of the African Big-headed ant, *Pheidole megacephala* has recently been recorded in bushland in Perth, Western Australia. This unexpected discovery prompted an investigation into the effects of the incursion on the native ant assemblages. Extensive pitfall trapping in invaded and non-invaded areas revealed that the incursion had a significant negative impact on ant species richness, diversity and evenness. Approximately 53% of native ant species present in non-invaded bushland were not sampled in areas occupied by *P. megacephala*, while the remaining species suffered considerable declines in frequency of occurrence. Many of these species perform important ecosystem functions, and their loss was thought to have had serious consequences on the ecosystem. Changes to the prevalence of the various ant Functional Groups indicated major disruptions to the composition of the assemblage as the abundance of *P. megacephala* increased. Ants that avoided direct competition with *P. megacephala*, by occupying temperature-dependant temporal niches, were more persistent in its presence. Estimates of the ant biomass sampled indicated that the invasive population was larger than that of all other ant species combined by several orders of magnitude. A feeding trial revealed intensified exploitation of food resources in invaded areas, which could have flow-on effects on other invertebrates and plants. Changes to predation, decomposition, and soil amelioration regimes, as well as possible disruptions to ant-plant interactions and invertebrate symbioses resulting from the disappearance of native ant species, were thought to have further eroded the conservation values of the ecosystem.

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INTRODUCTION

Invasive tramp ant species are recognized as some of the world's most serious economic and environmental pests (Williams 1994; Holway *et al.* 2002). While some species such as the Argentine ant, *Linepithema humile* (Mayr), and the Red Imported Fire ant, *Solenopsis invicta* (Buren), have received much public attention in Australia, due to their economic effects, other species that have less direct impact on humans have received far less attention (Wetterer 2007). One such ant is the African Big-headed ant (or Coastal Brown ant) *Pheidole megacephala* (Fabricius)*,* which has been known to occur in urban Western Australia for more than 50 years (Majer 1993). Until recently, this ant had not been considered a serious threat to conservation in Perth due to its prevalence only in highly altered, human-made habitats (van Schagen *et al.* 1993; Heterick 1997; M. Widmer pers. comm.). However, visual searches carried out in 2004 revealed a major infestation of *P. megacephala* in remnant bushland abutting Daran Park in Mt Claremont, Perth (S. Callan pers. obs.). This incursion represented the first known infestation of *P. megacephala* in bushland in the Perth metropolitan area, despite many observations of its presence in local suburban gardens (Heterick *et al.* 2000; Kain *et al.* 2002).

Incursions of *P. megacephala* have had serious negative impacts upon other ants and other invertebrate species in many environments around the Pacific (Hoffmann *et al.* 1999; Heterick 1997; Wetterer 2002) and around the world (Wheeler 1908; Broekhuysen 1948; Haskins and Haskins 1965; Heterick *et al.* 2000). The detrimental impacts of *P.*

megacephala on ant and invertebrate biodiversity have frequently been recorded from island environments such as Hawaii (Zimmerman 1948), Puerto Rico (Torres and Snelling 1997) and Bermuda (Haskins and Haskins 1965) The impacts of *P. megacephala* in Hawaii are particularly well-documented, and have included the displacement of beetles (Reimer *et al.* 1990), spiders (Gillespie & Reimer 1993), crickets (LaPolla *et al.* 2000), and ground-dwelling flies (Zimmerman 1970). In addition, the ant's capacity to form facultative symbiotic associations with homopterans such as mealybugs and scale (Jahn and Beardsley 1993;Reimer *et al.*1993; Lach 2003) is thought to be a threat to the conservation of susceptible native vegetation communities. In contrast to the above mentioned island environments, Australia's xeric ecosystems are believed to be comparatively resistant to invasive ants, due to the harsh, dry environmental conditions (Hoffmann 1998; Heterick *et al.* 2000), and the highly aggressive and abundant native ant fauna, characterised by the genus *Iridomyrmex.* (Hoffmann *et al.* 1999; Thomas and Holway 2005; Walters and Mackay 2005; Lach and Thomas 2008). Nevertheless, most studies on the impacts of *P. megacephala* in Australia have shown that incursions are associated with significant reductions in the richness and abundance of most native ant species (Heterick 1997; Vanderwoude *et al.* 2000).

The disappearance of the native ant fauna from invaded ecosystems is thought to have major direct and indirect impacts on biodiversity (Hoffmann 1998; Vanderwoude *et al.* 2000) and ecosystem functioning (Lach and Thomas 2008). Ant assemblages are recognised as particularly important components of Australian terrestrial ecosystems due to their ubiquity (Andersen 1997), their high biodiversity (Folgarait 1998), their participation in complex symbioses with other invertebrates (including members of the Hemiptera, Lepidoptera and Coleoptera) (Lach and Thomas 2008), and the many vital ecosystem services they perform (Holldöbler and Wilson 1990). Ants are recognised as major predators, scavengers (Petal 1980), and seed dispersers (Berg 1975), as well as "ecosystem engineers" (Folgarait 1998) because of their pedogenetic roles. Ants perform important soil amelioration functions such as the turning and aerating of soils, increasing water infiltration, and influencing nutrient cycles (Folgarait 1998; Lobry de Bruyn 1999). It is recognised that ant invasions can cause disruptions to these processes by replacing the native ant fauna with a single species that may perform such functions differently to the species it has displaced (Holway *et al.* 2002).

It is widely believed that water availability and humidity are highly influential on the distribution of *P. megacephala* (May and Heterick 2000; Hoffmann 1998; Heterick *et al.* 2000), along with related factors such as the ant's thermal tolerances and the availability of microhabitats that may act as a refuge from desiccation (Hoffmann *et al.* 1999). The high co-incidence of favourable conditions in human-altered environments may explain the prevalence of *P. megacephala* in urban habitats such as parklands and gardens (May and Heterick 2000). Incursions of *P. megacephala* in undisturbed bushland in good condition have been extremely rare in Australia (Majer 1985; Hoffmann *et al.* 1999). A notable exception was reported from Queensland, where an infestation was discovered in "long undisturbed forest" (Vanderwoude *et al.* 2000) near Maryborough. However, it was noted that the incursion may have been initially seeded by an undetected human vector (Vanderwoude *et al.* 2000). Interestingly, the results of this study did not support the idea of higher biological resistance in this undisturbed habitat, particularly with regard to the displacement of the Dominant Dolichoderinae. While the majority of Australian studies have found that *P. megacephala* prevails in disturbed or altered environments, it remains unknown whether changes to the physical environment or to the biological environment have a greater influence on the likelihood of invasion.

Invasive tramp ants such as *P. megacephala* are predisposed to accidental transport by many common human activities, such as landscaping, gardening and building. Urban landscapes are intrinsically at the highest risk of

invasion, due to a high likelihood of human-mediated introduction and a prevalence of altered or disturbed habitats suitable for fostering invasive ant populations (Holway *et al.* 2002). Consequently, urban bushland remnants are at high risk of incursion due to edge effects from the surrounding urban matrix. The literature suggests that *P. megacephala* reproduces by colony budding rather than by flight (Broekhuysen 1948), which typically results in continuous infestations. Incursions into bushland areas may therefore occur by gradual spread from nearby altered habitats and infrastructure (Heterick 1997), or from the accidental transport of reproductives into areas frequented by people and vehicles (Hoffmann and O'Connor 2004). The status of urban bushland remnants as important refugia for native invertebrate populations in urban landscapes, and the nature of invertebrates as critical drivers of ecosystem functions, necessitates that threats to invertebrate conservation in urban bushland should be taken seriously.

