

**Invasion dynamics of exotic ants:
interactions with native ants on Fraser
Island, in south-east Queensland**

PHD THESIS

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Executive Summary

This thesis investigates the mechanisms of invasion by the introduced ant *Pheidole megacephala* and interactions with native ant biodiversity in the World Heritage listed Fraser Island, an area with high biological diversity values. The research showed that Fraser Island is rich in ant fauna with 172 species from 57 genera collected, and predicted species richness approaching 300 species. The lack of behaviourally dominant taxa and high relative abundance of opportunistic species makes the Fraser Island ant fauna potentially susceptible to invasion by exotic taxa.

The introduced ants *Pheidole megacephala* and *Paratrechina longicornis* were associated with low native ant species richness and abundance in disturbed native vegetation at Kingfisher Bay and *P. megacephala* was identified as a particular threat. Annual variation in *P. megacephala* infestation boundaries were documented at Dilli Village, where vegetation management by Queensland Parks and Wildlife Service interacted with that infestation. The clearing of vegetation by mechanical means had varying effects with a general expansion of the *P. megacephala* infestation followed by retreat in a regeneration area, with expansion being followed by stability in continually managed areas. Management fires in native vegetation promoted the expansion of the *P. megacephala* infestation from edge populations.

At Dilli Village *P. megacephala* stopped foraging above 40°C or below 20% relative humidity in open areas, but they foraged 24 hours a day in native vegetation areas. *Iridomyrmex bicknelli* and *Monomorium sydneyense* were able to displace *P. megacephala* on baits when the invader reached these limits of temperature and humidity tolerance.

The use of longitudinal studies allowed the comparison of changes in native ant assemblages before and after advance or retreat on the *P. megacephala* infestations. In undisturbed native vegetation at Dilli Village and Lake Wabby, there were very rich native ant faunas and no difference in native ant biodiversity indicators, including species turnover between pitfall traps with and without *P. megacephala*. When there was no reduced native ant species richness pre-invasion, there was no reduced native ant species richness post-invasion. These results cast doubts over the interpretations of many published Australian studies that commonly suggest that *P. megacephala* cause lower native ant species richness but such studies generally do not contain pre-invasion data.

There was no evidence to support the suggestion that *P. megacephala* is a threat to native ant assemblages in undisturbed native vegetation on Fraser Island. However because of their competitive nature and sheer abundance they may be a potential threat to ecosystem services provided by ants. Experiments that examine how *Pheidole megacephala* invasions affect ecosystem services, such as soil engineering, tendering scale, viability and/or seed dispersal are required to elucidate the impacts on ant invaders on these important processes in this World Heritage Area.

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Certificate of Authorship

I WAYNE ROBINSON hereby declare that this submission is my own work and that, to the best of my knowledge and belief, it contains no material previously published or written by another person nor material which to a substantial extent has been accepted for the award of any other degree or diploma at Charles Sturt University or any other educational institution, except where due acknowledgment is made in the Thesis. Any contribution made to the research by colleagues with whom I have worked at Charles Sturt University or elsewhere during my candidature is fully acknowledged.

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27 July 2011

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Chapter 1: Introduction

1.0 Ants and exotic ant invasions

Ants are extremely abundant and diverse, rivalling people as the dominant organisms on land (Hölldobler and Wilson 1990, 1994, Majer et al. 2004). Functionally, ants are one of the most important animals in natural and disturbed ecosystems. In natural ecosystems, ants are important distributors of seeds (e.g. Andersen and Morrison 1998, Auld 1999, MacMahon et al. 2003), distributors of nutrients (Eldridge and Myers 1998, Nkem et al. 2000, MacMahon et al. 2003) and movers of soil (Folgarait 1998, Lobry de Bruyn 1999). They have been described as ecosystem engineers (Jones et al. 1994) and are responsible for changes in soil structures, including aeration and drainage characteristics (Eldridge and Myers 1998, Folgarait 1998, Lobry de Bruyn 1999, Nkem et al. 2000). In disturbed ecosystems, ants are an essential component of the colonisation, succession and recovery processes (Majer 1985a, Majer and de Kock 1992, Hoffmann and Andersen 2003, Majer et al. 2004). It is the composition of the ant faunas present that dictates how these roles are carried out within ecosystems.

The composition of ant assemblages in natural areas is primarily determined by abiotic factors like climate, soil and vegetation types (Greenslade and Thompson 1981, Majer et al. 2004). But, locally, they can be affected by biotic factors like predation (e.g. Gotelli 1996), prey or resource availability (e.g. Shattuck and McMillan 1998), inter-specific competition (Greenslade 1971, Fernández-Escudero and Tinaut 1999, Morrison 2000) and intra-specific competition (e.g. Holway et al. 2002a, Tsutsui and Suarez 2003). Some ant assemblages are

dominated by aggressive taxa that limit the activity of other taxa that generally nest and forage in spatial and temporal gaps left by the dominant taxa (Andersen and Patel 1994, Majer et al. 1994, Andersen 1995, Delabie et al. 1995, Andersen 1997, Peng et al. 1999, Wetterer et al. 1999, Johnson 2001, Gibb and Hochuli 2003, MacMahon et al. 2003). The role of dominant taxa can be quite complex and be part of a cascade of interactions between dominant, subordinate and subdominant taxa (Arnan et al. 2011). On the other hand, some ecosystems do not have many dominant taxa present naturally (Reimer 1994, Krushelnycky et al. 2005) and some disturbed ecosystems have reduced numbers of aggressive taxa (Human et al. 1998, York 2000, Hoffmann and Andersen 2003, Andersen et al. 2004). Thus these ecosystems may offer less interference competition and be more vulnerable to invasion by new ants introduced to the system.

1.1 Tramp and invasive ants

Almost 150 species of ants have been recorded outside their natural habitat and those ants that are commensal with humans are often transported by humans (McGlynn 1999b, Tsutsui and Suarez 2003, Hoffmann 2004). Most of these 150 species are restricted to human habitations when they occur, and are often described as “Tramp ants”. Tramp ant species were described by Hölldobler and Wilson (1990) as having the following characteristics:

- polygyny (multiple queens occur in a colony);
- unicoloniality (there is a lack of intraspecific aggression between colonies);
- budding (dispersal is not from winged nuptial flights, founding queens walk a short distance from the existing colony, usually taking some workers to help establish the new colony);

- largely dispersed throughout the world by human commerce, and;
- live in close associations with humans.

Tramp species generally have small worker castes and sterile workers (Passera 1994). Tramp ants are also opportunistic in their nesting preferences and always aggressive in competitive encounters (Brandao and Paiva 1994). Other tramp characteristics since identified are opportunism for food and nest location and fast nest relocation after perturbation (Le Breton et al. 2003). Several tramp species have been associated with homoptera as a food source (e.g. Way 1963, Rao et al. 1989, Reimer et al. 1990)

Many ant species, even within their range of origin are collected in non-native habitats, but tramp ants have the ability to establish long term populations in new areas (McGlynn 1999b). Tramp species are not necessarily a huge problem economically nor ecologically because they characteristically only occupy niches which are unoccupied by native species and don't necessarily interrupt ecosystem services performed by other ants (McGlynn 1999b). Hence they are common in locations where urban development is a regular feature (e.g. Collingwood et al. 1997) or ecosystems with naturally low ant species richness (Reimer 1994, Wetterer et al. 1999). When ant species are introduced to a new area and can displace native ants or disrupt ecosystem services, they are generally classified as "invasive".

Invasive ant species typically have the same characteristics as tramp species (Brandao and Paiva 1994, McGlynn 1999a, Tsutsui and Suarez 2003), but can dominate local taxa by monopolising food and other resources (Hoffmann 1998, McGlynn 1999b, Heterick et al. 2000, Vanderwoude et al. 2000, Holway et al. 2002a, Le Breton et al. 2003). The success of invasive ant species varies between locations according to environmental and biotic factors including biotic resistance (Ward 1987, Holway 1998b, Holway and Case 2001, Suarez et

al. 2001, Holway et al. 2002a). For example, in California, the invasive *Linepithima humile* appear to be primarily limited by the physical environment (Holway et al. 2002b) but in Western Australia they appear limited by native *Iridomyrmex* species (Majer 1994).

Some species may be considered tramps in some locations and invasive in others (Holway and Case 2001). For example, the Black Crazy Ant *Paratrechina longicornis* is not considered a major threat to biodiversity and only weakly interacts with native species in Kakadu National Park, Australia (Hoffmann and O'Connor 2004) but in the Biosphere II project in the Arizona Desert *P. longicornis* was ecologically dominant and skewed the entire arthropod diversity in a way that favoured the ants (Wetterer et al. 1999).

There are five invasive ant species that are such a serious concern they are listed in the top 100 of the world's most serious invaders (Baskin 2002). The general characteristics of the six most serious invasive ant species are reasonably well documented in the literature (For a comprehensive literature review start with Holway et al. 2002a) and their ranges are summarised in Table 1.1. In Australia there are at least 13 exotic ant species, including all six of considerable concern (Table 1.1; Hoffmann 2004).

1.2 The impacts of invasive ants

Although there have been many studies in since Elton's monumental book (Elton 1958), invasion ecology is still a rapidly growing field. Recognition of the significance of research into the causes, consequences and management of biological invasions is extremely important (Lodge 1993, Vermeij 1996, Vitousek et al. 1996, Byers et al. 2002), particularly

for biodiversity and conservation of ecosystem integrity. Although scientists have known about invasive ants for over a century (Wheeler 1908, Tryon 1912, Illingworth 1935, Greenslade 1971, 1972, Reimer 1994), research into the effect and control of invasive ant species has particularly benefited from several key studies in the past two decades; notably significant works are those by Ward (1987), Williams (1994), McGlynn (1999b) and Holway *et al.* (2002a).

Table 1.1. Global distribution of the six most serious invasive ants (adapted from Holway *et al.* 2002a).

Species	Common Name	Native Range	Introduced Range
<i>Anoplepis gracilipes</i>	Long-legged Ant, Crazy Ant, Yellow Crazy Ant	Africa?/ Asia?	Africa, Asia, Australia, Caribbean, Indian Ocean (islands)
<i>Linepithema humile</i>	Argentine Ant	South America	Africa, Atlantic Ocean (islands), Asia, Australia, Mediterranean, North America
<i>Pheidole megacephala</i>	African Big-headed Ant, Big-headed Ant, Brown House Ant, Coastal Brown Ant	Africa	Africa, Australia, North America, Caribbean, Indian Ocean, Mediterranean, Pacific Ocean (islands), South America
<i>Solenopsis invicta</i>	Red Imported Fire Ant	South America	Asia, Caribbean, North America, Australia, New Zealand
<i>Solenopsis geminata</i>	Tropical Fire Ant	Central & South America	Africa, Asia, Australia, Pacific Ocean, Caribbean, North America, Indian Ocean
<i>Wasmannia auropunctata</i>	Little Fire Ant	Central & South America	Africa, Caribbean, Australia, Pacific Ocean, Middle East, South America, North America

Ant biomass in invaded areas can remain unchanged (Holway 1998a) or be higher than uninvaded areas (e.g. Porter and Savigno 1990, Hoffmann et al. 1999, May and Heterick 2000). However, because invasive ants are generally smaller than native ants (McGlynn 1999a), there are usually more individual ants in an infested area even if biomass is the same (May and Heterick 2000). Areas that are invaded by exotic ants almost always have lower overall ant species richness (e.g. Delabie et al. 1995, Holway 1998a, Suarez et al. 1998, Hoffmann et al. 1999, Kaspari 2000, Holway et al. 2002a, Le Breton et al. 2003, Sanders et al. 2003). In some instances, the lower richness may contribute to the susceptibility of invasion in the first place (e.g. Collingwood et al. 1997), but in some cases the invasion may be causing the lower richness (Holway et al. 2002a). The latter case is of great concern and there have been only a few studies (using experiments or well-designed observational studies) where it has actually been documented (e.g. Holway et al. 2002a, Hoffmann and Parr 2008).

Sanders *et al.* (2003) sampled plots before invasion by *L. humile* and determined no pre-invasion difference in native ant fauna richness before invasion in uninvaded and invaded plots. Subsequently, the disassembly of the native ant community in the invaded plots after invasion was able to be attributed to the effect of the invaders (Sanders et al. 2003). This still doesn't mean the plots weren't different in some external factor that promoted the infestation, but it does suggest *L. humile* can displace native ants in some circumstances. Even without many well-designed experimental studies, the weight of evidence for the relatively well-studied invasive ant species such as *L. humile* and *S. invicta* suggests that they do displace or affect many native ant communities. Displacement in this context can

mean to remove, exterminate, exclude, or prevent from returning after removal, possibly by disturbance.

Invasive ant infestation impacts can differ both spatially and temporally as the density of the invader varies (e.g. Sanders et al. 2001, Sanders et al. 2003). Long-term studies are needed to document such processes and to understand factors influencing variability in densities and dominance. For example Tryon (1912), left no doubts to the dominance exerted by *P. megacephala* in the Brisbane region early last century:

- “Scarcely any other insect can exist where it has become established—soil or arboreal dwellers”
- “The dearth of insect life generally in Brisbane is largely attributable to their voracious hordes”
- “Remarkably, other kinds of ants vanish before them”
- “They will quite exterminate the large communities of the ‘meat-ants’—*Iridomyrmex* and of *Lasius* sp. as well as Formicidae—*Camponotus*, *Polyrachis*, *Leptothorax*, *Crematogaster*, *Monomorium*, etc. Even *Ectatomma metallica*”.

It sounded so bad that one may have expected no other insects in Brisbane 100 years later but that isn't the case (256 ant species were collected in Brisbane in 2005 (Churchill 2007)). It is possible that evolutionary changes may allow integration of invasive ants into native assemblages (Heterick et al. 2000). There is also evidence that an equilibrium occurs in some environments where the invader numbers decline after a period of time (e.g. Morrison 2002). This could be related to competition with other invasive ant species (Haskins and Haskins 1965, Passera 1994, Morrison 2002, Wetterer and Wetterer 2004), abiotic factors of the environment (e.g. Hoffmann et al. 1999) or interactions with native species. Regardless, short-term impacts of invasive ant species may not accurately predict the long-term

consequences on the recipient ant and other arthropod communities (Morrison 2002). Well-designed long-term studies are needed to resolve these issues.

1.3 Biotic resistance

Biotic resistance (Elton 1958) implies that when there are few unused niches, it is difficult for dominant species or invaders to get a foothold and that species rich areas are not often invaded successfully by other taxa (Holway 1998b). For example, a combination of local minor species was able to restrict the usually dominant *Iridomyrmex cordatus* in the Solomon Islands (Greenslade 1972). In Australia, biotic resistance can also refer to interference competition as it may not be the diversity of native ants but the presence of aggressive native species that is the key to invaders not being successful in some areas (Majer 1994, Hoffmann 1998, Hoffmann et al. 1999). For example, the existence of the diverse and ubiquitous fauna of *Iridomyrmex* spp. in Western Australia has probably contributed to the containment of *L. humile* outbreaks (Majer 1994). Either way, biotic resistance from native ants probably varies regionally (Holway et al. 2002a)

Biotic resistance may also be related to other factors such as disturbance and habitat. Tramp species in general are highly successful in and around human structures and we know the native ant faunas associated with human structures are generally depauperate (Fowler et al. 1994). For example, *L. humile* infestations in Western Australia occur in obviously disturbed areas with simplified ant faunas such as market gardens, grassed areas around lakes, and rubbish dumps (Majer 1994).

The role of biotic resistance in restricting invasion by invasive ant species may be very important (e.g. Greenslade 1972, Holway 1998b) yet it is one of the least understood components of invasive ant ecology probably because there are ethical issues that make manipulative experiments difficult to perform (Holway 1998b). Most published studies researching invasive ant impacts use anecdotal or present correlative evidence only (Holway et al. 2002a) and are simply snap shots that lack pre-invasion data on natural ant community structure or ecosystem functioning (Sanders et al. 2003). The problem with these studies is that intact and invaded areas may differ in some way other than the presence of the invasive ant (Sanders et al. 2003). For example, differences could be because of the features of the sites that the invasive ants prefer, rather than the invasive ants themselves (Ward 1987).