The parkland of Daran Park and the adjacent suburban gardens represented habitat types where *P. megacephala* thrives in the Perth metropolitan area, including landscape features such as mulched garden beds, watered lawns, ponds, and human infrastructure. In the context of Perth's dry Mediterranean climate, it was thought that *P. megacephala* would be limited to such habitats and was not likely to spread into bushland. The discovery of the *P. megacephala* incursion throughout large parts of the bushland abutting Daran Park caused concerns that the incursion may spread to Bold Park, a regionally significant conservation reserve located immediate north (Figure 1). Consequently, a field survey was undertaken to determine the effects of the invasive ant population on native ant assemblages and to assess the level of threat to the remnant ecosystem. The research aimed to: a) determine the distribution of *P. megacephala;* b) outline the effects of *P. megacephala* on the native ant assemblages and their food resources; and c) provide an assessment of the level of threat that the incursion presented to the conservation of the bushland remnant.

[**insert figure 1**]

MATERIALS AND METHODS

The approximate location of the study site was 31° 57' 31" S (-31.9589 degrees), 115° 46' 31" E (115.7755 degrees). The site was a dry-land remnant of *Eucalyptus gomphocephala* (Tuart) and *Banksia attenuata* woodland (BGPA 2000), on Quindalup dune-system soils (Bastian 1996). The understorey vegetation was infested with grass weeds such as *Erharta calycina* (veldt grass), and *Avena barbata* (wild oats), as well as garden species such as *Pelargonium alchemilloides* (geranium). Weed infestation and signs of human disturbance, such as the dumping of garden refuse, were evident throughout the bushland, particularly in the northern and eastern parts that adjoined the garden beds of Daran Park. The bushland area was roughly triangular in shape, bounded by the curve of Rochdale Road to the south-west, and Stephenson Road to the north-west, extending over approximately 3.5 ha (Figure 1).

Observation and hand collections were used to confirm the presence of *P. megacephala* in Daran Park and in surrounding suburban areas. Pitfall trapping was used to obtain ecological information on the ant assemblages of invaded and non-invaded areas of the bushland abutting Daran Park in April of 2004. Approximately 300 pitfall traps were laid in a single, large grid, designed to cover the majority of the bushland (approximately 2.7 ha), with traps placed at the intersection of transect lines 10 m by 10 m apart. This layout was designed to cover the full extent of the incursion and to extend beyond into non-infested bushland. Traps consisted of plastic vials of 28 mm diameter; half filled with 80% ethylene glycol, dug in to ensure that the rim of each trap was level with the ground and left open for

four days. Care was taken to minimize soil disturbance during installation, although it was not possible to cover the traps for any period to avoid digging-in effects, due to a shortage of trap lids.

The ants sampled were identified to species using keys, and voucher specimens were deposited in the JDM Western Australian Ant Collection at Curtin University of Technology. Species abundances were recorded from each trap, and entered into a data matrix for analysis. Where numbers of individual ants exceeded 500, abundance was estimated by sorting individuals into a single layer covering the surface of one or several petri dishes, the surface area of which was known. Grid paper of 10 mm by 10 mm was laid under the dish, and the number of individuals with their entire alitrunk within the boundaries of a chosen square were counted. This was conducted for five squares at varying distances from the middle of the dish, and the mean count was multiplied by the surface area of the dish for an estimate of abundance. Traps that had exhibited a disturbance were excluded from abundance counts.

Preliminary examination of the data revealed that samples displaying *P. megacephala* abundances within certain ranges had similar ant assemblages. For this reason, samples were grouped into 'zones' of *P. megacephala* abundance, which were later found to approximate the geographical spread of the invasion from the gardens into the bushland (Figure 2). The zones and their abundance levels are listed as follows: NoBHA: Samples with no *P. megacephala*; Zone 1 = 1 – 20 ants; Zone 2 = 21 – 100 ants; Zone 3 = 101 – 500 ants; Zone 4 = 501 – 1000 ants; and Zone 5 > 1001 ants.

[insert Figure 2]

In order to examine trends in native species occurrence, occurrence frequency data were calculated for each species in each zone. These data were expressed as a percentage of the total number of traps in each zone, in order to overcome differences in sample size. Species in each zone were sorted into rank order, from Zone 5, where *P. megacephala* abundance reached its highest level, to the NoBHA zone. This was designed to illustrate the varying levels of persistence of each native ant species as the abundance of *P. megacephala* increased across the zones.

Native ant species were classified into Functional Groups (following Andersen 1997) in order to illustrate changes to the ant assemblages at the Functional Group level as the abundance of *P. megacephala* increased across the zones. The Functional Group classification scheme used follows:

- Dominant Dolichoderinae - highly active, aggressive and competitive species such as *Iridomyrmex* spp., *Anonychomyrma* spp.;
- Subordinate Camponotini - associated with but behaviourly submissive to Dominant Dolichoderinae, genus *Camponotus*;
- Hot Climate Specialists - taxa which avoid direct competition with Dominant Dolichoderinae by foraging during warmer temperature extremes such as *Melophorus spp.*, and certain species of *Monomorium* and *Meranoplus*;
- Cold Climate Specialists - taxa which avoid direct competition with Dominant Dolichoderinae by foraging during cooler temperature extremes, such as genus *Stigmacros* and certain species of *Monomorium*;
- Generalised Myrmicinae - cosmopolitan genera commonly occurring in most habitats e.g., *Crematogaster* spp., *Monomorium* spp., *Pheidole* spp.;

- **Opportunists** - unspecialised common species that benefit from disturbance e.g., genus *Rhytidoponera*, *Ochetellus*, *Doleromyrma* and *Tetramorium*, and some species of *Monomorium*;
- **Cryptic species** - soil and leaf litter foragers which have little interaction with epigaeic ants e.g., *Hypoponera* spp., *Pachycondyla* spp., and *Solenopsis* spp.

No members of the Specialist Predators or Tropical Specialists groups were sampled. Introduced species other than *P. megacephala*, and *P. megacephala* itself, were dealt with in separate categories in these analyses. Species presence data of ants sampled in each zone were ordered in a table to illustrate the changes to Functional Group composition as the abundance of *P. megacephala* increased.

A feeding trial was carried out to determine whether levels of food resource exploitation were influenced by the presence of *P. megacephala*. Three types of bait were chosen to reflect the food resources of nectar or honeydew (golden syrup), prey (SPAM® canned meat), and seeds (peanut butter). A standard teaspoon of each bait type was set on an upturned petri-dish, placed equidistant apart in a triangle formation, pushed in to ground level. Five baiting stations were placed at random intervals inside and outside of the boundary of the incursion. Baits were checked after 30, 60, 120 and 240 minutes, and restocked as required, so that the attractiveness of the bait was not diminished over time. Ant abundance at each bait type was estimated during each inspection, by making a quick count of up to 20 individuals, and estimating what proportion of the remainder that comprised. Ant abundance was scored according to the following 7-point scale: 0 = No ants; 1 = 1 ant; 2 = $2 - 10$ ants; 3 = $11 - 30$ ants; 4 = $31 - 50$ ants; 5 = $51 - 100$ ants; and $6 > 100$ ants.

Ant species feeding at baits were hand collected and identified to species. The type of bait being exploited by each species was recorded as well as species changes over time. Additional observations on ant feeding behaviour were recorded by observing one set of baits continuously for an hour, both inside and outside of the incursion.

STATISTICAL ANALYSES

The software package PRIMER® (version 5) was used to calculate the Shannon-Wiener Diversity index (H′), and Pielou's Evenness index (J′) for each trap in the analysis. The Shannon-Wiener Diversity index was calculated as:

$$H' = n \log n - [(\textstyle\sum f_i \log f_i)/n]$$

(Shannon and Weaver 1949) where n is the total number of individuals in a sample, and f_i is the frequency of individuals of a single species in the same sample. Pielou's evenness statistic (J′) was calculated from this, as:

$$J' = H'/\log_e S$$

(Pielou 1969) where S is the total number of species in the sample being tested. Mean species richness (number of species), and diversity and evenness values for each zone were compared using one-way ANOVA in the software package SPSS® (version 11). Post-Hoc testing was conducted using Scheffé's test.

To assess the ant biomass sampled, the lengths of representatives of all ant species were measured, and individual mass was calculated from length, using the following power model derived by Brady and Noske (2006):

$$Y = A + B^X \text{ or } \log_e Y = \log_e A + B (\log_e X)$$

where Y = mass in mg, X = length in mm, $A = 0.001 \pm 0.000$, $B = 2.330 \pm 0.151$. The standard error of the estimate = 0.496, and the R^2 value of the model = 0.708 (Brady and Noske 2006). It was acknowledged that the biomass analysis was an under-estimate of the total ant biomass in the environment, because of characteristics of the sampling protocol, the method of abundance estimation in samples of higher abundance, and general characteristics of ant behaviour. All

available castes of each species were measured, and where caste ratios were known (e.g., *Pheidole* caste ratios were applied from Holldöbler and Wilson (1990)), they were applied to the calculation. Where caste ratios were not known, biomass was calculated from the mean length of all castes measured. Once calculated, individual mass was multiplied by the abundance of each species in each sample, to indicate the total biomass sampled.

RESULTS

Observations and baiting detected *P. megacephala* throughout all of the gardens and lawns of Daran Park, as well as the majority of suburban gardens in the surrounding area (Figure 1). It was also present on road islands between suburban infestations along Rochdale Road and the southern tip of Bold Park, as well as in two small areas of Bold Park itself: one immediately adjacent the infested Rochdale Road, and the other at the juncture between the south western part of the Park and Christchurch Grammar School's playing fields (Figure 1). The ant was also present throughout an approximate 2 ha area in the northern and eastern parts of bushland abutting Daran Park, to a distance of approximately 90 m from the bushland/ parkland boundary (Figure 1). It was observed that the highest densities of *P. megacephala* in the bushland area were closest to the boundaries of Daran Park gardens, particularly in proximity to the artificial wetlands (Figure 2).

A total of 36 ant species were sampled during the survey, including 32 native species, and four introduced species including *P. megacephala*. Considerably fewer species were sampled in *P. megacephala* infested zones than in the non-invaded bushland, representing a reduction between 66% (20 species absent in zone 1) and 95% (34 species absent in zone 5) of the total species richness sampled (Table 1). The 18 native species and three introduced species that were sampled inside of the boundary of the incursion showed marked declines in frequency of occurrence as the abundance of *P. megacephala* increased (Table 1). Particularly as the abundance of *P. megacephala* increased to exceed 100 ants per trap (in zones 3 – 5), the frequencies of other ants in the samples declined to negligible levels. Some species of *Melophorus* and *Monomorium* were relatively persistent at higher abundances of *P. megacephala*, particularly *Melophorus wheeleri* sp. complex JDM 783, which was the only other species present in the most highly abundant areas of the incursion.

[insert Table 1]

The ant assemblages exhibited changes in the composition and relative abundances of each Functional Group as each group itself declined in the prevalence of *P. megacephala* (Figure 3). Hot Climate Specialists were the most frequently occurring in all zones, but relatively more so at higher abundances of *P. megacephala*. While Generalised Myrmicinae and Opportunist groups were not as frequently occurring as Dominant Dolichoderinae in the non-infested samples, they declined less rapidly than the Dolichoderinae as the abundance of *P. megacephala* increased. Subordinate Camponotini disappeared entirely in the presence of *P. megacephala*, whereas Cryptic Species, Cold Climate Specialists and Introduced Species were persistent at some level, at all but the highest abundance zones (zones 4 and 5).

[insert Figure 3]

The disappearance of native species across the zones of incursion translated to significant declines in ant species richness ($\alpha = 0.05$; F = 16.075; df = 6,323; $p < 0.001$), species diversity ($\alpha = 0.05$; F = 31.412; df = 6,323; $p < 0.001$)

and sample evenness (α = 0.05; F = 41.19; df = 6,323; p < 0.001). Samples in non-infested bushland revealed 34 species in total, although the mean richness per trap was only 2.59 species SE = 0.12 (Figure 4). Infested zones showed a richness of 16 species in zone 1 (mean = 2.62 species per sample, SE = 0.33), to only 2 species in zone 5 (mean = 1.07 species per sample, SE = 0.07), while the mean abundance of *P. megacephala* in the samples increased from 9.14 ants (SE = 1.24) in zone 1 to 1996.50 ants (SE = 325.68) in zone 5 (Figure 4).

[insert Figure 4]

Mean sample evenness and species diversity declined in very similar fashion to mean species richness. Differences in mean diversity and evenness were significant between three distinct groups of samples. Samples from NoBHA and zone 1 grouped together, as did samples from zone 3, zone 4 and zone 5, while zone 2 samples were distinct from either of the other two groups (Figure 5).

[insert Figure 5]

The rise in abundance of *P. megacephala* across the six zones corresponded to substantial increases in total ant biomass from NoBHA to zone 5 (Figure 6). This was entirely attributed to the *P. megacephala* population, as the biomass of other ant species declined to negligible levels in the prevalence of *P. megacephala*. The maximum estimated biomass of ants other than *P. megacephala* was 0.504 g per sample in NoBHA zone, while the maximum estimated biomass of *P. megacephala* reached 29.879 g per sample in zone 5 as the biomass of all other species combined declined to 0.007 g per sample.

[insert Figure 6]

The level of food resource exploitation in invaded areas was orders of magnitude greater than that observed in non-invaded areas. The feeding trial demonstrated that *P. megacephala* consistently located baits faster than ants in non-invaded areas, as well as recruiting to baits faster, and in higher numbers (Figure 7). Although protein and seed-based food sources (SPAM® and peanut butter) were preferentially fed upon by *P. megacephala,* it was observed exploiting all three bait types simultaneously. The only species observed at bait stations within the boundaries of the incursion was *P. megacephala*. In non-invaded areas, ant abundances at baits were comparatively lower (Figure 7). Baits visited by *Iridomyrmex chasei* (golden syrup only) had the highest level of ant visitation, while some baits were observed to have several species present simultaneously (e.g., *Iridomyrmex mattiroloi splendens* and *Melophorus* sp. ANIC 3 on a SPAM® bait). Species change-over between observations was not recorded at any of the bait stations.

[insert Figure 7]

The arrival of major workers of *P. megacephala* at food resources was observed to have a noticeable effect on the ant's collective feeding behaviour. Prior to the arrival of major workers at baits, the minor workers engaged primarily in individualistic feeding and recruiting. However, after majors arrived, groups of minor and major workers began engaging in co-operative behaviours, circling food sources as if patrolling, and breaking off portions of solid food to transport them back to the nest. These observations represented noticeably different behaviour patterns to any of the native ant species observed (e.g., *Iridomyrmex chasei*, *Crematogaster laeviceps chasei*).