1.4 Pheidole megacephala

The *P. megacephala* (Big Headed Ants or BHA) type specimen was collected in Mauritius in 1793 with other early records coming from Portugal in 1862 (Tryon 1912). They have been described as of East Indian origin (Wheeler 1908, Wilson 2003) but are generally thought to originally be from Tropical or Northern Africa (Wilson and Taylor 1967, Greenslade 1972, Fowler et al. 1994, Haines et al. 1994, Jahn and Beardsley 1994, Passera 1994, May and Heterick 2000, Holway et al. 2002a).

P. megacephala do best in relatively moist, disturbed habitats, and hence thrive around human habitations and cultivated land (Wilson 2003). Tryon (1912) reported that *P. megacephala*'s ability to spread rapidly with human assistance was noted in Mayr's 1864–85 voyage notes. There are records of *P. megacephala* occurring at least in England

in 1861, South Africa, Algeria, Turkestan in 1883, New Guinea in 1887, Cairns in 1901 with the species already being well established in Brisbane and Hawaii by the first Australian paper on their occurrence here (Tryon 1912). *P. megacephala* is likely to have been in Darwin by the 1930's (Hoffmann and O'Connor 2004).

P. megacephala is restricted to coastal and nearby urban districts in Australia, with records along the East coast from Eden to the tropics (Nikitin 1979, Vanderwoude et al. 2000) and similar environments in south Western Australia (van Schagen et al. 1994, May and Heterick 2000) and Darwin and the Northern Territory (Hoffmann 1998).

Like all ant species, *P. megacephala* can be patchily distributed locally (Wilson 2003) and numbers can fluctuate regularly, probably because of competition or abiotic factors (Greenslade 1971, Heterick et al. 2000). Successful colony establishment by *P. megacephala* may be determined by prevailing meteorological conditions (Tryon 1912). Propagule size, in particular, the number of workers present with the queen, is also likely to be an important factor in determining colony survival after a translocation (Holway et al. 2002a).

Biotic resistance is a possible factor in limiting the distribution of *P. megacephala* in Australia (Hoffmann et al. 1999). After sand mining on Stradbroke island, *P. megacephala* were able to invade remote but native ant species depauperate areas (Majer 1985a). *P. megacephala* were unable to spread into adjacent plots, probably because of competitive exclusion by the relatively rich native ant fauna of the ground layer (Majer 1985a). In the Solomon Islands, *P. megacephala* should be well suited to the lowland forest climate, but

were absent, probably because of competitive exclusion by the relatively rich native ant fauna in the forest litter layer there (Greenslade 1972).

The role of disturbance in invasions varies according to interactions with biotic and abiotic factors (Lodge 1993). Disturbance of any kind can provide new habitats and stress, or can remove native species allowing for the movement of introduced or dominant species (Stiles and Jones 1998, Gibb and Hochuli 2003). Many of the native ant species missing from rehabilitated areas on Stradbroke Island were cryptic litter dwelling species and wood nesters, or ants with strong arboreal foraging or nesting traits (Majer 1985a). In other words, the disturbance itself may have reduced the biotic resistance, making the sites vulnerable to *P. megacephala* invasion. *P. megacephala* are common along urban corridors in coastal Australia and are probably expanding their range coincident with the ongoing disturbance through urban development and human expansion. There are no studies that have been able to isolate the roles of disturbance and biotic resistance in facilitating invasion by *P. megacephala*.

The site of Vanderwoude *et al.* (2000) is of interest, as it has had no timber harvesting for at least 30 years and no evidence of recent disturbance. However, there is evidence of some kind of post-European settlement structure in the vicinity of the infestation, probably the remnants of a cattle yard (Cas Vanderwoude, Pers. Comm. 2012). Regardless, this site and those of Majer (1985) illustrate that even long after the disturbance has been removed, once *P. megacephala* have a foothold, it is very difficult for them to be removed.

P. megacephala invasions on the Hawaiian islands and Bermuda are in pristine areas, but these areas also have low natural biotic resistance (Haskins and Haskins 1965, Gillespie and

Reimer 1993, Reimer 1994, Wetterer and Wetterer 2004). Individual *P. megacephala* had ventured small distances into natural bushland from a few points of the disturbed area on Mount Coot-tha (Heterick 1997) but seldom moved away from drainage lines at Howard Springs in the Northern Territory (Hoffmann et al. 1999). *P. megacephala* probably don't move out of rainforest because of desiccation and competition with *Iridomyrmex* at Howard Springs (Hoffmann 1998). *P. megacephala* can sometimes appear restricted to disturbed areas, with occasional movement over small distances into surrounding undisturbed areas if microhabitat sites are suitable (Heterick 1997, Hoffmann et al. 1999). *P. megacephala* have been found in long undisturbed areas (Vanderwoude et al. 2000) and in areas with unknown but apparently never disturbed histories (W Robinson, pers. obs.; J. D. Majer pers. comm. 2004). A recent study looked at *P. megacephala* in a remnant bushland area within an urban neighbourhood in Western Australia (Callan and Majer 2009) but even then the site displayed some evidence of disturbance such as decreased native vegetation cover and density, increased weediness and dumping of rubbish. On top of that, proximity to known disturbed areas may in itself be a form of disturbance because of the reduced pool of native species in the region.

Generally speaking, there are few studies on ecological impacts of *P. megacephala* in naturally species rich habitats that haven't been disturbed (Hoffmann et al. 1999). This may be because there aren't any where it has successfully invaded or there aren't many habitats that haven't been disturbed by humans.

1.5 Impacts of *P. megacephala* on native ants

Every published study of *P. megacephala* invasions in Australia is observational and, as such, the characteristics of native ants in invaded areas cannot be attributed to the invasion. For example, in heavily disturbed areas like urban gardens or highway fringes, where *P. megacephala* are present they are highly numerous and native ants are in lower abundance and richness than uninfested areas (Samways et al. 1997, Heterick et al. 2000, May and Heterick 2000). This only means that most (dominant) native ants and *P. megacephala* are mutually exclusive, as are many native ants and disturbance (e.g. Andersen 1995, York 2000). The same reasoning of disturbance facilitating the invasion can be applied consistently across observational type studies; Native species may have been eradicated in the Perth region by an earlier baiting campaign against *L. humile* (May and Heterick 2000); many urban gardens don't have suitable nesting habitat for native ants, hence favour *P. megacephala* and their opportunistic nesting requirements (Heterick et al. 2000). In other words it is possible that the removal of the nest sites, not the arrival of the *P. megacephala*, that removed the native ants (Heterick et al. 2000).

Even where an exotic ant invaded area has been observed before and after invasion, there is usually potential for spatial and/or temporal confounding (Holway 1998b). The only published repeat visit study of *P. megacephala* and native ant relationships in Australia (Hoffmann and Parr 2008) cannot absolutely resolve that the changes observed in native ant assemblages were the cause or the effect of the observed changes in the *P. megacephala* populations.

In spite of the lack of true experiments, the weight of evidence continues to build and has led to a widespread acceptance that invasion by *P. megacephala* seriously devastates native ant and arthropod faunas wherever they occur (e.g. Heterick 1997, Samways et al. 1997,

Hoffmann et al. 1999, May and Heterick 2000, Hoffmann and Parr 2008, Callan and Majer 2009). There is also little doubt, that once infested by *P. megacephala*, an area is extremely unlikely to recover from disturbance or ever have similar ant assemblages to those had it been uninfested (e.g. Majer 1985a). *P. megacephala* supercolonies in non-urban areas in Australia are commonly known to cover areas larger than 10 ha (Vanderwoude et al. 2000, Hoffmann and O'Connor 2004), with the Howard Springs population covering at least 25 ha (Hoffmann et al. 1999). When they have successfully colonised an area, *P. megacephala* exclude most other ant species (Majer 1985a, Reimer 1994, Hoffmann et al. 1999, Heterick et al. 2000, Vanderwoude et al. 2000, Wilson 2003, Hoffmann and O'Connor 2004) (Table 1.2). If impact and/or displacement are not thought of as direct killing, but rather as exclusion of, or prevention of recolonisation by native ants, then the evidence is substantially greater. For example, increases in native ant species richness were observed after *P. megacephala* were poisoned (Heterick et al. 2000, May and Heterick 2000). Hoffman (2009) showed that restoration of native ant assemblages was achievable when a *P. megacephala* infestation was suppressed.

Whilst *P. megacephala* consistently make up more than 90% of actively foraging ants at sites where they have invaded (Table 1.2), the effects on overall ant abundance varies between habitats and *P. megacephala* is apparently most damaging in tropical and subtropical areas (Heterick et al. 2000). The types of impacts are also quite likely to be different in regions depending on the prevailing biotic and abiotic factors. Studies like Majer (1985) and Heterick (1997) may have experienced less severe impacts because they were in open vegetation types, unlike the rainforest sites at Howard Springs (Hoffmann et al. 1999, Hoffmann and Parr 2008). In Monsoonal rainforest in the Northern Territory, overall ant

abundance was 37 to 110 times the abundance of all native ants combined at uninfested sites (Hoffmann 1998). Yet, overall ant abundance wasn't different between infested and uninfested sites in the studies by Heterick (1997) and Vanderwoude et al. (2000). The study of Heterick (1997) suffered from low replication and low statistical power and his result reflects this, as there was an average of 998 workers per *P. megacephala* plot compared to 318 in the uninfested plots. Callan and Majer (2009) reported their results in 'zones' of *P. megacephala* abundance and, as such, offer a data set with added value for investigating interactions with native ant species richness.

The studies shown in Table 1.2 are usually only comparing catches of foraging ants made in pitfall traps or another selective sampling strategy, and there is a general lack of quantitative comparisons of the true density and biomass of invasive and native ants (Holway et al. 2002a). This is made even more difficult in the case of *P. megacephala*, as they maintain diffuse supercolonies composed of ephemeral and poorly defined nests which vary in size (Broekhuysen 1948, Holway et al. 2002a). There is quite a range of the numbers of native ant species observed in the infested zones for the different studies (Table 1.2); this may be related to the differing numbers of species naturally occurring (using the ant species richness of the uninfested zones as a guide) and the density of the invaders or the diffuse supercolonies. Callan and Majer's (2009) use of zones of invader numbers may be useful, but used frequency in pitfall traps rather than absolute abundances of native ants (presumably to avoid the notorious effect of skewed data from some pitfall trap abundances) making direct comparisons inappropriate.

Given the consistent association of *P. megacephala* with reduced native ant diversity in Australia (Table 1.2) and recent evidence that *P. megacephala* have the ability to invade

native vegetation areas (Majer et al. 2004) the implications for conservation are serious (Callan and Majer 2009). Conservation of biological diversity clearly matters in the global context (Wardle 1999) and the conservation value of highly significance areas would be clearly compromised if they are vulnerable to *P. megacephala* invasions.



Plate 1: *Leptomyrmex cnemidatus* on Fraser Island.

Table 1.2. Abundance and species richness of foraging ants in areas infested by *P. megacephala* in Australian studies. Average species richness is total species richness if only one area is sampled. All except Tryon (1912) used pitfall trapping in sampling.

Source	Habitat	% Ants that were <i>P. megacephala</i> in infested areas	Average # species in uninfested areas	Average # species in infested areas	Native species co-existing with <i>P. megacephala</i> (> 3 individuals collected)
(Tryon 1912)	Urban Brisbane	Virtually all	At least eight listed, but not quantitatively sampled		One small black ant, possibly <i>Ochetellus</i> 'glaber', <i>Monomorium</i> sp. or <i>Anonychomyrma</i> sp.
(Heterick 1997)	Urban Brisbane	89%	27*	16*	<i>Camponotus aenopilosus</i> , <i>Mayriella</i> , <i>Oligomyrmex</i> , <i>Stigmacros</i> , <i>Pheidole</i> spp., <i>Paratrechina</i> sp.
(Heterick et al. 2000)	Urban Perth	95.4%	10.8*	2.0*	Virtually none
(May and Heterick 2000)	Urban Perth	88%*	9.4	4.5	<i>Iridomyrmex chasei</i> , <i>Tetramorium simillimum</i> , <i>Brachyponera lutea</i>
(Majer 1985a)	Rehabilitated exposed high sand dune, Stradbroke Island, Queensland	99%*	28*	6*	<i>Monomorium</i> sp. 5
(Hoffmann et al. 1999)	Howard Springs Nature Reserve, Northern Territory	>99%*	26.3*	5.3*	Cryptic and Opportunistic species of <i>Hypoponera</i> , <i>Tapinoma</i> and <i>Cardiochondyla</i>
(Vanderwoude et al. 2000)	Native open hardwood forest, South eastern Queensland	94%	25*	2.0*	None in main area, some Opportunistic species in intermediate zone
(Natrass and Vanderwoude 2001)	Urban Brisbane Remnant vegetation reserve	82%*	Not sampled	9.0*	<i>Rhytidoponera</i> sp. 31 <i>Paratrechina</i> 'obscura'
(Hoffmann and Parr 2008)	Howard Springs Nature Reserve, Northern Territory	>99%*	21*	1*	nil
(Callan and Majer 2009)	Urban Perth Remnant vegetation reserve	na	31	2–16^	<i>Melophorus</i> sp × 2 <i>Monomorium</i> sp × 2 <i>Doleromyrma darwiniana</i>

* = Calculated from published data. ^ = 2 species in traps with >1000 *P. megacephala*, 16 species in traps with 1–100 *P. megacephala*.

1.6 Guide to this Thesis

The thesis investigates the mechanisms of invasions by invasive ants and interactions with native ant biodiversity in an area with high biological diversity value, the World Heritage listed Fraser Island. Specifically, it aims to determine:

- the characteristics of the Fraser Island native ant assemblages in undisturbed habitats, their biodiversity value and vulnerability to exotic ant invasions;
- the native ant biodiversity values in areas invaded by *Pheidole megacephala*, and;
- the roles of disturbance and biotic resistance in the spread of *P. megacephala* on Fraser Island.

The thesis begins by describing the ant biodiversity values of Fraser Island, by documenting the ant species associated with each of the island's major habitats, and analysing their biogeographic and functional significance and vulnerability to invasion by exotic ants (Chapter 2). It next describes the extent to which native ant biodiversity differs in areas where the exotic ants *Paratrechina longicornis* and *Pheidole megacephala* have already invaded native bushland (Chapter 3). This identifies *P. megacephala* as associated with low native ant biodiversity, and the remainder of the thesis presents a detailed examination of the invasion dynamics of this species.

Chapter 4 reports on the dynamics of *P. megacephala* invasion boundaries over a 5-year period, and how they are influenced by anthropogenic disturbances. Changes in native ant biodiversity relative to advances and retreats in a *P. megacephala* invasion are then examined (Chapter 5). Chapter 6 uses a manipulative experiment to identify abiotic factors that allow some native ants to co-exist in areas invaded by *P. megacephala*. Chapter 7 uses a

longitudinal experiment to attempt to elucidate the roles of disturbance, biotic resistance and abiotic factors in *P. megacephala* invasions, and to describe the consequences of invasion in undisturbed native vegetation.

The thesis summary section follows the final Chapter and summarises the findings making recommendations to direct future research into *P. megacephala* infestations of Fraser Island.

Chapter 2: Ant biodiversity values of Fraser Island

2.1 Introduction

Documenting the biodiversity in internationally recognized protected areas is an important step in managing species and ecosystem processes of such areas of high conservation significance (Byers et al. 2002). Relevantly, Fraser Island in south-east Queensland, which is the largest sand island in the world, having an area of over 166,000 ha. Fraser Island was designated World Heritage Status in 1992, primarily because of its unique geological processes. However, after the natural heritage criteria were reviewed in 2002, it was recognised that Fraser Island demonstrates universal qualities across all four revised criteria viz: (1) ongoing geological and geomorphic processes; (2) ongoing ecological and biological processes; (3) natural phenomena and areas of exceptional natural beauty, and; (4) presence of exceptional biodiversity and threatened species (EPA 2005). However, there is very little published literature on ecological and biological processes or the biodiversity, on Fraser Island. In particular, research on the biodiversity of its invertebrate fauna is conspicuous by its absence from the scientific literature.

Ants are ideal organisms to study when documenting patterns of biodiversity because they are ecologically important, ubiquitous, abundant and relatively easy to sample (Folgarait 1998, Parr and Chown 2001, Majer et al. 2004). Ants are so abundant and diverse that they rival people as the dominant organisms on land, playing ecologically important roles in shaping ecosystems (Hölldobler and Wilson 1990, 1994, Majer et al. 2004). In natural ecosystems, ants are important distributors of seeds (Andersen and Morrison 1998, Auld

1999, MacMahon et al. 2003), distributors of nutrients (Eldridge and Myers 1998, Nkem et al. 2000, MacMahon et al. 2003) and movers of soil (Folgarait 1998, Lobry de Bruyn 1999). They have been described as ecosystem engineers (Jones et al. 1994) and are responsible for changes in soil structures, including aeration and drainage characteristics (Eldridge & Myers 1998; Folgarait 1998; Lobry de Bruyn 1999; Nkem *et al.* 2000).

Ants are so linked to their environment that distributions of many species are linked with soil type and this is often manifested by changes in vegetation type (e.g. Greenslade and Thompson 1981). The vegetation types on Fraser Island follow a distinct succession from East to West (Sinclair and Morrison 1990), making sampling and comparison of ant faunas within and between vegetation types a practical and suitable method for documenting ant biodiversity on the island. The specific aims of this chapter are to:

- provide an overview of the ant fauna of Fraser Island;
- identify affinities of the ant faunas with the Fraser Island vegetation communities;
- compare the Fraser Island ant faunas with other Australian faunas in terms of functional and biogeographical affinities, and;
- determine relative abundance of native behaviourally dominant species (a potential measure of biotic resistance to exotic ant invasions).

2.2 Methods

2.2.1 Study sites

Fraser Island has a subtropical climate and generally has the coolest months in July and August, driest months in August and September, hottest Months in December to March and wettest months in January and February. There are nine broad categories of vegetation types defined for Fraser Island, based on the Stanton vegetation typing (Craig 1985). Seven categories that were deemed suitable ant habitats (swampland and mangrove areas were excluded) plus Mixed Forest with Cypress, an additional more recently described vegetation type with only two small patches (QPWS 2005) were included in this study. Two replicate sites were chosen for each vegetation type for sampling and their main features are described in Table 2.1. The replicate sites were at least 2 km apart, separated by at least one other vegetation type, and spread out where possible to encompass the width and breadth of the island (Figure 2.1).

Table 2.1. Location and vegetation characteristics of study sites for ant surveys on Fraser Island in April and September 2004. Sites were selected using the Craig (1985) classifications except Mixed forests with Cypress, which were selected using local knowledge and this vegetation type was officially described by QPWS (2005).

Vegetation type as described by; Craig (1985) or [QPWS (2005)]	Site code	Location	Vegetation characteristics (Craig 1985) except *(W Robinson pers obs.)
<i>Banksia</i> shrubland [Forest/Heath]	BSH101	S25035.733' E153004.904'	Mostly shrub communities in which <i>Banksia serratifolia</i> is the dominant or co-dominant canopy species with <i>Eucalyptus signata</i> and <i>E. gummifera</i> . Trees over 14m mostly less than 25% of canopy
	BSH102	S24023.518' E153004.810'	
Tall <i>Eucalyptus pilularis</i> forest [Tall eucalypt forest]	TEP41	S25034.490 E153002.791'	Over 26 m and mostly over 30 m. Canopy almost entirely formed by <i>Eucalyptus pilularis</i> .
	TEP42	S25024.527' E153005.464'	
Low to medium open Eucalypt Forest [Scribbly gum or Wallum forest]	LME51	S25024.240' E153003.794'	Low to medium Eucalyptus forest. Over 25% of canopy formed by trees over 12 m and generally less than 22 m.
	LME52	S24059.246' E153017.734'	
Carrol scrub [Vine forest]	CVF31	S25024.587' E153005.501'	Vine forest dominated by <i>Backhousia myrtifolia</i> (Carrol). May have <i>Araucaria cunninghamii</i> as the main emergent.
	CVF32	S25023.521' E153004.815'	
Tall closed forest [Tall closed forest]	TCF21	S24059.255' E153017.782'	Tall closed forest with canopy cover over 25% of <i>Syncarpia hillii</i> and/or <i>Tristania conferta</i> . Generally over 30 m. Vine understorey may be present.
	TCF22	S25021.880' E153006.604'	
unnamed [Mixed forest with Cypress]	MFC201	S25024.518' E153000.805'	*Medium to tall open to semi-open forest dominated by <i>Callitris macleayana</i> . Understorey mostly woody debris, with sparse vegetation
	MFC202	S25023.229' E153001.968'	
Mixed shrubland [Coastal forest]	MSH111	S25036.691' E153005.381'	Open to closed shrublands with scattered small areas of grassland. Usually in exposed coastal positions. Trees over 14 m generally less than 25% of canopy cover.
	MSH112	S24056.684' E153017.816'	
Grassland [Grassland]	GLD131	S25047.589' E153004.480'	Grassland with occasional shrubs
	GLD132	S24057.802' E153020.978'	

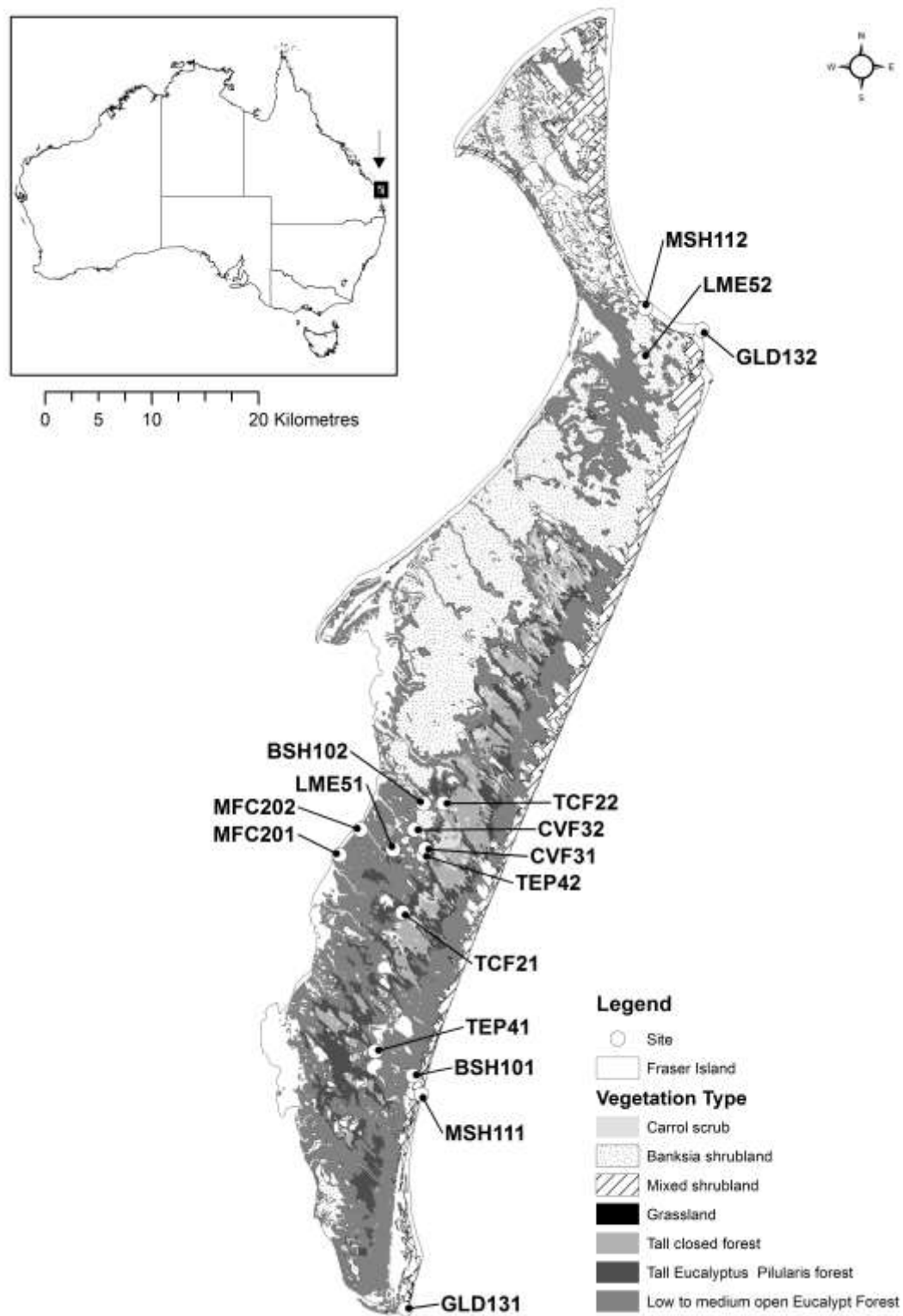


Figure 2.1. Approximate location of study sites on Fraser Island, Queensland. Precise latitude and longitudes are given in Table 2.1.

2.2.2 Sampling strategy

Simple species lists of ant assemblages can be obtained by sampling epigaeic (ground foraging) ants using pitfall traps (Andersen 1991, Andersen et al. 2002). However, pitfall trapping is only moderately effective for sampling litter ants (Bestelmeyer 2000), so cannot give complete inventories of species richness. Some authors supplement pitfall trapping with active or hand searching (King et al. 1998), but these methods may also be biased towards ground foraging ants or conspicuous species. Improved species lists can be obtained by sampling more than once (Hinkley and New 1997) or by including litter sampling (Bestelmeyer 2000, York 2000, Parr and Chown 2001). Winkler sacks have become the common form of litter sampling overseas (Fisher 1999, Delabie et al. 2000, Vasconcelos et al. 2000, Soares et al. 2001) and more recently are gaining popularity in Australia. Whilst Winkler sacks may collect more ants than other methods, they may also not be exhaustive (Fisher 1999). More recently, another method has been to use bait traps under the surface to attract subterranean ants (Andersen and Brault 2010) and this may lead to discovering a completely new ant fauna (Wilkie et al. 2007), although this method alone may be selective because it uses baits. This study aimed to collect as many ant species as possible by using a variety of sampling methods, using the vegetation classification to stratify sampling, taking replicate samples within each vegetation type and sampling in two seasons.

Collection of ants for all sites occurred during 19th March to 2nd April and 24th September to 6th October 2004. At each site three or four methods were employed for ant collection on each date (Table 2.2). The data collected in March were used by Peter Collier in his Honour's Thesis (Collier 2004).

Pitfall traps

Plastic vials (42 mm internal diameter x 109 mm deep) were half filled with 70% ethanol and 3% glycerol solution and buried so that the rim of the trap was flush with the soil surface. The traps were placed in a 5 x 3 grid with 10 m between traps. Displacing soil whilst deploying pitfall traps can attract opportunistic ant species (Greenslade 1973) but this was not of concern because all substrate was sand that could be displaced with minimal disturbance. Traps were left open for four days in both surveys.

Litter extractions

Upon removal of the pitfall traps in the April survey, five × 1 m² quadrats were randomly placed in the pitfall grid sampling area. Large sticks were broken or removed and all remaining litter was sieved to remove large leaves, then returned to the field station in sealed plastic bags and hung in individual Winkler sacks for 72 hours. Using this method, on occasions, there were more samples than Winkler sacks available and several samples were unusable by the time sacks were available. Therefore there are no litter samples for MSH112, MTEL 52 and CTF21 in April. In the September survey the five samples were combined, sub-sampled and hung in two Winkler sacks in the field. Litter samples were not taken from grassland sites on either date because there was no litter.

Subterranean sampling

A novel sampling method was trialled in the September survey using sub-surface baiting. Pitfall trap vials had access holes (11 mm diameter) drilled into their walls and a teaspoon of tuna placed inside, then buried 30 cm beneath the sand with the lid secured (Figure 2.2).

Five traps per site were randomly located within the pitfall grid and positioned and collected at the same time as the surface pitfall traps. Samples were transferred to sealed vials and fixed with 70% ethanol upon collection. The subterranean traps were regularly lost after being dug up by dingoes or goannas. A small number of the pitfall traps were also lost to animals in the September sampling. The actual number of samples available for each method in each site-date is given in Table 2.2.

Hand sampling

Two people searched actively at each site for a minimum of 30 minutes and until no new species were collected within a five minute period. The hand sampling was conducted within a 10 m perimeter of the pitfall grid, giving an effective sampling area of 2400 m² per site. The time taken for each site was 30–60 minutes and was always conducted between the hours of 10:00 and 16:00. Samples were transferred to sealed vials and fixed with 70% ethanol upon collection.

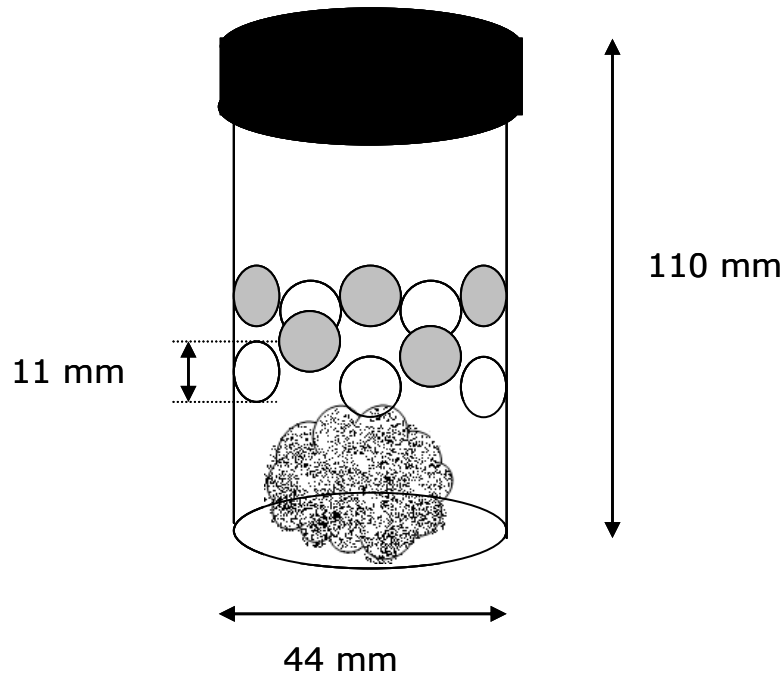


Figure 2.2. Subterranean traps with tuna bait for sampling ants used on Fraser Island in September 2004. Dimensions are external measurements.

2.2.3 Ant identification

Ants were identified to species or species group following Andersen (2000), with unique species assigned a letter unique to this study (Alan Andersen pers. comm.). All species were assigned to functional group and biogeographic affinities as described by Andersen *et al.* (2004). Voucher specimens are lodged at the CSIRO Tropical Ecology Research Centre (TERC), Darwin, Australia.

Table 2.2. Sampling effort for ants in 16 sites on Fraser Island in 2004. The area covered by each leaf litter sample in September is equivalent to 2.5× the area covered by the April leaf litter samples. Dashes indicate samples not collected or all samples lost to an external disturbance.