DISCUSSION

The patterns of occurrence of *P. megacephala* in the parkland of Daran Park and in nearby suburban gardens fit with what is known about the ant's habitat preferences (Broekhuysen 1948; Hoffmann 1998). Within these environments, *P. megacephala* was associated with shade, high water availability (as observed by the condition of lawns and vegetation), human infrastructure, and mulched garden beds. The ant was most regularly observed between the cracks of block-paved footpaths, brick-paved driveways, and at the verge between lawns and the road kerb, which may represent different preferred microhabitats in these highly altered areas (Hoffmann 1998). It was observed that the spread of colonies was limited by bituminized surfaces such as roads or driveways, supporting previous observations that such surfaces are effective barriers to *P. megacephala* incursions (Hoffmann and O'Connor 2004).

The incursion in Daran Park may have come about by gradual spread from residential areas, although it may have been introduced during the parkland's construction, during which potted plants, turf grass, soil and mulch were imported (S. Crossman, City of Nedlands pers. comm. 2004). Although it is acknowledged that the current data do not indicate causality, it is clear that the invasion of the bushland abutting Daran Park has been facilitated by the presence of a highly altered environment in direct proximity. Infested areas throughout the bushland were observed to be lower in native vegetation density and canopy cover, and more infested with grassy weeds than some non-invaded areas of the remnant, as well as exhibiting signs of disturbance such as dumped garden refuse and bushwalking tracks. These observations concur with what is known about the ant's habitat preferences (Wetterer 2007). In the bushland, *P. megacephala* was observed utilising microhabitats at the base of plants, rocks, logs and trees as preferred sites for nest entrances (Broekhuysen 1948; Hoffmann and O'Connor 2004).

The *P. megacephala* invasion was associated with a significant reduction in ant biodiversity, relative to non-invaded areas. Despite the lack of data on pre-invasion ant assemblages, it seems clear that *P. megacephala* has had a negative effect on the native ant fauna, consistent with observations of its ecological impacts elsewhere (Heterick 1997; Hoffmann *et al.* 1999; Vanderwoude *et al.* 2000; Hoffmann and Parr 2008). While it is possible that habitat disturbance may have undermined the ant assemblages, it is unlikely that any of the other environmental impacts observed in the remnant (e.g., weed infestation, bushwalking, dumping of refuse) could have resulted in such pronounced differences between invaded and non-invaded ant assemblages. Ant species richness, diversity and evenness declined most markedly between zone 2 (*P. megacephala* abundance 21-100 ants per trap) and zone 3 (101-500 ants per trap) (Figures 3, 4, 5). This may correspond to a density threshold of *P. megacephala* after which most native ant species are unable to persist.

Over the same space as the abovementioned changes, an overwhelming increase in ant biomass was recorded in the samples (Figure 6). It is commonly observed that invasive ant populations can reach abundances and biomass far in excess of native ant assemblages (Porter and Savignano 1990; Holway 1998; Abbott 2005). The resulting numerical advantages over native ant species are compounded by comprehensive foraging strategies (Nonacs and Soriano 1998; Holway *et al.* 2002), and rapid recruitment of workers *en masse* to food resources (Holway 1999; Rowles and O'Dowd 2007). The impact on food resource exploitation is evident in Figure 7, although a more precise measurement is required to demonstrate the rate of recruitment within the first 30 minutes. The ability of *P. megacephala* to locate and exploit food resources appears to be considerably greater than that of the native ant species; a finding similar to that of other invasive ant feeding trials (Holway 1999; Walters and Mackay 2003; Human and Gordon 1999). Dejean *et al.*

(2005) revealed that the detection of certain territorial marking chemicals from competitor species elicited a higher recruitment response from *P. megacephala*, particularly in the soldier caste, at food resources. In addition to enhancing its competitive ability, rapid recruitment could also be advantageous to *P. megacephala* in interspecies conflict (Dejean *et al*. 2005). High competitive ability, high aggression (more so between species than within species), and massive population sizes are all thought to be key mechanisms for the displacement of native ant species by invasive ants (Holway *et al*. 2002).

As various species declined and disappeared with increasing abundances of *P. megacephala,* ants from the various Functional Groups displayed different levels of persistence, reflecting changes to the structure of the assemblage (Figure 3). There is much evidence in the literature regarding the persistence of ants which can avoid competitive exclusion or interference competition from invasive ants, including small, innocuous species (Porter and Savignano 1990), Opportunists (Vanderwoude *et al*. 2000; Heterick *et al*. 2000), cryptic species and soil foragers (Ward 1987; Heterick 1997; Heterick *et al*. 2000), ants with strong stinging defenses (Heterick 1997; Porter and Savignano 1990) and temperature specialists (Hoffmann 1998; Thomas and Holway 2005). In the current study, Hot Climate Specialists (e.g., *Melophorus* spp.) remained relatively frequent in all but the highest abundances of *P. megacephala.* This species is able to forage at temperatures lethal to *P. megacephala* (Andersen 1997), thereby occupying a temporal niche in the heat of the day, which is unavailable to the invasive species (Hoffmann 1998). Opportunists and Cold Climate Specialists, while not as persistent as the Hot Climate Specialists at the highest abundances of the incursion, still made up a large proportion of the persistent ant biodiversity at lower abundances of *P. megacephala* (Table 1). While the low diversity of Cryptic Species in the samples may have been a result of the paucity of leaf litter in the majority of the remnant (S. Callan pers. obs.), the absence of the Subordinate Camponotini in the presence of *P. megacephala* follows with what is known of this group (Hoffmann *et al.* 1999; Vanderwoude *et al*. 2000).

Meanwhile, the lack of Dominant Dolichoderinae species in higher abundance zones (Table 2) is in notable contrast to theories that ants such as *Iridomyrmex* spp. can resist invasions because of their highly active and aggressive nature (Majer 1993; Andersen 1997; Hoffmann *et al*. 1999; Thomas and Holway 2005). The non-invaded ant assemblage was not dominated by dolichoderine ants in terms of percentage occurrence (Table 1 shows *Iridomyrmex chasei* at 36.62% occurrence in NoBHA zone, second to *Monomorium sordidum* at 71.83%), perhaps suggesting an effect of disturbance, or at least that these species may not have been dominant prior to the invasion. Nevertheless, as the abundance of *P. megacephala* increased in zones 1 and 2, the Dominant Dolichoderinae (e.g., *Iridomyrmex chasei*) displayed a far more rapid decline than Generalist Myrmicines (such as *Monomorium sydneyense*) and Opportunists (such as *Rhytidoponera violacea*) (Figure 3, and Table 1). These findings (with regard to the persistence of Opportunists and Generalised Myrmicines) are somewhat in line with the effects of *P. megacephala* on ant Functional Groups in the bushland of Maryborough State Forest (Vanderwoude *et al*. 2000). Ants such as *M. sydneyense* may fit into the aforementioned 'small/ innocuous' category, while *Rhytidoponera* spp. are known to have powerful stings, which may help them to persist in infested areas (Heterick 1997). Conversely, *Iridomyrmex* spp. may be relatively susceptible to displacement because they are in direct competition with *P. megacephala* for carbohydrate food resources such as homopteran honey-dew. Although Figure 7 shows that carbohydrate-based food resources are the least preferred by *P. megacephala,* the ant's rapid rate of recruitment and higher abundance at golden syrup baits suggests that it has the ability to out-compete any of the native species that were sampled at similar bait types during the trial.