Site	April-2004			September-2004		
	Pitfall traps	Leaf litter samples	Subterranean traps	Pitfall traps	Leaf litter samples	Subterranean traps
BSH101	15	5	-	15	2	3
BSH102	15	5	-	15	2	5
MFC201	15	5	-	15	2	5
MFC202	15	5	-	15	2	2
CVF31	15	5	-	15	2	3
CVF32	15	5	-	15	2	5
TCF21	15	-	-	15	2	4
TCF22	15	5	-	15	2	5
GLD131	15	-	-	15	-	1
GLD132	15	-	-	15	-	5
MSH111	15	5	-	15	2	2
MSH112	15	-	-	14	2	4
LME51	15	5	-	11	-	1
LME52	15	-	-	14	2	2
TEP41	15	5	-	13	2	5
TEP42	15	5	-	15	1	2

2.2.4 Statistical analysis

Overall ant species composition and richness

To estimate the overall ant species richness for Fraser Island species accumulation curves were generated for the entire island using the species lists for the 32 site-dates as samples. Accumulation curves were generated from bootstrapping algorithms purpose-written in SAS®, following those described by Codwell and Coddington (1994). Each accumulation curve was generated from 200 bootstrapped samples and the sampling evaluated for efficiency by (1) comparing the median observed species richness in the last two pitfall traps of the bootstrapped data sets to determine whether the last pitfall trap added no new species, and (2) calculating whether the median observed species richness was within 10% of the predicted richness (Peterson and Slade 1998). Predicted species richness for each sample

was based on the Chao 2 estimator for incidence based data (Chao 1987, Colwell et al. 2004). Results from pitfall traps alone and from all methods combined were compared.

Ant species richness within and between vegetation type and dates

Epigaeic ant species richness among vegetation types and date of sampling were compared using factorial analysis of variance (ANOVA). Only the pitfall trap data (all traps pooled per site) were used because of different sampling efforts from the other methods. Significant effects were tested using the Student-Neuman-Keuls multiple comparisons procedure and the assumptions of normality and homoscedasticity were checked using residual analysis.

Ant community composition within and between vegetation type and dates

The ant species data using all methods for each site and date were converted to presence and absence and Bray-Curtis dissimilarity calculated between each pair of site dates. ANOSIM was then used to test for consistencies in the similarity of community composition between; 1) the eight vegetation types; 2) the two sampling dates, and 3) the 16 sites. I calculated the actual F ratio (between/within group variation) and possible F ratios from 1000 randomised group allocations of the data. When the F ratio was significant, I determined which groups showed significant within group affinities by repeating the procedure for each pair of comparisons. All analysis of similarities were carried out using PATN 3.12 (Belbin 1989).

A Kruskal-Wallis medians test was used to identify taxa that had significantly different abundances between the eight vegetation types. The two sites and dates within each vegetation type were treated as four independent replicates for each vegetation type.

Community composition of Fraser Island ant faunas

Ant species were assigned to one of nine functional groups (Table 2.3) based on global responses of their species groups to environmental stress and disturbance (Andersen 1995, 1997). The functional groups were: Dominant Dolichoderinae, Generalized Myrmicinae, Opportunists, Subordinate Camponotini, Hot-, Cold- and Tropical-climate Specialists, Cryptic Species, and Specialist Predators. The relative abundance of foragers within the functional groups were compared between sites using only the pitfall trap data. To give equal weight to each sampling period, the percent foragers in each functional group were calculated separately for the March and September periods and averaged. The averages were then converted back to percentages to ensure 100% cumulative contributions for taxa in each site and presented in graphs, as were the % species composition in the functional groups.

Comparisons with other regional faunas

The Fraser Island ant fauna were compared with seven published ant faunas from various regions of Australia with moist climates (Table 2.4). The regional faunas were chosen to ensure that a range of ant assemblages were represented, so that a spread of values in univariate analyses and some disaggregation of results in multivariate analyses was ensured.

A comparison of ant fauna biodiversity values was performed by calculating and comparing the number of species per genus for each regional fauna. The relationship of species/genera to total species was plotted and the position of Fraser Island to the other faunas interpreted.

The percent functional group composition of the Fraser Island sites were compared with the seven regional ant faunas. A two-way classification table was generated to show groups of sites with similar ant functional groups and groups of functional groups that had similar site affinities. All analyses used Bray-Curtis similarities, flexible UPGMA clustering and were performed using PATN version 3.12 (Belbin 1989). The functional group affinities with the groups identified by the classification were tested using the Kruskal-Wallis medians test and followed up using ANOVA on the mean of the ranks. The regional faunas used in the comparisons were from the published lists with the exception of the ant species list from North Stradbroke Island (Majer 1985a) which was based on the taxonomy updated in 2011 (Jonathan Majer pers. comm. April 2011).

Table 2.3. Ant functional groups used to examine ant functional composition, following Andersen (1995; 1997).

Functional group	Characteristics	Major taxa in study region
Dominant Dolichoderinae	From a global perspective, dominant ants are those at the top of the dominance hierarchies of the most productive ant communities, and such ants are characteristically dolichoderines	<i>Iridomyrmex</i> , <i>Anonychomyrma</i>
Generalised Myrmicinae	This group comprises the cosmopolitan genera <i>Pheidole</i> , <i>Monomorium</i> and <i>Crematogaster</i> , which are among the most abundant ants throughout the warmer regions of the world. From a global perspective they can be considered subdominant to Dominant Dolichoderinae	<i>Pheidole</i> , <i>Monomorium</i> , <i>Crematogaster</i>
Opportunists	These are unspecialised, poorly competitive species, often with wide habitat distributions. They predominate only at sites where stress or disturbance severely limits ant productivity and diversity, and consequently where behavioural dominance is low	<i>Nylanderia</i> , <i>Rhytidoponera</i> , <i>Papararatrechina</i>
Subordinate Camponotini	<i>Camponotus</i> and allied genera are ubiquitous in ant communities; they tend to be behaviourally submissive to dominant dolichoderines, and many are ecologically segregated from them due to their large body size, nocturnal foraging, and/or arboreal habits	<i>Camponotus</i> , <i>Polyrhachis</i> , <i>Stigmacros</i>
Hot- climate specialists	These are taxa occurring primarily or exclusively in arid regions, and exhibit highly specialised behaviour such as granivory or extreme thermophilia	<i>Melophorus</i>
Tropical- and cold-climate specialists	These are taxa whose distributions are heavily centred on the ground-layer of temperate and tropical forests respectively. The abundance of dominant dolichoderines is generally low in these habitats, and aside from their habitat tolerances, Cold- and Tropical-Climature Specialists are typically unspecialised ants	<i>Mayriella</i> , <i>Notoncus</i> , <i>Stigmacros</i>
Cryptic species	These are small to minute species, predominantly myrmicines and ponerines, that nest and forage primarily within soil, litter and rotting logs. They are ecologically removed from the mainstream ant community	<i>Solenopsis</i> , <i>Carebara</i> , <i>Hypoponera</i>
Specialist predators	This group comprises medium-sized to large, highly active predators with well developed sight, and most have powerful stings	<i>Colobostruma</i> , <i>Myrmecia</i>

Table 2.4. Regional ant faunas compared with 16 Fraser Island ant communities. Sampling methods are only the methods considered when compiling data for this chapter. For example, Andersen *et al.* (2009) used arboreal methods but these data are not included in this comparison.

Code	Author	Study location	Habitat description	Sampling methods
SEQ_TEF	(Osunkoya <i>et al.</i> 2011)	Brisbane–Gold Coast, south east Queensland	Tall open eucalypt (dry sclerophyll) forest and subtropical (microphyll vine) rainforest	Ground pitfall, subterranean
SEQ_TEP	(Majer 1985a)	North Stradbroke Island, south east Queensland	Coastal dune similar to Fraser Island, including <i>Eucalyptus pilularis</i> , <i>Banksia aemula</i> as dominants	Hand, ground pitfall, leaf litter and arboreal
NT_MRF	(Andersen <i>et al.</i> 2007)	Wildlife Park, near Darwin, Northern Territory Australia	Monsoonal Rainforest	Litter, ground pitfall, baited arboreal pitfall,
WA_TEB	(Callan and Majer 2009)	Remnant native vegetation in Urban Perth, Western Australia	<i>Eucalyptus gomphocephala</i> and <i>Banksia attenuata</i> woodland	Ground pitfall traps
VIC_HTH	(Andersen 1986)	Wilson’s Promontory, Victoria	Heathland, dominants <i>Lepotspermum mercenoides</i> , <i>Allocasuarina pusilla</i>	Ground pitfall traps, hand
VIC_WDL	(Andersen 1986)	Wilson’s Promontory, Victoria	Woodland, dominated by <i>Eucalyptus baxteri</i>	Ground pitfall traps, hand
NSW_TEF	(Andersen <i>et al.</i> 2009)	Eden, south east New South Wales	Dry sclerophyll forest, dominated by mixed Eucalypt species	Ground pitfall traps

Comparisons of the biogeographic affinities of the Fraser Island and regional ant faunas were made by assigning each species to one of four biogeographic classes based on the distribution of their species group within Australia, following Andersen (2000); Torresian (occurring primarily in the tropical north), Bassian (primarily in the cool-temperate south), Eyrean (primarily in the arid zone), and Widespread (represented throughout Australia).

Greenslade and Thompson (1981) collected ants in the nearby Cooloola/Noosa region and whilst there is no species list available, some features relating to common species and relative frequency of dominant taxa were used for further comparisons with the Fraser Island taxa.

2.3 Results

2.3.1 Fraser Island ant species composition and richness

There were 157 species from 6173 ants collected in March and 119 species from 4503 ants in September. Across the two dates there were 172 ant species including 105 from hand samples, 129 from pitfall traps, 82 from litter samples and 25 from subterranean traps (Table 2.5). There were 55 genera, with the most diverse being *Polyrhachis* (14 spp.), *Camponotus* (11) and *Stigmacros* (10). The two numerically dominant genera were *Rhytidoponera* 24% (2499 individuals) and *Pheidole* 22% (2266). *Aphaenogaster longiceps* and *Rhytidoponera metallica* made up 11.2 and 9.2 % of all ants collected, respectively, whilst only *Nylanderia* sp. A (vaga gp.) occurred in every site (Table 2.5).

The species accumulation curves using either all data pooled or only data from pitfall traps, did not approach an asymptote with neither curve suggesting more than 75% of species were collected. The predicted ant species richness for Fraser Island was 232 for all methods and 170 for just pitfall traps (Figure 2.3).

2.3.2 Ant species richness within and between vegetation types

There were significantly different average numbers of species of ants in the pitfall traps in the different vegetation types ($F = 8.11$, $df = 7, 16$, $p < 0.0005$). The *Banksia* Shrubland

(mean = 27.5) and Mixed Forest with Cypress sites (25) had significantly more species in pitfall traps than the Grasslands (16.5), Carrol Scrub (15.25) or Tall *Eucalyptus* (13.25) sites whilst the remaining sites were intermediate in species richness. When all methods and dates were combined, the mixed Cypress woodlands had the highest individual site ant species richness, with 54 and 49 species, whilst the Grassland sites were lowest with 26 and 32 species collected.

2.3.3 Ant community structure within and between vegetation types, sites and dates

There was a significant affinity of the site dates with the eight vegetation types ($F = 1.31$, $p < 0.001$). All site dates showed stronger ant community affinities within than between vegetation types except the 12 site dates comprising the *Banksia* shrublands, Mixed shrublands and Low to Medium open *Eucalyptus* forests. There was no significant affinity of the ants to the collection date (ANOSIM $F = 0.9999$, $p = 0.45$). There was also a strong overall affinity for the date replicates to be closer within than between sites ($F = 1.54$, $p < 0.001$). The exceptions were; the two Mixed Forest with Cypress (MFC) sites and one of these was also similar to one of the Low to Medium *Eucalyptus* forest sites, and; the two Carrol Scrub Vine forest sites which were similar to each other and to one each of the Tall *Eucalyptus pilularis* sites (TEP41) and Closed Tall Forest sites (CTF21).

Table 2.5 (cont.). Ants collected in 16 sites on Fraser Island, 2004.

Taxa	Biogeographic affinity	Functional group	BSH101		BSH102		CVF31		CVF32		GLD131		GLD132		LME51		LME52		MFC201		MFC202		MSH111		MSH112		TCF21		TCF22		TEP41		TEP42	
			M	S	M	S	M	S	M	S	M	S	M	S	M	S	M	S	M	S	M	S	M	S	M	S	M	S	M	S	M	S	M	S
Subfamily Formicinae (cont.)																																		
<i>Camponotus</i> sp. nr. <i>Consobrinus</i> (Erichson)	B	SC																																
<i>C.</i> sp. A (<i>novaehollandiae</i> gp.)	T	SC																																
<i>C.</i> sp. B (<i>novaehollandiae</i> gp.)	T	SC																																
<i>C.</i> sp. C (<i>discors</i> gp.)	W	SC																																
<i>C.</i> sp. D (<i>novaehollandiae</i> gp.)	T	SC																																
<i>C.</i> sp. E (<i>novaehollandiae</i> gp.)	T	SC	2	H			4			1			16			3	1	1	3	3	3	8	1	3	3			2			1	1	1	1
<i>C.</i> sp. H (<i>innexus</i> gp.)	T	SC																																
<i>Melophorus</i> sp. A (<i>mjobergi</i> gp.)	E	HCS																																
<i>M.</i> sp. B (<i>bruneus</i> gp.)	E	HCS																																
<i>Notoncus</i> sp. A (<i>enormis</i> gp.)	B	CCS																																
<i>N.</i> sp. B (<i>enormis</i> gp.)	B	CCS																																
<i>N.</i> sp. C (<i>enormis</i> gp.)	B	CCS																																
<i>N.</i> sp. D (<i>enormis</i> gp.)	B	CCS																																
<i>N.</i> sp. E (<i>gilberti</i> gp.)	B	CCS																																
<i>Nylanderia</i> sp. A (<i>vaga</i> gp.)	T	O	5	7	LH	7	7	15	24	13	4			2	39	9	4	7	10	27	13	34	H	5	10	18	26	23	16	8	7	3	14	12
<i>N.</i> sp. B (<i>obscura</i> gp.)	W	O																																
<i>N.</i> sp. C (<i>vaga</i> gp.)	T	O																																
<i>Parapatrechina</i> sp. D (<i>minutula</i> gp.)	W	O																																
<i>P.</i> sp. E (<i>minutula</i> gp.)	W	O																																
<i>P.</i> sp. F (<i>minutula</i> gp.)	W	O																																
<i>Plagiolepis</i> sp. A	B	CCS																																
<i>P.</i> sp. B	B	CCS																																
<i>Polyrhachis ammon</i> (Fabricius)	T	SC	L	2	2			2					H	1	H			1	H	1	H	3			H	H								
<i>P. augusta</i> (Forel)	T	SC																																
<i>P. australis</i> (Mayr)	T	SC																																
<i>P. daemeli</i> (Mayr)	T	SC	H	1																														
<i>P. hookeri</i> (Lowne)	T	SC																																
<i>P. lydiae</i> (Forel)	T	SC																																
<i>P.</i> sp. nr. <i>obscura</i>	T	SC																																
<i>P. pilosa</i> (Donisthorpe)	T	SC																																
<i>P. ruffemur</i> (Forel)	T	SC																																
<i>P. semiaurata</i> (Mayr)	T	SC																																
<i>P.</i> sp. A (<i>appendiculata</i> gp.)	T	SC																																
<i>P.</i> sp. D (<i>atropos</i> gp.)	T	SC																																
<i>P.</i> sp. H (<i>hedomyrma</i> gp.)	T	SC																																
<i>P. tubifera</i> (Forel)	T	SC	LH	H																														

Table 2.5 (cont.). Ants collected in 16 sites on Fraser Island, 2004.