The levels to which certain ant species persist in the presence of *P. megacephala* may be of vital importance to the continuation or cessation of the ant assemblage's ecosystem functions. For example, the relatively persistent Hot Climate Specialists include many seed-distributing ants such as *Melophorus* spp. and *Meranoplus* spp. (Andersen 1997). While *P. megacephala* is known to be a rapacious harvester of seeds (Majer 1985; Hoffmann 1998), it is not known whether dispersal by *P. megacephala* facilitates germination to the same extent as native ant dispersal (Majer 1985). The ultimate fate of ant-dispersed seeds relies upon a number of co-evolved factors, and it is generally thought that invasive ants may cause a disruption to the patterns of dispersal and therefore plant reproduction (Majer 1985; Holway *et al.* 2002; Lach 2003; Ness *et al.* 2004). Conversely, there is some evidence to suggest that certain plant species may be promoted by *P. megacephala* (Compton and Robertson 1988; Cushman *et al.* 1998; Hoffmann 1998; Bach 1991).

Detailed ecological information is required to adequately determine what ecosystem functions may be lost by the displacement of certain ant species. In addition, it is likely that the ecosystem functions performed by the massive invasive ant population itself differ to those of the diverse, sparsely-populated ant assemblages present in non-invaded areas of the bushland. The literature reports that ecological processes such as myrmecochory (Bond and Slingsby 1984), predation and competition for prey (Porter and Savignano 1990; Human and Gordon 1997), and nutrient cycling (Folgarait 1998) may be affected by ant invasions. Further impacts may be caused by the upheaval of ant-plant and ant-invertebrate mutualisms, such as the tending of floral and extra-floral nectaries which could affect native pollinators and herbivores (Lach 2003; Lach 2005). Increases to populations of ant-mutualist Homoptera (Bach 1991; Jahn and Beardsley 1993; Gonzalez-Hernandez *et al.* 1999) may in turn have negative effects upon the health of the vegetation.

Few impacts of *P. megacephala* upon vertebrate animals have been recorded, although the ant has been observed attacking bird hatchlings (Wetterer 2007; S. Callan pers. obs.), and has been implicated in local extinctions of insectivorous birds through its impact on invertebrates (Banko and Banko 1976).

To date, only one further study has been done on the ants of the bushland abutting Daran Park. Baiting and field observations conducted by students of the Department of Environmental Biology at Curtin University of Technology indicated that the non-infested (in 2004) areas in the south-west of the remnant remained free of *P. megacephala* in 2006 (R. Harris pers. obs.).

CONCLUSIONS

The *P. megacephala* incursion in the remnant bushland abutting Daran Park is the first of its magnitude recorded in the Perth metropolitan area, although it is difficult to determine from the current data why this particular incursion has been successful, while other bushland remnants nearby remain free of the pest. This highly competitive, extremely abundant incursion has been associated with a comprehensive simplification of the native ant fauna, which presents a serious threat to urban bushland conservation. Unsurprisingly, the impacts of the incursion on the native ant assemblages and their food resources were much more pronounced at higher levels of invasive ant biomass, which corresponded geographically to the more disturbed areas of the bushland in closest proximity to human-made habitats. This indicates a need for more appropriate management of disturbance in urban bushland, and the incorporation of buffer zones to better protect remnants from suburban impacts at their exposed edges. At a research level, there is a need for long-term study of such incursions to detail the specific factors influencing the distribution of *P. megacephala* in Australian ecosystems, and the likelihood of incursions into bushland of various conditions. Recent observations in

Perth have revealed another significant *P. megacephala* incursion in nearby bushland at Allen Park, in Cottesloe (R. Harris unpubl. data; S. Callan pers. obs. 2006). Given the scale of ecological impacts revealed in this and other recent Australian studies, and the widespread distribution of *P. megacephala* around Australia, there is a clear need for comprehensive, co-ordinated assessment of the threats to inform management.

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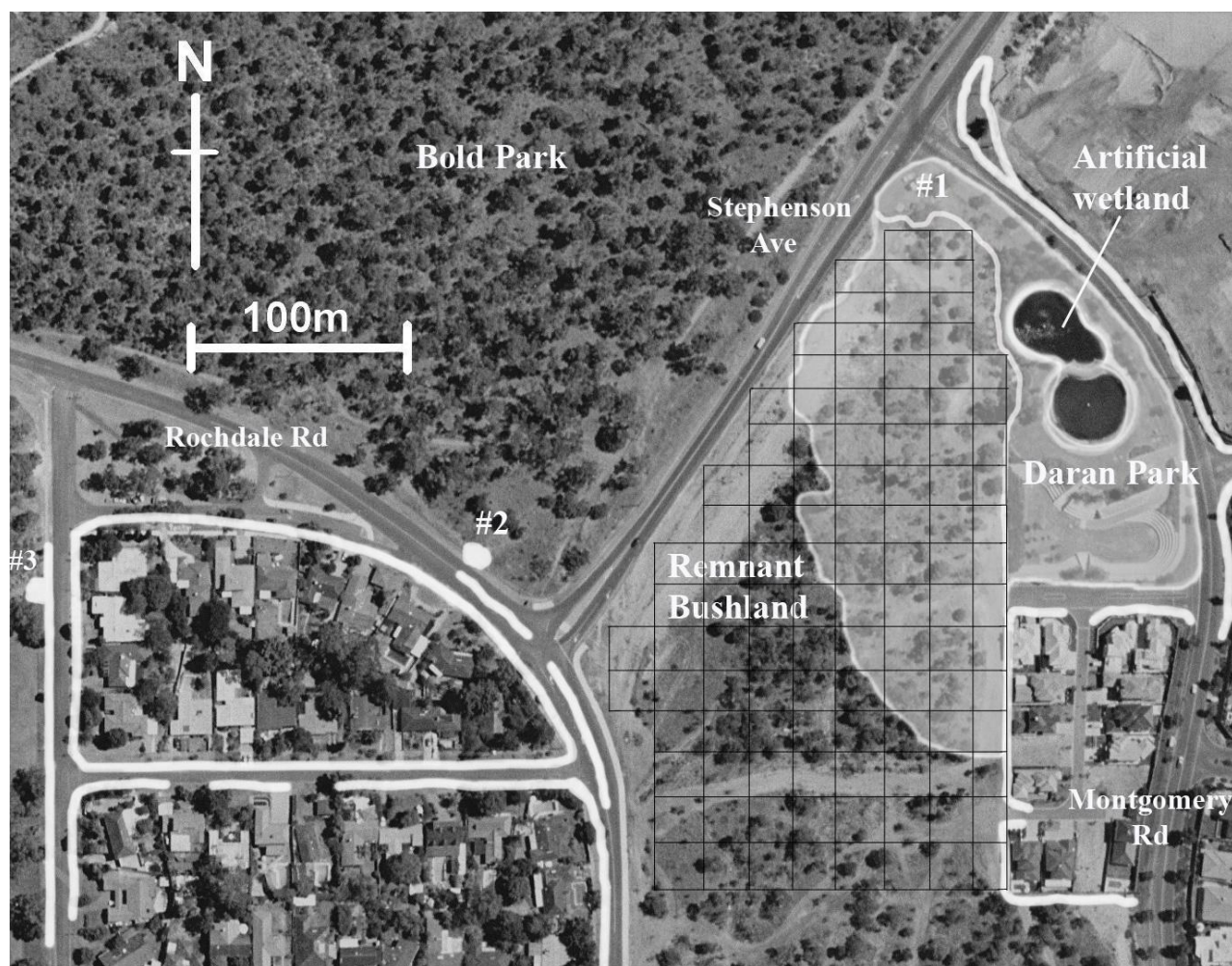
Fig. 1. Pheidole megacephala distribution in Daran Park, adjacent bushland, and surrounding suburban areas. Presence of *P. megacephala* is indicated by white lines in suburban infestations, and translucent shading. Approximated pitfall