Taxa	Biogeographic affinity	Functional group	BSH101		BSH102		CVF31		CVF32		GLD131		GLD132		LME51		LME52		MFC201		MFC202		MSH111		MSH112		TCF21		TCF22		TEP41		TEP42		
			M	S	M	S	M	S	M	S	M	S	M	S	M	S	M	S	M	S	M	S	M	S	M	S	M	S	M	S	M	S	M	S	M
Subfamily Myrmicinae (cont.)																																			
<i>Monomorium</i> sp. A (<i>laeve</i> gp.)	E	GM																								2									
<i>M.</i> sp. B (<i>laeve</i> gp.)	B	CCS					L	1	L	2					1	4			1		3	2				2		3	L				LH	1	
<i>M.</i> sp. C (<i>tambourinense</i> gp.)	B	CCS					1																						1	L	1				
<i>M.</i> sp. D (<i>carinatum</i> gp.)	T	GM	L			3					22	3	48																						
<i>M.</i> sp. E (<i>nigrius</i> gp.)	T	GM				3						9											1												
<i>M.</i> sp. F (<i>nigrius</i> gp.)	T	GM	4	4							4				L		5	1	1			2	8								1				
<i>M.</i> sp. H (<i>rubriceps</i> gp.)	T	TCS					L																												
<i>M.</i> sp. O (<i>rubriceps</i> gp.)	B	CCS																																	H
<i>Myrmecina australis</i> (Wheeler & Wheeler)	T	TCS					1			L																	1								
<i>Orectognathus</i> sp. A	T	SP							L	1																								LH	2
<i>Pheidole</i> sp. A (<i>variabilis</i> gp.)	W	GM	66	2	10	2	20								1		29	5	56	25	132	1	16	11	23	H		20	1	4			H		
<i>P.</i> sp. C (group E)	T	GM	46	1	3	7					5			38		9	3	1				5	4	1	3										
<i>P.</i> sp. D (<i>variabilis</i> gp.)	W	GM	L	16				8	11	4																	2		10						
<i>P.</i> sp. E (<i>athertonensis</i> complex)	T	GM	4	3		1	32	2	28	3					7	1				22	11	2	48	12	16	4	48	3	11	1	16	LH	7	2	
<i>P.</i> sp. F (group C)	W	GM			1																						8		25	1					3
<i>P.</i> sp. J (<i>ampla</i> gp.)	T	GM			6		23			19				8								213	132								61	4	53	1	
<i>P.</i> sp. L (group C)	W	GM					3							34	4							1												L	
<i>Podomyrma gratiosa</i> (Smith)	T	TCS																							L										
<i>P.</i> sp. B (<i>omniparens</i> gp.)	B	CCS	L																																
<i>P.</i> sp. C	B	CCS					H																												
<i>Rhopalomastix</i> sp. A	T	C																		1															
<i>Solenopsis</i> sp. A	W	CS											H	5								3				1									
<i>S.</i> sp. B	W	CS																																	
<i>S.</i> sp. C	W	CS			3	2			10		4				1		1	L	3	1	1	18	1												
<i>S.</i> sp. D	W	CS	12																																1
<i>Strumigenys</i> sp. B	T	CS																																	
<i>S. deuterus</i> (Bolton)	T	CS	1				2			L																									
<i>S. emmae</i> (Emery)	T	CS	L															L																	
<i>S. harpyia</i> (Bolton)	T	CS																																	L
<i>S. zygon</i> (Bolton)	B	CS																																	
<i>T. bicarinatum</i> (Nylander)	Invasive	O									H																								
<i>T.</i> sp. B (<i>striolatum</i> gp.)	E	O									21	4	2																						
<i>Tetramorium</i> sp. C (<i>striolatum</i> gp.)	T	O									2																								
<i>T.</i> sp. D (<i>ornatum</i> gp.)	T	O																																	
<i>T. turneri</i> (Forel)	E	O							LH			4			4						1	1		2				5		1				1	
<i>Gen. nov.</i> (<i>Stenammini</i>)	T	CS																																	

Table 2.5 (cont.). Ants collected in 16 sites on Fraser Island, 2004.

Taxa	Biogeographic affinity	Functional group	BSH101		BSH102		CVF31		CVF32		GLD131		GLD132		LME51		LME52		MFC201		MFC202		MSH111		MSH112		TCF21		TCF22		TEP41		TEP42								
			M	S	M	S	M	S	M	S	M	S	M	S	M	S	M	S	M	S	M	S	M	S	M	S	M	S	M	S	M	S	M	S	M	S					
Subfamily Myrmicinae (cont.)																																									
<i>Myrmecia brevinoda</i> (Forel)	B	SP	1																																						
<i>M. fulviculis</i> (Forel)	B	SP																																							
<i>M. nigrocincta</i> (Smith)	B	SP	H																																						
<i>M. ?queenslandica</i>	B	SP																																							
<i>M. sp. A (urens</i> gp.)	B	SP	H																																						
Subfamily Ponerinae																																									
<i>Amblyopone australis</i> (Erichson)	W	CS																																							
<i>Anochetus ?rectangularis</i>	T	SP																																							
<i>A. sp. B (graeffei</i> gp.)	T	SP																																							
<i>Bothroponera</i> sp. A	T	SP	2																																						
<i>B. ?oculata</i>	T	SP	H																																						
<i>B. sp. B (porcata</i> gp.)	T	SP																																							
<i>Brachyponera lutea</i> (Mayr)	W	CS	1	S	1	5			2	7	2	5			1			1	1			1	1			1	2	2			1	L	L	2							
<i>Discothyrea extensa</i>	T	CS			L	L																																			
<i>Heteroponera ?imbellis</i>	B	CCS			6	8	1																																		
<i>Hypoponera</i> sp. A	W	CS	1			2	LH																																		
<i>H. sp. B</i>	W	CS																																							
<i>H. sp. C</i>	W	CS																																							
<i>H. sp. D</i>	W	CS	1		1		L			1			L	1	L	LH			L			LH																			
<i>H. sp. E</i>	W	CS																																							
<i>H. sp. F</i>	W	CS	L	L																																					
<i>H. sp. G</i>	W	CS	L																																						
<i>Leptogenys anitae</i> (Forel)	T	SP			1																																				
<i>L. angustinoda</i> (Clark)	T	SP	5																																						
<i>L. ?bidentata</i>	T	SP																																							
<i>L. sjostedti</i> (Forel)	T	SP			3				1	4	L	H			1	4	L	H			H			1	H			1			L	L									
<i>Mesoponera australis</i> (Forel)	T	SP	3	H	6		1		H	LH	H			10	2	H		8	7	5	1		4	L	H			H			9	S			L	L					
<i>Odontomachus</i> sp. A (<i>turneri</i> gp.)	T	O																																							
<i>Ponera</i> sp. A	T	CS			L	L																																			
<i>Prionopelta robynmae</i> Shattuck	T	CS																																							
<i>Proceratium</i> sp. A	T	CS			L				L			L			L			L			L			4																	

Table 2.5 (cont.). Ants collected in 16 sites on Fraser Island, 2004.

Taxa	Biogeographic affinity	Functional group	BSH101		BSH102		CVF31		CVF32		GLD131		GLD132		LME51		LME52		MFC201		MFC202		MSH111		MSH112		TCF21		TCF22		TEP41		TEP42			
			M	S	M	S	M	S	M	S	M	S	M	S	M	S	M	S	M	S	M	S	M	S	M	S	M	S	M	S	M	S	M	S		
Subfamily Ectatomminae																																				
<i>Rhytidoponera</i> sp. A (<i>convexa</i> gp.)	E	O		15	1						51	91			H		8		4	1					24											
<i>R. chalybaea</i> (Emery)	T	O		2		23		5															20	74			11	9	2	7	H	8	13	9		
<i>R. croesus</i> (Emery)	B	O											12																							
<i>R. metallica</i> (Smith)	W	O	16	7	16	4					2	441	46	13	7	10	84	8	26	18	26	2	85	93									4	2		
<i>R. sp. nr. metallica</i>	W	O	5	2		2					513	55		1	6	5	49	1			2		23	17											2	
<i>R. sp. 1 nr. victoriae</i>	B	O					16		14															1				29	9	55	33	7				
<i>R. sp. 2 nr. victoriae</i>	B	O																					47	10			11									
<i>R. sp. nr. cristata</i>	E	O		59	18										18	H																				
Species Richness			47	49	39	35	26	32	38	40	49	54	40	37	34	32	34	21	23	34	34															
Genera Richness			26	26	26	26	16	21	20	24	32	31	25	22	24	21	23	23	23	23	23															
Species/Genera			1.8	1.9	1.5	1.3	1.6	1.5	1.9	1.7	1.5	1.7	1.6	1.7	1.4	1.5	1.5	1.5	1.5	1.5	1.5															

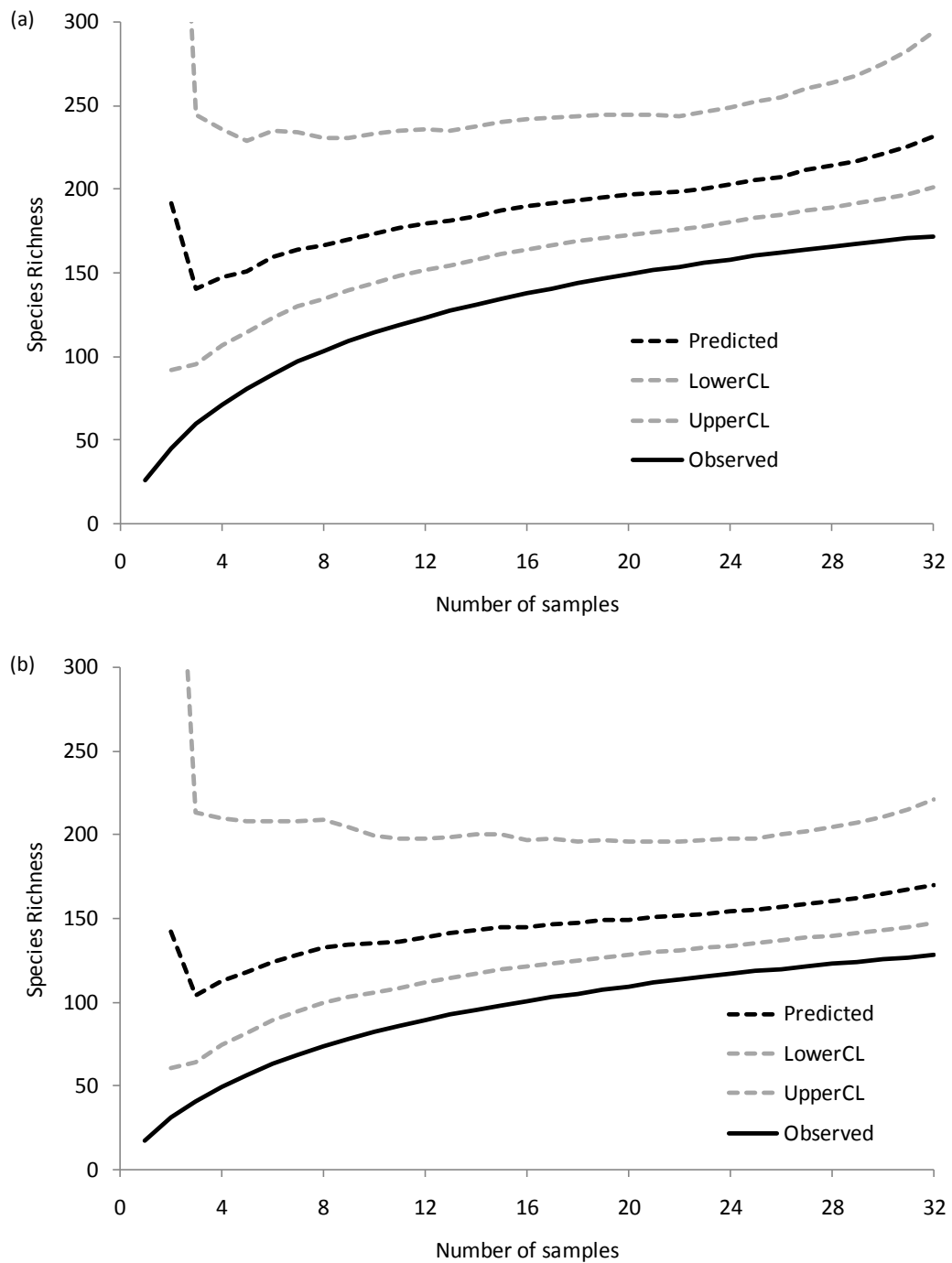


Figure 2.3. Observed and predicted ant species richness on Fraser Island using (a) combined methods and (b) pitfall traps only. Predicted richness and confidence intervals are calculated using the CHAO2 measure.

2.3.4 Ant biodiversity values of Fraser Island compared with other regional faunas

The individual sites generally had between 1.3 and 1.9 species per genera (Table 2.5), whilst across the whole island there was 3.0 species per genera (172/57). In comparisons with the regional faunas, Fraser Island had the greatest number of species per genus (Figure 2.4). Yet the individual Fraser Island sites tended to have lower numbers of species per genera than most other faunas (Figure 2.4).

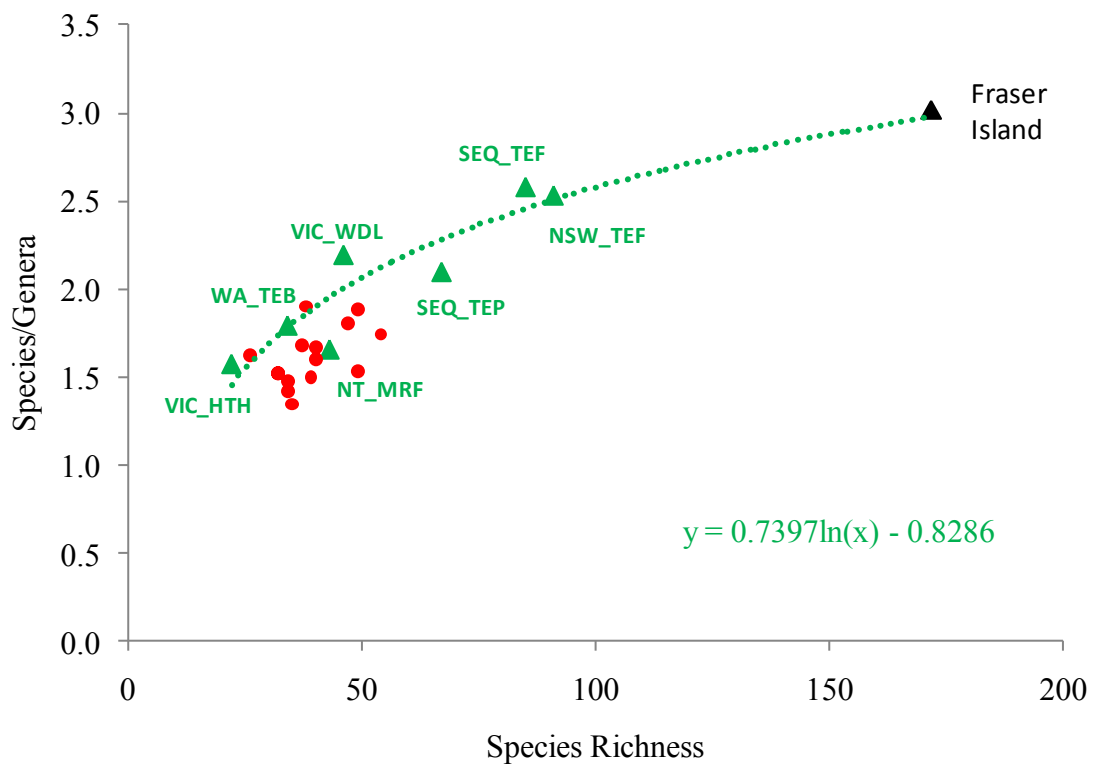


Figure 2.4. Comparison of number of species per genus for Fraser Island and other regional ant faunas. Circles are 16 Fraser Island sites, black triangle is overall Fraser Island ant fauna. The regression line is shown only as a guide and was calculated using the regional faunas and the overall Fraser Island fauna.

2.3.5 Functional Group affinities of Fraser Island ant communities

There was considerable variation in the ant functional group compositions between the Fraser Island vegetation types (Figure 2.5). Cold climate specialist, Cryptic species, Generalised myrmicines and Opportunists occurred in every site (Figure 2.5). Opportunists were the most common foraging ants, making up more than 45% of foragers in 13 of the 16 sites, but only making up 26 and 27% of ants in the two *Banksia* shrubland sites (Figure 2.5a). Dominant Dolichoderinae (DD) occurred in nine of the sites and were dominant in *Banksia* shrubland site BSH102 on both occasions (36% and 42% of individuals) but not recorded in BS101 on either occasion. DD were also dominant (42%) in LME51 and GLD131 (37%) in the September samples but made up less than 16% of ants in the other sites when they occurred. Hot climate specialists (HCS) were also scarce on Fraser Island, occurring in only six sites. HCS made up 7% of individuals in GLD131 and 10% in BSH102 in the September samples, but less than 1 % of individuals in their four other sites.

The functional groups of the species collected were much more evenly distributed (Figure 2.5b) but it is noted that there were several habitats where groups were not represented. Notably, Dominant Dolichoderinae were only in nine of the sites (figure 2.5b) and only more than 10% of epigaeic foraging ants in three of the sites (Figure 2.5a). Hot climate specialists occurred in only six and Tropical climate specialists in 11 of the sites. There were no specialist predators in one of the grassland sites (Figure 2.5b).

Variability in the functional group similarity between replicates within the same vegetation classification was also apparent in the comparisons with the regional ant faunas (Figure 2.6). The two Closed Tall Forest sites were extremely similar (> 90%), yet the two *Banksia* sites

and the two Grassland sites had only about 50% similarity. Of the regional comparison faunas, the two sites at Wilson's Promontory in Victoria had about 90 % similarity in functional group faunas even though they were quite distinct vegetation types, heath and woodland.

The Fraser Island and regional fauna functional group compositions fell into four distinct groups using a cut off of 70% similarity (Figure 2.6). The regional faunas (VIC_WDL, VIC_HTH, SEQ_TEP, NSW_TEL) were included in a group which was characterised by high proportions of Cool Climate Specialists and Dominant Dolichoderinae but low representation of Opportunists. A second group included the site from Western Australia (WA_TEB) and one Fraser Island Grassland and one Fraser Island *Banksia* shrubland site and was characterized by low Specialist Predators and high Hot Climate Specialists (Figure 2.6). The Monsoonal Rainforest from the Northern Territory (NT_MRF) was found to be similar to a group of Fraser Island sites that included both Carrol Scrub/Vine forest replicates, both Closed Tall Forest replicates and one of the *Eucalyptus pilularis* replicate sites (Group D, Figure 2.6). This rainforest/vine forest group was characterized by high relative proportions of Cryptic species and Specialist Predators and the absence of Hot Climate Specialists. The south east Queensland ant fauna from the Gold Coast and Brisbane hinterlands (SEQ_TEF) grouped with both the Fraser Island mixed Tall *Eucalyptus*, one each of the Mixed Forest with Cypress, Grassland and *Banksia* shrubland sites (Group C, Figure 2.6). These mixed woodland sites had low Dominant Dolichoderinae and high subordinate Camponotini.

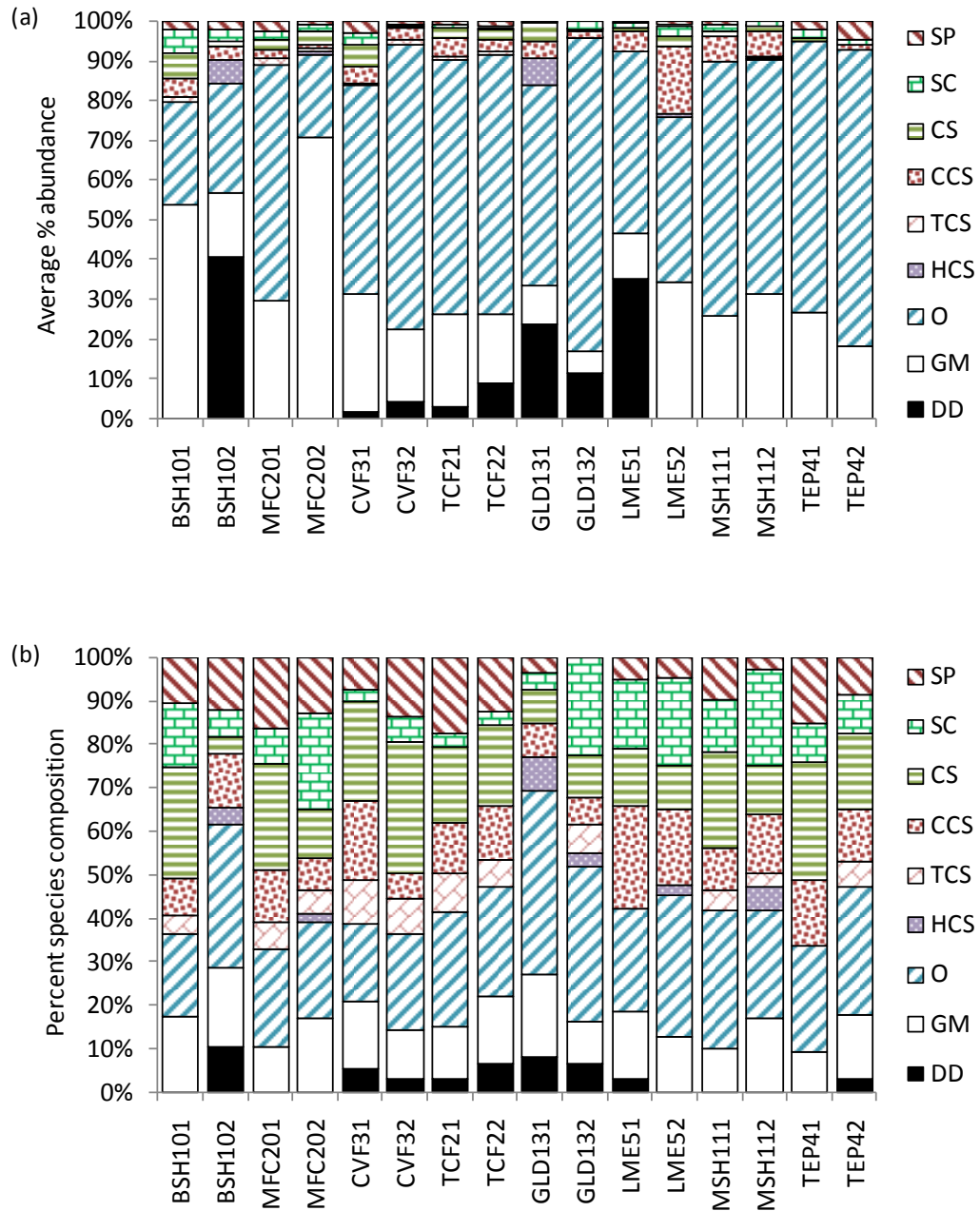


Figure 2.5. Functional group profiles for ant foragers collected in 16 sites on Fraser Island. (a) Pitfall trap forager abundance % is averaged between March and September 2004. (b) Species composition across all sampling methods. HCS = Hot climate specialists, DD = Dominant Dolichoderinae, TCS = Tropical climate specialists, SP = Specialist predators, SC = Subordinate Camponotini, O = Opportunists, GM = Generalised Myrmicines, CS = Cryptic species, CCS = Cold Climate specialists.

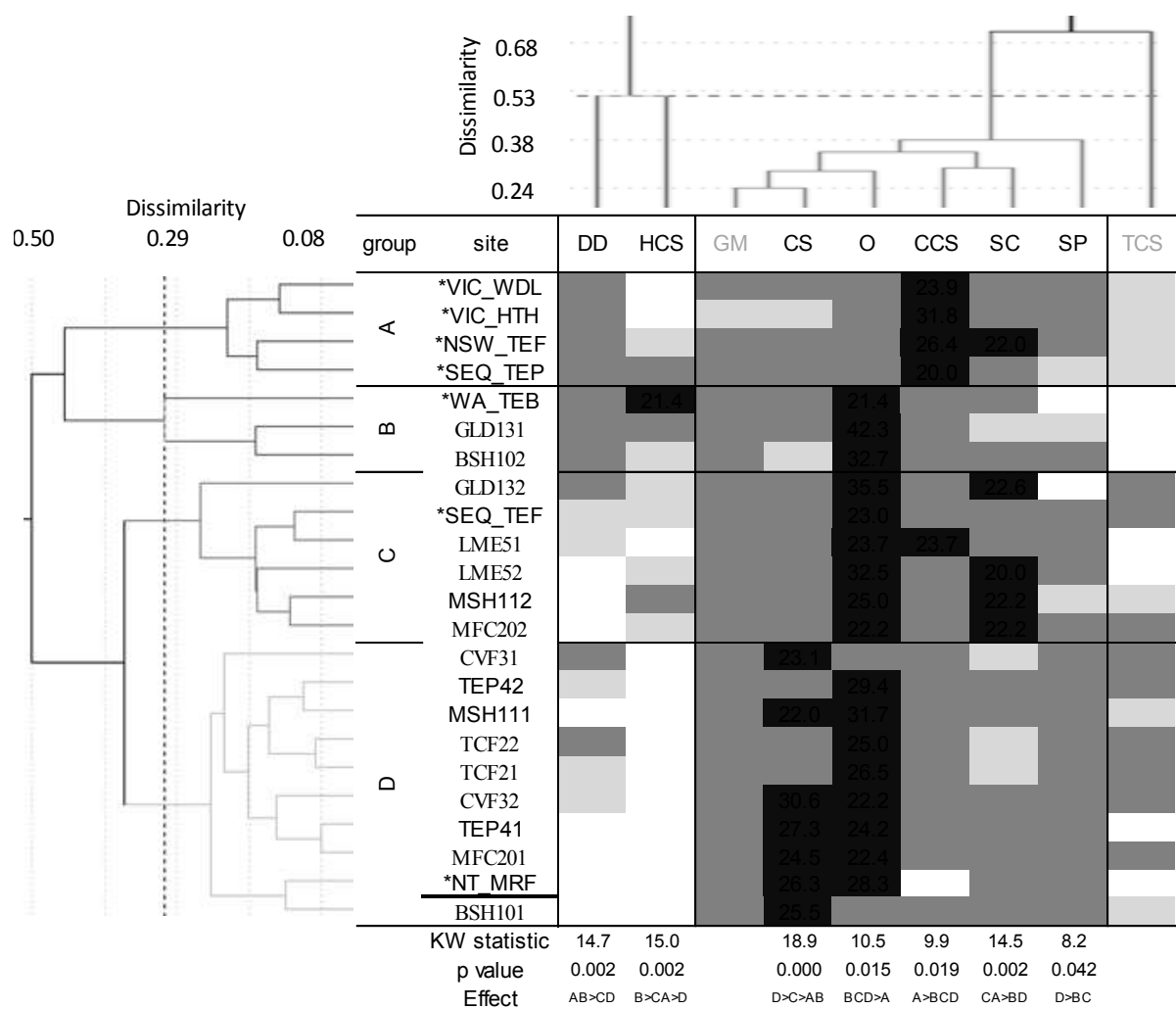


Figure 2.6. Two-way classification of 16 Fraser Island and seven regional Australian ant communities (notated by *) using % species composition in functional groups as community attributes. Darker dotted lines on dendrograms are suggested cut-offs for groups at 70% similarity between ant assemblages and 50% similarity between functional groups. The four levels of shading are 0, < 5%, < 20% and > 20% (maximum is 43%). Lower box represents significant Kruskal Wallce tests and identifies median differences between the site groups.

2.3.6 Biogeographical affinities

Widespread species made up between 14 and 28% of ant taxa in all faunas compared (Figure 2.7). Fraser Island had 44% Torresian species which was only higher in the

Monsoonal rainforest site of the NT (70%), whilst the Victorian sites and the Western Australian sites had 0–5% from this group. Of the remaining 35% of ant species on Fraser Island, the greatest affinity was with cooler climate groups, as the Bassian fauna made up 27% and Eyrean groups only 8 % (Figure 2.7). The Fraser Island affinities were generally more similar to the North Stradbroke Island [SEQ_TEP] affinities (41% Torresian) than the Brisbane–Gold coast hinterland fauna [SEQ_TEF] (27% Torresian). A major difference was the Brisbane–Gold coast fauna having twice as many Eyrean species as North Stradbroke Island and three times as many as Fraser Island (Figure 2.7).

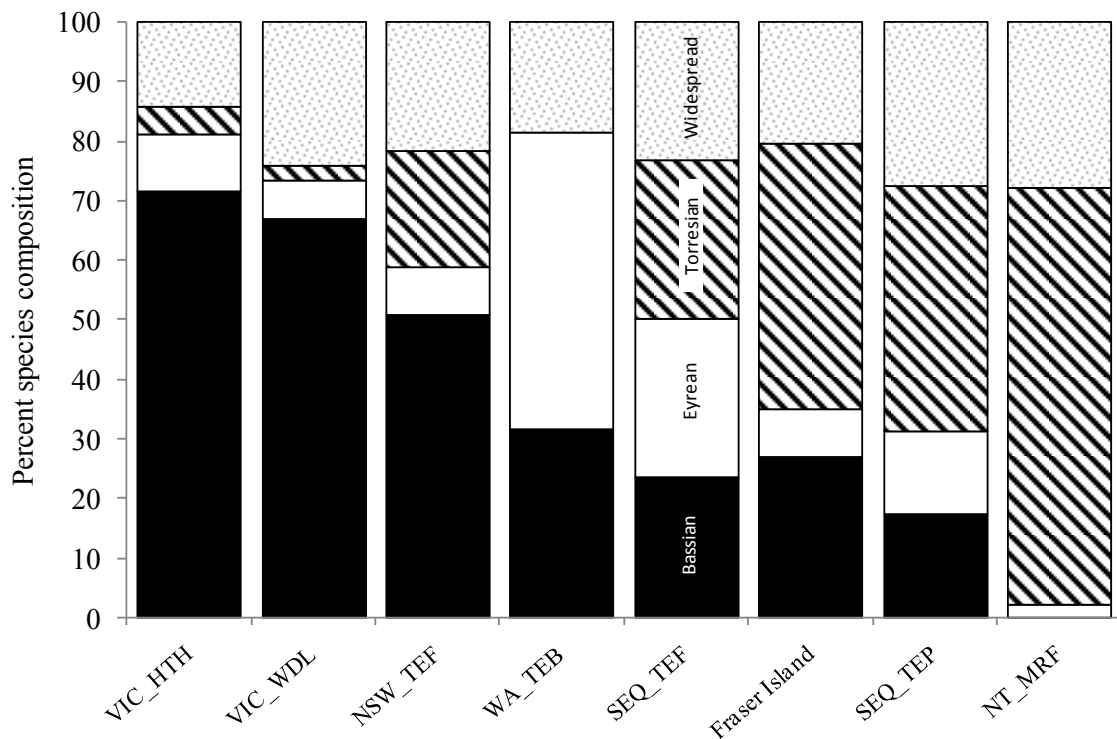


Figure 2.7. Biogeographic affinities of ant taxa collected across Fraser Island and 7 regional Australian ant communities. Regional site codes are described in Table 2.4.

2.4 Discussion

Fraser Island supports a rich and diverse ant fauna, with 172 species recorded during this study, and total species richness just in the 16 sites sampled is estimated to be well over 200. The species accumulation curve used to make the prediction was far from an asymptote, however, so the actual richness could be much higher as indicated by the upper confidence interval which was 300 (Figure 2.3a). A singleton is a species that is represented by only one individual in a survey and the percent singletons influences the prediction of how many taxa were present but not yet captured (Chao 1984, Coddington et al. 2009, Colwell 2009). In a complete inventory, the observed curve should asymptote and singletons should tend to zero (Coddington et al. 2009) but in the whole-of-Island data set or individual site data (Table 2.5) of this study, there was an average of 20% singletons. This maybe an over-estimate of singletons caused by edge effects and under-sampling which is known to cause systematic negative bias of species richness (Coddington et al. 2009). Nevertheless, considering that this study sampled only 16 sites, then a more intensive spatial sampling effort could reach the 300 species recorded in the nearby Cooloolo/Noosa region by Greenslade and Thompson (1981). More intensive sampling within each site would also return many more species, as indicated by the high number of singletons in the pitfall traps or ants only collected by hand searching in Table 2.5.