trapping grid is represented by black lines, with traps placed at the intersection of lines at 10 m intervals. Numerals mark out the following *P. megacephala* incursions; #1 - Daran Park, #2 - southern part of Bold Park, #3 - south western part of Bold Park.
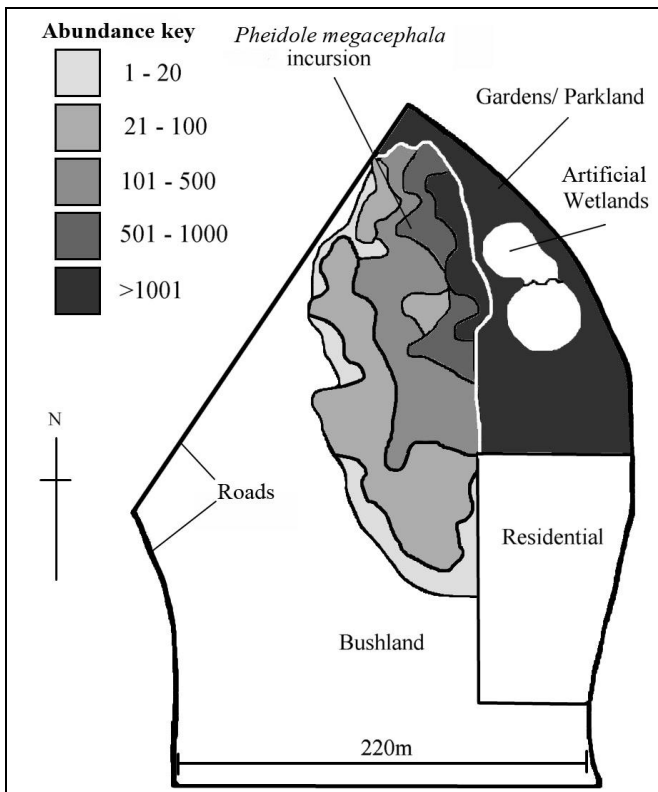

Fig 2. P. megacephala incursion into bushland adjacent Daran Park, classed into abundance zones. Zones reflect the number of *P. megacephala* individuals sampled by pitfall traps laid at 10 m intervals in a single large grid throughout the bushland, left open for four days in April 2004.
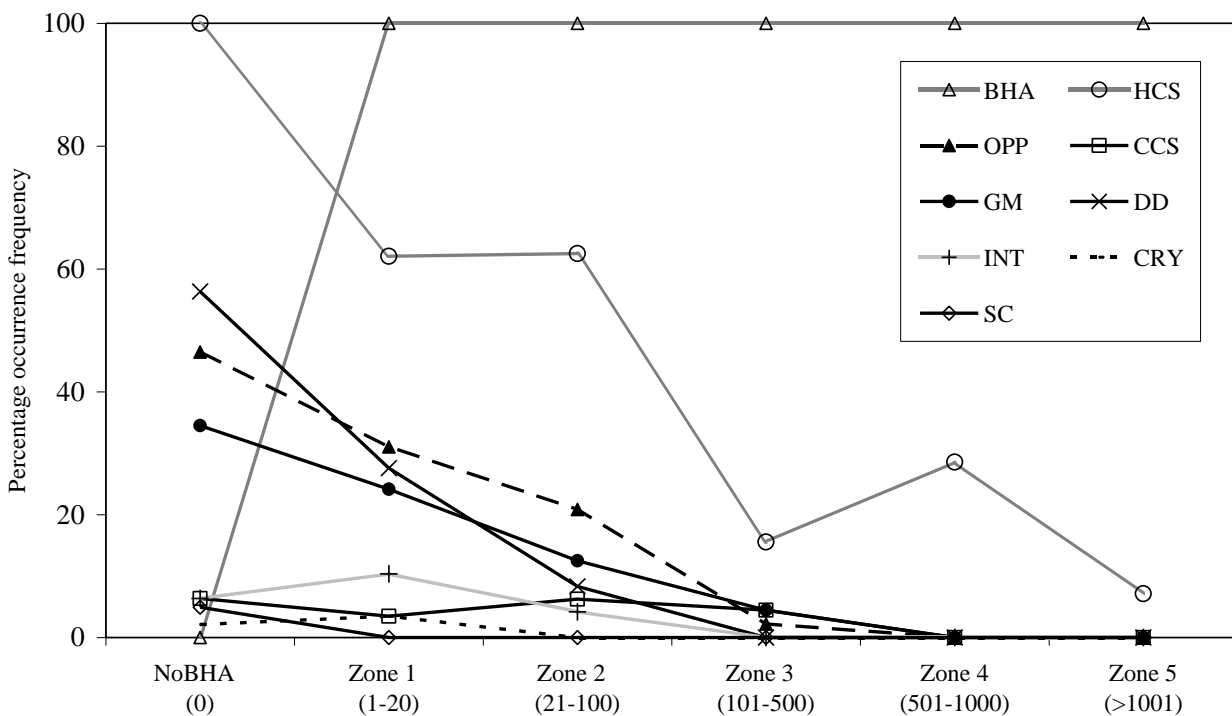

Fig 3. Frequency of occurrence of ant Functional Groups (as in Andersen 1997) plotted against the abundance of *P. megacephala* in each zone. Frequency of occurrence expressed as a percentage of the total number of traps in each abundance zone. BHA = *P. megacephala*; HCS = Hot Climate Specialists; OPP = Opportunists; CCS = Cold Climate Specialists; GM = Generalist Myrmicinae; DD = Dominant Dolichoderinae; INT = Introduced species other than *P.*