The Fraser Island ant fauna had very high within-genus diversity, averaging three taxa per genus, significantly more than any of the other faunas compared. This is partly because species and genera cannot accumulate at the same rate, hence increased species richness in general is associated with increased species/genera as identified in Figure 2.4. But it also

reflects the type of genera present at Fraser Island. In particular the large contributions to the overall species list from the very diverse Formicine sub-family genera, namely *Polyrhachis*, *Camponotus* and *Stigmacros*.

The Fraser Island fauna in general can be characterised as having low numbers of dominant/aggressive native taxa. *Iridomyrmex*, in particular, were poorly represented. The most diverse genera, *Polyrhachis*, *Camponotus* and *Stigmacros* are generally poor competitors with aggressive taxa and their diversity on Fraser Island reflects the absence of dominant/aggressive native taxa. *Iridomyrmex* spp. were only recorded in the two Grasslands and one *Banksia* site in this study and were similarly restricted to well-insolated shrubland, woodland and open forest in Cooloola/Noosa (Greenslade & Thompson 1981).

The most abundant ants on Fraser Island, *Aphaenogaster longiceps* and *Rhytidoponera metallica*, and the most ubiquitous, *Nylanderia* sp. *A. (vaga* gp.), are all widespread and opportunistic species, occurring in most Australian ecosystems (Andersen 1995). *Aphaenogaster longiceps* and *Rhytidoponera metallica* were both widely distributed in relation to vegetation in the Cooloola/Noosa region (Greenslade and Thompson 1981). My results support Greenslade and Thompson's (1981) finding that *A. longiceps* distribution is closely tied to soil properties and is independent of vegetation and associated microclimates. *A. longiceps* was only observed on the sandy soils in the Cooloola/Noosa region (Greenslade and Thompson 1981). The sandy soils must provide excellent nest substrate for *A. longiceps* as in many of the heavily forested parts of Fraser Island its characteristic excavations of fresh sand over the dark leaf litter can be observed as far as the eye can see. *Aphaenogaster longiceps* made up more than 10% of individual ants collected and, because of their above average size, it is predicted that more than 1/6th of all ant biomass on Fraser Island is

A. longiceps. The high overall *Rhytidoponera metallica* abundances are remarkable considering they were never recorded in the closed Tall Forests or Carrol Scrub, as was also the case in Cooloola/Noosa (Greenslade & Thompson 1981). A third widespread taxa in the Cooloola/Noosa study, *Camponotus nigreanus* was not recorded in this study (Table 2.5). This is probably because of a taxonomic mismatch and it may be assumed that the *Camponotus aeneopilosus* (Mayr) is the same taxa (Alan Andersen, pers. comm. 2011) and was less widespread on Fraser Island.

All of the species recorded in this study have been recorded elsewhere and there were no apparently endemic taxa. Of interest, however, are the single *Rhopalomastix* sp. A and three *Gen. nov.* (*Stennammini*) individuals collected in the different Mixed Forest with Cypress replicates. Both these taxa have limited records and the latter is from an as yet unnamed genus. These two MFC sites had the smallest stands of vegetation types sampled (they weren't on Craig's 1985 classification) but the greatest observed ant species richness. It may be that the high species richness of these smaller stands may actually be because the samples are actually from two vegetation types, as ants from adjacent vegetation types could have been inadvertently collected. The two MFC sites were both on the western side of the island, and were amongst the oldest sites sampled, as Fraser Island shows a succession of vegetation types from West to East as new sand dunes are continually being formed and older ones become more protected and stable (Sinclair and Morrison 1990). MFC202 was the most ant species rich of all the sites sampled and, remarkably, is only a small patch of less than two ha and is fully within the Kingfisher Bay Resort and Village lease. This vegetation stand is within 100 metres of a picnic area and 200 metres of human dwellings and large infestations of the tramp ants *Paratrechina longicornis* and *Pheidole megacephala*

(see Chapter 3). The richness of these sites does, however, fit in with the Greenslade and Thompson's (1981) prediction that increased productivity in the form of increased ground cover along with some insolation getting through the canopy allow for an increase in ant carrying capacity. The Carrol Scrub and Tall *Eucalyptus pilularis* sites were intermediate in ant species richness and this is probably because shade and low temperatures become critical and diversity falls (Greenslade and Thompson 1981). The youngest sites in this study were the grasslands, and they had no litter and obviously reduced primary productivity and ant carrying capacity.

Most of the Fraser Island vegetation types generally have low insolation and this results in a lack of aggressive species, as confirmed by the few representatives from the Dominant Dolichoderinae (Figure 2.4). Members of this group are dominant, effectively requiring other ant community members to fit their distributions in with this dominance (Greenslade and Thompson 1981, Andersen 1995). Only in occasional sites on Fraser Island in this study did the DD reach anything like the dominance observed by Greenslade and Thompson (1981) in the Cooloola and Noosa regions. In dry areas of the Cooloola/Noosa region, epigaeic Dolichoderinae, generally *Iridomyrmex*, made up to 30% of individual ant records (Greenslade and Thompson 1981). It should be noted that even if I included the now redefined Opportunistic ant *Leptomymex* as a DD in the Fraser Island calculations to make the data comparable to Greenslade and Thompson (1981), the DD only achieved proportions of 30% or greater on four of the 32 site-dates in this study.

There were also more Dolichoderinae species recorded on North Stradbroke Island (Majer 1985a) than in this study on Fraser Island and this may reflect the more open habitats sampled on North Stradbroke, where many sites were also rehabilitated, mined areas. There

were generally fewer taxa caught per site on North Stradbroke Island by Majer (1985) but those samples were mostly from rehabilitated sites and therefore a lower richness may be expected. Using pitfall traps, arboreal shaking, leaf litter and hand searches, there were still only 26–30 species in the control plots on North Stradbroke Island however (Majer 1985a).

The use of regional ant faunas for comparison with the Fraser Island site faunas was successful, because the range of faunas that were included ensured a division would be detectable. The groups of sites (Figure 2.6) that were generated by the functional group classification are intuitive. The Fraser Island Grassland and *Banksia* replicates (BSH102 and GLD131) that grouped with the Western Australian site were both observed to be drier and more open than their other replicates (W Robinson pers. obs.). This probably highlights an issue of trying to fit only a limited number of vegetation classifications to the whole island. Obviously, there will be some heterogeneity within some vegetation classes and these results support that notion. The functional groups that were significantly related to the classifications were sensible and easy to interpret. For example, a high proportion of Dominant Dolichoderinae and Cold Climate Specialists would be expected in Victorian (VIC_HTH & VIC_WDL) and south east New South Wales (NSW_TEF) sites where the climate is cool wet winters and dry hot summers. The lack of discrimination between groups of sites by the Generalised Myrmicines reflects the evenness of the contribution of this functional group to the classification groups and this may reflect that all faunas except those of Majer (1985) are from undisturbed habitats.

If there are any unexpected groupings then it may be the placing of the North Stradbroke Island [SEQ_TEP] fauna (Majer 1985) with the Bassian group of NSW and VIC sites, making it 30% different to the two drier habitat Fraser Island faunas above, and at least 50%

different to the remaining Fraser Island functional group compositions. This may be an artifact of the inclusion of arboreal samples or simply just the drier habitats that were sampled by Majer (1985).

The classification groups supported the general framework of the functional group concept. For example, the Hot Climate Specialists and Dominant Dolichoderinae were grouped as having similar site affinities and this reflects the taxa within those groups such as *Iridomyrmex* spp. (DD) and *Melophorus* spp. having preferences for similar, drier, open habitats (Andersen 1995). Interestingly, the Generalised Myrmicines (GM) and Cryptic Species (CS) were the two most similar of all the functional groups. Even though CS showed a definite preference for the rainforest/vine forest type locations their similarity with GM was influenced by both groups providing lower relative contributions to the fauna when there was higher DD present.

The Fraser Island biogeographic affinities were more similar to the North Stradbroke Island [SEQ_TEP] affinities than when using the functional groups for comparisons. This confirms that the two approaches act in a different manner. The main driver of the similarity between Fraser and Stradbroke Islands was the large number of Torresian affiliated taxa. In contrast, the Western Australian site had more taxa that were Eyrean affiliated. This is hardly surprising given that south west Western Australia is a long way from the tropical region with the Torresian boundary being several thousand kilometres north of Perth, near Broome (Andersen 2000). Additionally, the pooling of the faunas from several obviously different habitats on Fraser Island for this comparison probably also contributed to difference.

In conclusion, Fraser Island has a very rich (>200 species) and diverse (> 55 genera) ant fauna. The diversity of the Fraser Island ant fauna is similar to the adjacent mainland fauna (Cooloola/Noosa region). However because Fraser Island has less open drier habitats, the fauna have fewer dominant aggressive native ant species present. Subsequently, the fauna is numerically dominated by opportunistic and widespread taxa such as *Aphaenogaster longiceps*, *Rhytidoponera metallica* and *Nylanderia vaga*. The functional group composition of species between sites on Fraser Island can be quite variable and even considerably different between replicate sites of the same vegetation type. There were three distinct type of ant faunas on Fraser Island, namely; 1) There were two hotter drier sites (one Grassland, one *Banksia* shrubland) with high abundances of Hot Climate Specialists and Dominant Dolichoderinae; 2) mixed *Eucalyptus* and Cypress woodland ant faunas that had high relative proportions of subordinate camponotini and moderate levels of Cryptic species, and; 3) Rainforest/Vine forest sites that were low in Hot Climate Specialists and high in specialist Predators.

2.5 Conclusions

- *This chapter presents the first known ant species list for WHA listed Fraser Island.*
- *Fraser Island is rich in ant fauna with 172 species from 57 genera collected.*
- *The Fraser Island ant species richness is predicted to approach 300 species.*
- *Replicates of Closed Tall Forest, Tall Eucalyptus pilularis and Closed vine Forests ant assemblages were all similar to each other in ant functional composition*
- *Associations within vegetation types were not always distinct, with up to 50% dissimilarity in ant assemblages between replicates of the same vegetation type*

- *The ant fauna are characterised by the low relative species richness, frequency of occurrence and abundance of Eyrean biogeographic ant groups and Dominant Dolichoderinae functional groups.*
- *The dominant foragers in almost all sites sampled were opportunistic species with *Aphaenogaster longiceps* predicted to contribute more than 1/6th of all ant biomass on Fraser Island.*
- *The lack of behaviourally dominant taxa and high relative abundance of opportunistic species makes the Fraser Island ant fauna potentially susceptible to invasion by exotic taxa.*



Plate 2. *Polyrhachis hagiomyrma* gp. Near Lake Wabby, Fraser Island, 2006.

Chapter 3: Exotic ant invasions and native ant biodiversity at Kingfisher Bay

3.1 Introduction

Invasions by non-native ants are usually associated with low native ant diversity (e.g. Cook 2003, Sanders et al. 2003, Hoffmann 2004) and are therefore an important conservation concern (Holway et al. 2002a). The concern may be intensified when dealing with high conservation value environments, where native ant biodiversity may be even more important for ecosystem function (Folgarait 1998). Fraser Island, in south-east Queensland is one of 16 World Heritage Areas in Australia having been identified as having exceptional biodiversity values (QPWS 2005) and has rich native ant biodiversity value (Chapter 2). Part of the ongoing conservation management program for Fraser Island is the protection of the natural processes including provision for control of weeds and pests (QPWS 2005). During field work for the previous Chapter 2, the invasive ant species, *Paratrechina longicornis* and *Pheidole megacephala* were observed in large numbers at Kingfisher Bay on Fraser Island. Both these species have previously been identified as threats to native ant assemblages in other parts of the world (Holway et al. 2002a).

The Black Crazy Ant, *Paratrechina longicornis* has probably been in Australia for decades (Reichel and Andersen 1996) but has received little research focus compared with economically important ant invaders such as *Solenopsis invicta*, *Linepithima humile* and *Pheidole megacephala*. The African Big-Headed ant, *P. megacephala* is comparatively well researched and has been associated with considerable ecological damage in several

Australian ecosystems (Hoffmann et al. 1999, May and Heterick 2000, Hoffmann and Parr 2008, Hoffmann 2009). *P. megacephala* is deemed more destructive in tropical and subtropical areas (Heterick et al. 2000), but consistently makes up more than 80% of actively foraging ants regardless of climate where it has been observed (Table 1.2). *P. longicornis* can also be locally common in tropical and subtropical areas but may be poorly studied in Australia because it has generally been regarded as timid in the presence of other aggressive ant species (Banks and Williams 1989), and it is not considered a major threat to biodiversity because of perceived weak interactions with native species (Hoffmann and O'Connor 2004). Yet *P. longicornis* does share typical invasive ant biological attributes such as high fecundity, mass recruitment and efficient food procuring efficiency (Banks and Williams 1989, Fowler et al. 1994, Meier 1994, Wetterer et al. 1999, Stanley and Robinson 2007). It was able to numerically dominate its preferred baits in a minimally disturbed area with high native ant diversity on Fraser Island in South East Queensland (Stanley and Robinson 2007).

There are many different mechanisms that have been used to report on the magnitude of ant invasions or their associated impacts, including: invasive ant nest densities (e.g. Groden et al. 2005, Morrison and Porter 2005); average number of invasive ants per pitfall trap (Callan and Majer 2009); proportion of all ants recorded in the study area that are invaders (Wetterer et al. 1999, Heterick et al. 2000, Holway et al. 2002a, Le Breton et al. 2003); relative abundance of invasive and native ants in pitfall traps (Holway 2005); speed of resource monopolization by the invaders (Holway et al. 2002a); foraging invasive ant numbers at bait stations (Krushelnycky et al. 2004, Morrison and Porter 2005); total ant biomass of the invaded site (Morrison 2000, Hoffmann and Parr 2008, Callan and Majer 2009); total ant

abundance of the invaded site (Hoffmann 1998); presence of the invader (Ness and Bronstein 2004, Lafleur et al. 2005); proportion of pitfall traps the invaders occur in (Nicholls 2005), and: size or area of the invasive ant supercolony (Sanders et al. 2001). With so many options for reporting there is an obvious need to look at how the results presented and their interpretation may be influenced by the choice of reporting method used. In particular, the scale of reporting is open to influence by skewed count data that is collected when pitfall traps are positioned near nests or foraging trails (e.g. Greenslade 1973). Furthermore, reporting at a single scale (e.g. average ant species per pitfall trap) can miss a significant effect if the impact is at a different scale (e.g. when the regional ant species pool is impacted) (Nicholls 2005).

Further complicating the reporting of invasive ant infestations and their impacts, infestations often have irregular boundaries (e.g. DiGirolamo and Fox 2006) and there can be islands of native ants persisting within the area infested (Holway et al. 2002a). Hence, it should be expected that, in some surveys, not all of the samples in the pre-determined invaded area contain the invader. A dilemma then for the researcher is whether or not to include these traps in the analyses as they may not be representative, depending on the hypothesis being investigated.

Yet another complication arises in field ecology if the sampling effort between treatments becomes unequal, this commonly arises when the study: 1) plans to compare two or more treatments of different sizes; 2) starts with equal sized areas and part of a treatment area is disturbed or affected by an external agency in the course of the study, or; 3) treatment isn't homogenous or isn't contained within the pre-sampling defined treatment boundaries. Consequently, when there are differential sampling efforts between treatments, typical

comparative measures such as proportion abundance or biomass of the invader or total native species richness of the comparison areas may be biased and have the potential to be misleading.