megacephala; CRY = Cryptic Species; SC = Subordinate Camponotini. Zone definitions (*P. megacephala* abundance per trap) are shown in parentheses.
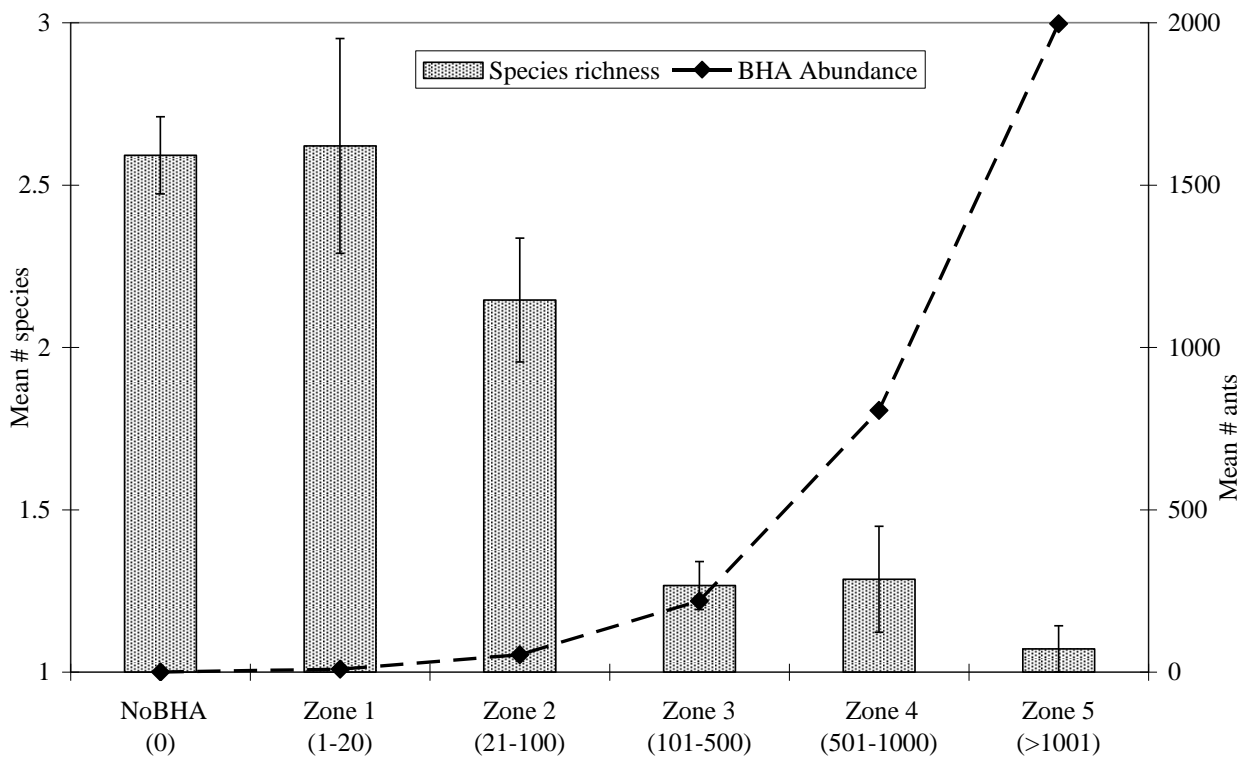

Fig 4. Mean species richness per zone, plotted against the abundance of *P. megacephala* in each zone. Zone definitions (*P. megacephala* abundance per trap) are shown in parentheses.
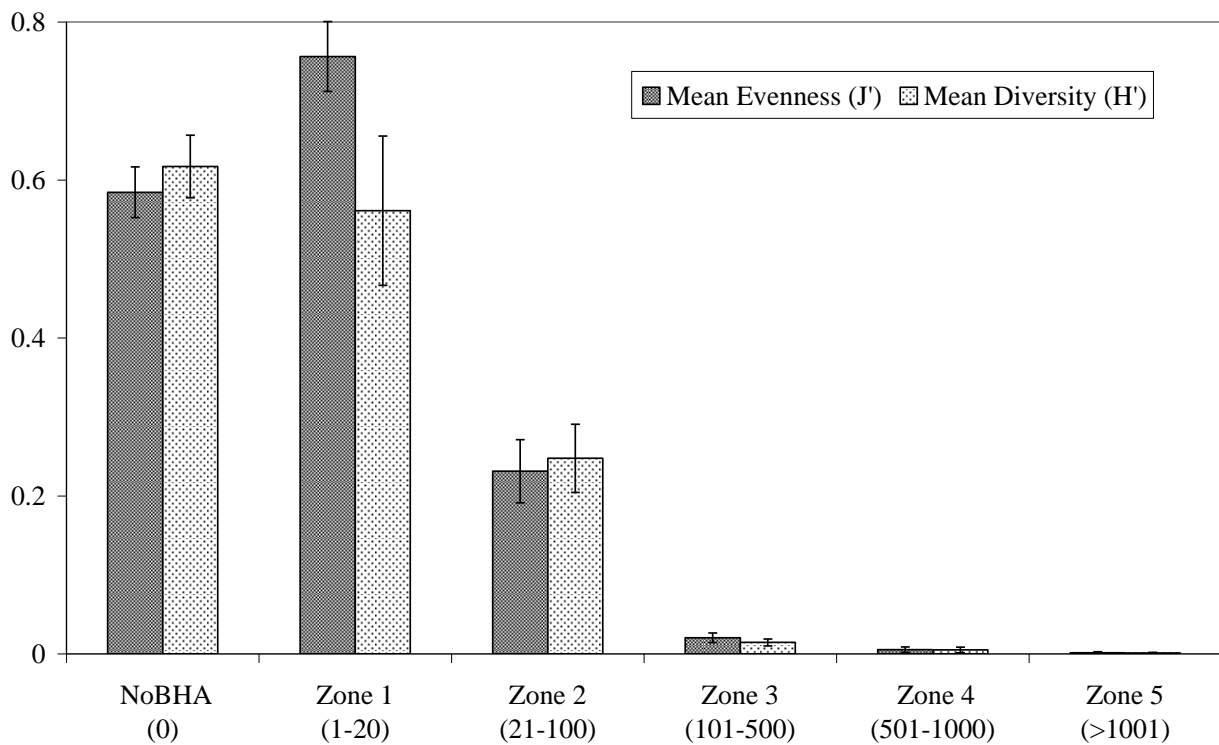

Fig 5. Mean sample Evenness (J') and Diversity (H') values plotted against the abundance of *P. megacephala* in each zone. Zone definitions (*P. megacephala* abundance per trap) are shown in parentheses.
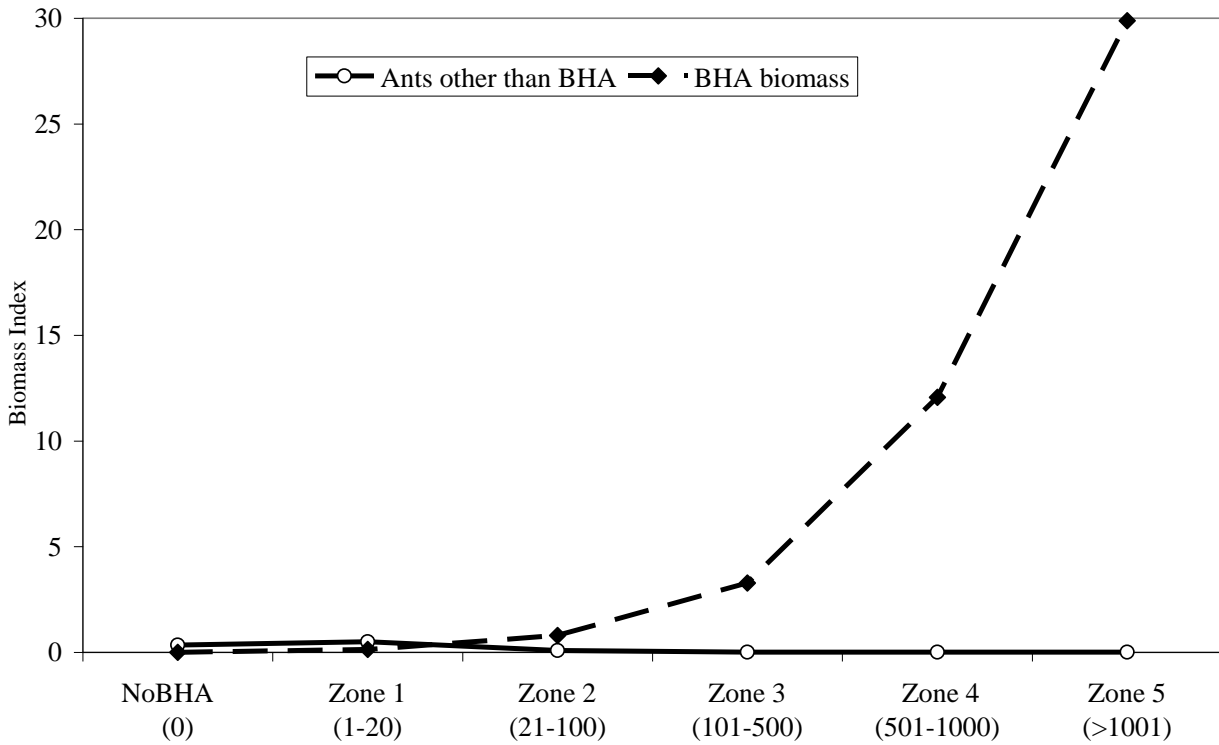
Fig 6. Biomass of *P. megacephala* plotted versus that of all other species combined plotted against the abundance of *P. megacephala* in each zone. Biomass index was calculated by individual ant mass (following Brady and Noske 2006) multiplied by total abundance sampled per zone, divided by the number of traps. Zone definitions (*P. megacephala* abundance per trap) are shown in parentheses.
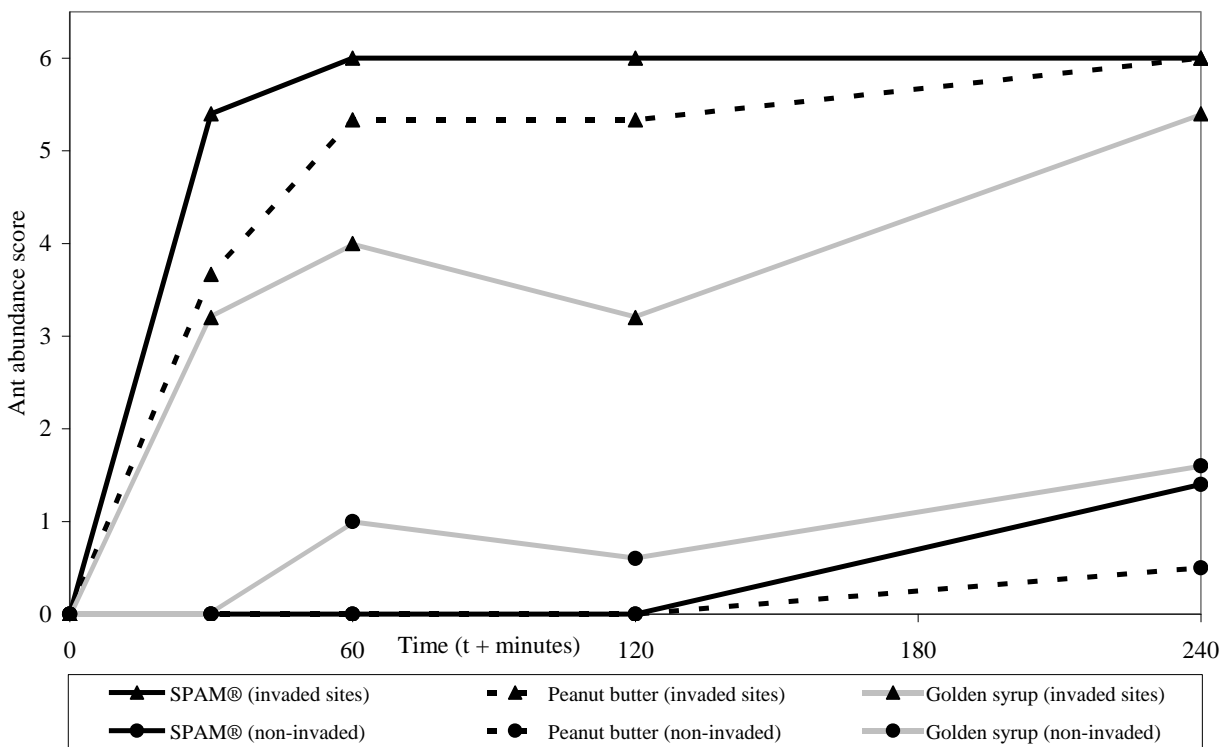

Fig 7. Ant abundance at feeding trial baits over time. ▲ = baits in *P. megacephala* infested areas, *P. megacephala* was the only species sampled at baits; ● = baits in non- infested areas, *Ochetellus glaber* sp. JDM 19, *Iridomyrmex chasei, Doleromyrma darwiniana*, *Crematogaster laeviceps chasei, Iridomyrmex mattiroloi splendens,* and *Melophorus* sp. ANIC 3 were sampled at baits.

Table 1. Persistence of ant species, in various Functional Groups, within each *P. megacephala* abundance zone. Frequency of occurrence of each species except *P. megacephala* is represented as a percentage of the total number of traps in each zone. Species within each Functional Group are ordered by the highest frequency of occurrence in the zone of highest *P. megacephala* abundance. Functional Groups (following Andersen 1997) are ordered in the table in the same fashion.

	NoBHA	Zone 1	Zone 2	Zone 3	Zone 4	Zone 5
Pheidole megacephala abundance per trap	**0**	1 - 20 ants	21 - 100	101 - 500	501 - 1000	> 1001 ants
HOT CLIMATE SPECIALIST						
Melophorus wheeleri sp. complex JDM 783	20.42	13.79	22.92	11.11	21.43	7.14
Melophorus ANIC sp. 3	3.52	3.45	12.50	2.22	7.14	
Monomorium sordidum	71.83	41.38	27.08	2.22		
Meranoplus ferrugineus	2.82	3.45				
Meranoplus rugosus	2.11					
Melophorus sp. JDM 500	1.41					
OPPORTUNISTS						
Doleromyrma darwiniana	6.34	10.34	4.17	2.22		
Rhytidoponera violacea	33.80	20.69	10.42			
Ochetellus glaber sp. JDM 19	2.11		4.17			
Rogeria flavigaster			2.08			
Rhytidoponera inornata	2.11					
Tetramorium impressum	1.41					
Monomorium decuria	0.70					
COLD CLIMATE SPECIALIST						
Monomorium leae	3.52	3.45	2.08	4.44		
Stigmacros clarki	2.11		2.08			
Stigmacros epinotalis			2.08			
Notoncus gilberti	0.70					
GENERALISED MYRMICINAE						
Monomorium sydneyense	28.17	24.14	12.50	4.44		
Crematogaster laeviceps chasei	2.82					
Crematogaster queenslandica gp. sp. JDM 428	2.11					
Pheidole ampla perthensis	1.41					
DOMINANT DOLICHODERINAE						
Iridomyrmex chasei	36.62	13.79	4.17			
Iridomyrmex mattiroloi splendens	1.41		2.08			
Iridomyrmex agilis gp. sp. JDM 85	12.68	6.90				
Anonychomyrma sp. JDM 835	0.70	3.45				
Iridomyrmex exsanguis		3.45				
Iridomyrmex discors	4.93					
INTRODUCED (other than *P. megacephala*)						
Cardiocondyla nuda	4.93	6.90	2.08			
Tetramorium bicarinatum	0.70		2.08			
Paratrechina bourbonica	0.70	3.45				
CRYPTIC SPECIES						
Hypoponera congrua		3.45				
Pachycondyla lutea	1.41					
Solenopsis clarki	0.70					
SUBORDINATE CAMPONOTINI						
Camponotus scratius	2.80					
Camponotus terebrans	2.11					
TOTAL SPECIES RICHNESS	31	16	16	7	3	2