This study uses observational research to characterise the native ant biodiversity values of neighbouring areas where *P. megacephala* and *P. longicornis* have invaded into native bushland at Kingfisher Bay, Fraser Island Australia. It acknowledges that the areas may have been different prior to invasion, and does not attempt to infer cause and effect nor make inferences about other areas invaded by these taxa. Specifically, the study determines the native ant abundance, species richness and species turnover in natural areas and nearby areas invaded by *P. megacephala* and *P. longicornis* at Kingfisher Bay, and investigates any relationship between *P. megacephala* and *P. longicornis* abundances with native ant abundance and diversity in infested areas.

Further, this study investigates how different indicators of the magnitude of an invasion and related native ant indicators can be affected by sampling effort, reporting scale, and whether the data are analysed using pre or post-sampling definitions of the boundaries of the invaded areas. Such detailed understanding of the nature and interpretation of ant abundance and richness data is important for statistical analyses and ecological conclusions in the remainder of this thesis. It also puts into context the conclusions drawn by other studies of ant invasions.

3.2 Methods

3.2.1 Study site

Fraser Island is located about 290 km N of Brisbane and Kingfisher Bay (Latitude 27° 37' 27 S, Longitude 153° 05' 32 E), is on the western side of the island. Large infestations of *Paratrechina longicornis* and *Pheidole megacephala* were noticed in the Kingfisher Bay area when sampling for Chapter 2. All sampling for this chapter was conducted within the grounds of Kingfisher Bay (Ecotourism) Resort and Village (KBRV) which was constructed between 1989 and 1991. To minimise disturbance to the local environment during KBRV construction, hundreds of plants were moved to a nursery while building work took place and then replanted *in situ* (KBRV 2009). Hence there are no non-indigenous plants at the resort and landscape disturbance was minimal. The resort covers approximately 65 ha and includes naturally landscaped gardens between buildings and a large area of never disturbed bushland. However, the nursery phase included importation of potting mix and nursery materials as well as the usual materials for building human dwellings. *P. longicornis* was probably transported to the island during the nursery phase, given that this area appears to be the origin of the infestation (Nicholls 2005). *P. megacephala* was probably introduced at about the same time, and although there is no clear sign of the origin of the infestation it tends to be associated with the resort buildings in the south west part of the resort (Figure 3.1).

3.2.2 Field sampling

A preliminary survey using peanut butter and jam baits and information from previous research at the site (Nicholls 2005, Stanley and Robinson 2007) were used to locate boundaries for *Pheidole megacephala* and *Paratrechina longicornis* infestations around KBRV in October 2006. This identified zones of approximately equal areas defined as *P. megacephala* zone, *P. longicornis* zone, *P. megacephala* + *P. longicornis* zone and a native ants only zone. Within each zone, 8–10 linear transects were established at least 20 m apart, each transect containing five pitfall traps 5 m apart (Figure 3.1). All invasive ant transects were in apparently undisturbed native bushland (Figure 3.2) and were generally positioned at least 20 m away from, but within 100 m of any buildings so could be said to be disturbed by proximity to buildings. The native ant transects were at least 200m from any buildings but within 20 m of a fire control road (Figure 3.1). The pitfall traps were plastic vials, 42 mm internal diameter x 109 mm deep half filled with 70% ethanol and 3% glycerol then buried so that the rim of the trap was flush with the soil surface. Traps were positioned on the 1st October 2006, opened 2nd October 2006 and collected on the 8th October 2006.

Prior to opening the traps, each pitfall trap was geo-referenced for mapping (Figure 3.1) and the percent cover of litter, bare ground, woody debris, ground vegetation and woody vegetation, and the number of woody plant stems within a 1 m² area around each pitfall trap were estimated. The maximum vegetation height and average vegetation height were also estimated for each transect. The same operators performed all habitat measurements.

3.2.3 Ant identification

Ants were identified according to *The Ants of Northern Australia* (Andersen 2000) and voucher specimens are lodged at the Tropical Ecosystems Research Centre at CSIRO, Darwin, Northern Territory.

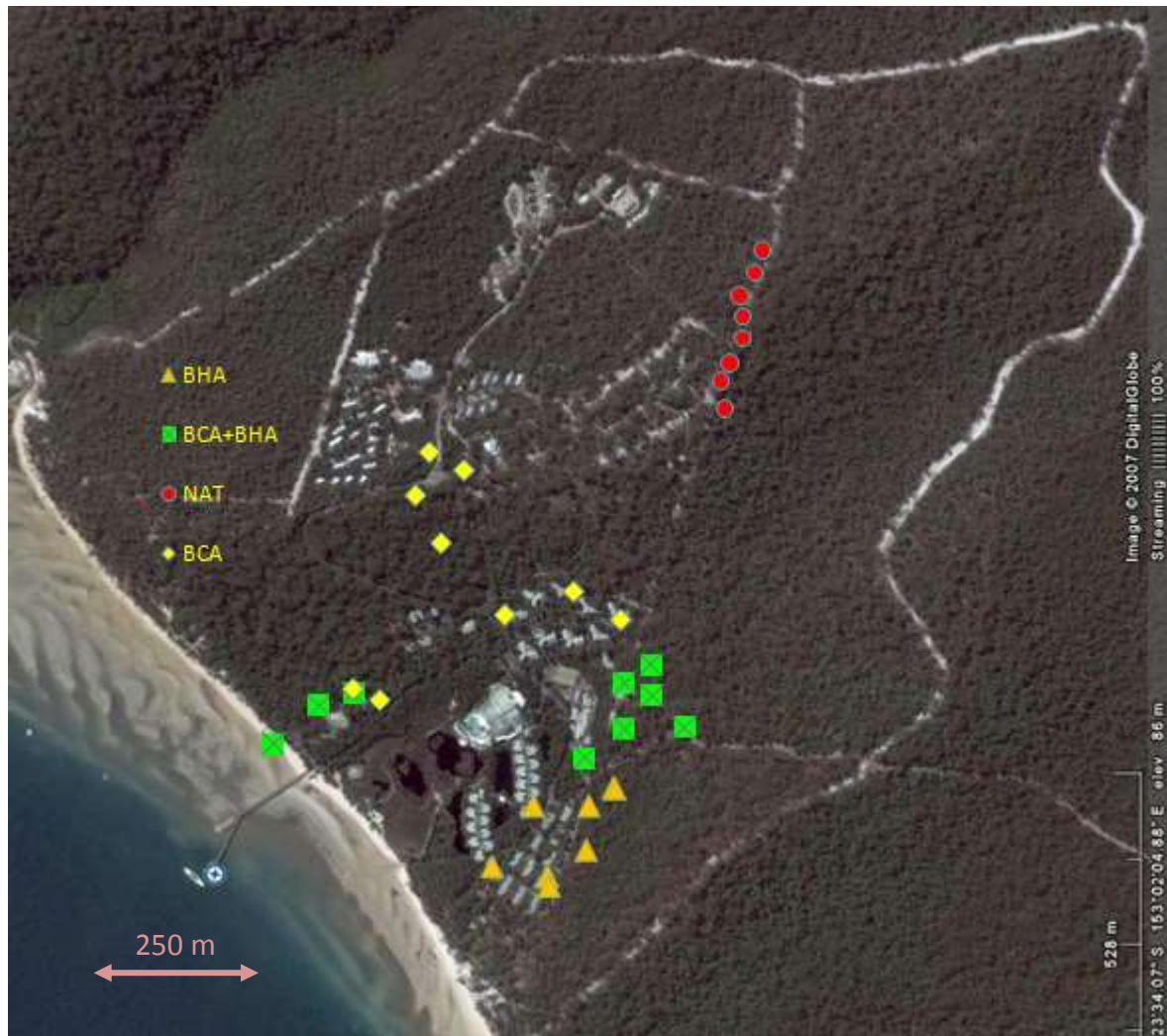


Figure 3.1. Position (± 10 m) of the middle trap of pitfall trap transects within Kingfisher Bay Resort and Village (lease boundary is outer fire break). Transects were allocated to zones (legend) based on pre-sampling defined boundaries. BHA = *Pheidole megacephala*, BCA + BHA = *Pheidole megacephala* + *Paratrechina longicornis*, NAT = Native ants, BCA = *Paratrechina longicornis*. Image is downloaded from Google-earth on 17th July 2007.



Figure 3.2. Examples of transect locations in four different zones. a) and b) *Pheidole megacephala* zone, c) and d) *Paratrechina longicornis* zone, e) and f) *Pheidole megacephala* + *Paratrechina longicornis* zone, g) and h) Native ant zone.

3.2.4 Statistical analysis

Sampling zones

Each trap and each transect were redefined as having either, both or neither of *P. longicornis* and *P. megacephala* present after the samples were sorted. I then created separate datasets for each trap, each transect (trap data pooled) and again for the zone (transect data pooled) for both pre and post-sampling definitions of zone. For example, consider a transect that had

all five traps intact and an invasive species present in only one trap. For the analysis of post-sampling defined zones, at the trap scale only that one trap would be classified as having the invader present, for the transect and zone scale analyses, all traps in the transect were classified as having the invader present. If the transect was in a zone defined prior to sampling as the *P.longicornis* zone, then all traps were classified as having *P. longicornis* in the pre-sampling defined dataset. All traps were treated as independent replicates within each dataset.

Native ant species turnover

To understand the relationship of native ant diversity with the invasions required comparisons of an indicator of diversity of the native ant assemblages in the invaded zones with the native ant zone. However, sampling effort (traps per unit area) was not the same in the different zones because of possible different starting zone sizes and the loss of some traps and transects from external disturbances. Thus, the samples of the zone's ant biodiversity, native ant species lists and total numbers of species collected, are not directly comparable and species accumulation curves (Colwell et al. 2004) were used to give an indication of species turnover for sampling effort. This equates to the "Relative Diversity" described by Greenslade and Thompson (1981). Species turnover was compared by graphing the average observed cumulative species richness per unit effort (pitfall trap) and per cumulative native ant abundance between sampling zones (Native, *P. longicornis*, *P. megacephala*, *P. megacephala* + *P. longicornis*).

To compare the species turnover between the zones and pre and post-sampling definitions of zone, the predicted species richness was calculated using the Chao1 measure (Chao 1984)

and the Estimates program (Colwell 2009). The predictions were compared using a two factor ANOVA without replication (Factor A was zone, Factor B was pre- or post-sampling). The predictions were all made at the same number of traps as determined by the zone with the fewest intact traps post-sampling.

Native and alien ant indicators

Biodiversity indicators were used to complement the species turnover analyses and to highlight the complications of comparing when sampling effort is unequal. The ant biodiversity characteristics of each zone was documented using native ant abundance, native ant species richness, native ant Simpson diversity (using the Simpson Reciprocal Index $1/D$, where D is the probability that two individuals randomly selected will belong to the same species), native ant evenness and total ant abundance. As an indicator of invasion magnitude, the proportion of ants that were invaders for each data set was calculated. I further investigated the effects on these indicators of: 1) reporting using pre- or post-sampling defined zones, and; 2) the scale at which the reporting was made.

Traps that were disturbed were excluded from all analyses and transect and zone scale results include only transects where all five traps were undisturbed. The trap and transect average native ant species richness, diversity, evenness and abundance were compared between post-sampling defined zones using ANOVA and are followed up with Tukey's Honestly Significantly different (HSD) tests. Abundances were log-transformed before analysis and residuals were checked to verify the assumptions of normality and homogeneity of variances were met. These analyses required the assumption that traps were independent within transects and zones and transects were independent within zones.

Relationships of invasive ant abundance and native ant biodiversity indicators

The abundance of the invasive species was used as an independent measure of the magnitude of the invasion and its relationship with the native ant biodiversity measures were investigated by testing for significant Spearman's rank correlations. There were insufficient replicates for statistical testing at the transect or zone scales, hence only pitfall trap associations are included and are compared between pre and post-sampling defined invasion zones.

Relationships with habitat

A Kruskal-Wallis test was used to compare the median of the local scale (pitfall trap and transect) habitat variables between the post-sampling groups. When the effect was significant, ANOVA and Student-Newman-Kuel's multiple range tests on the ranks of the raw data were used to identify significant differences. Spearman's rank correlation analysis was used to investigate the relationships between the habitat variables and the abundance of any ant taxa that occurred in at least 20 pitfall traps.

3.3 Results

3.3.1 Sampling zones

There were 5206 ants collected in 133 undisturbed traps with the other 37 traps lost to disturbance, probably by dingoes, goannas or humans. The pre-determined zones were not precise, with *Pheidole megacephala* and *Paratrechina longicornis* occasionally occurring in the zone thought prior to sampling to be exclusively dominated by the other species (Table 3.1). There were also considerably more traps that had only native ants present than was expected (Table 3.1). Only two transects in the *P. megacephala* zone and the shared *P. megacephala* and *P. longicornis* zones had all five pitfall traps intact (Table 3.1).

3.3.2 Native ant species turnover in invaded zones

Zones invaded by *P. megacephala* had lower observed native ant species turnover than those invaded by *P. longicornis* (Figure 3.3). Zones invaded by both or neither invasive taxa were intermediate in observed native ant species turnover but the magnitude of the differences was dependant on the definition of the zone (Figure 3.3a). Within the post-sampling defined zones, the zone with both invaders present had the highest gradient of species accumulation and the *P. megacephala* zone the lowest gradient (Figure 3.3a). This effect was markedly reduced using the pre-sampling defined zones where the curves were generally more similar to each other (Figure 3.3b).

Table 3.1. Number of undisturbed pitfall traps and transects collected from four different zones at Kingfisher Bay, Fraser Island. For example, there were a total of 25 traps collected in the zone determined as *Pheidole megacephala* prior to sampling, but 11 of these contained only native ants. Complete transects are where all five traps were undisturbed upon collection.

		Post sampling				
		<i>Paratrechina longicornis</i>	<i>Pheidole megacephala</i>	<i>P. longicornis</i> + <i>P. megacephala</i>	Native	Total
Pre sampling	<i>Paratrechina longicornis</i>	35	0	3	4	42
	<i>Pheidole megacephala</i>	0	13	1	11	25
	<i>P. longicornis</i> + <i>P. megacephala</i>	12	0	7	11	30
	Native	0	1	0	35	36
	Total traps	47	14	11	61	133
Complete transects		7	2	2	5	16

The species turnover as calculated by predicted native ant species richness after 11 pitfall traps was significantly different between zones ($F = 77.3$, $df = 3, 3$, $p < 0.005$) and sampling zone definition ($F = 12.7$, $df = 1, 3$, $p < 0.05$). The predictions were higher for the *P. longicornis* and *P. longicornis* + *P. megacephala* zones than the *P. megacephala* or native ant zones (Table 3.2). Across all zones, using post-sampling boundaries gave estimated total native ant species richness that was an average of 2.7 species higher than by using the pre-sampling defined zones (Table 3.2).

Table 3.2. Predicted native ant species richness after sampling in 11 pitfall traps in zones invaded and non-invaded by *Paratrechina longicornis* and *Pheidole megacephala* at Kingfisher Bay, Fraser Island.

Zone	<i>P. longicornis</i>	<i>P. megacephala</i>	<i>P. longicornis</i> + <i>P. megacephala</i>	Native only
Post-sampling	38.8	29.4	39.3	24.4
Pre-sampling	35.7	25.4	35.8	23.9

The average number of native ants per species was considerably fewer in all three post-sampling defined invasive ant zones than the native ant zone (Figure 3.4). Furthermore, there were noticeably fewer native ants in total collected per pitfall trap in the *P. megacephala* and *P. longicornis* zones than the native or combined invader zones (Figure 3.4). Had the pre-sampling defined zones been used the *P. megacephala* zone would have appeared very similar to the native ant zone (Figure 3.4b).

3.3.3 Native and exotic ant indicators and the effect of scale and zone

Overall, the proportion of invasive ants was considerably higher in the *P. longicornis* or *P. longicornis* + *P. megacephala* zones than in the + *P. megacephala* zone (Figure 3.5). The proportion of invasive ants that could be reported, however, was greatly different depending on the reporting scale or if using pre or post-sampling defined zones (Figure 3.5). The proportion of all ants that were *P. longicornis* was considerably higher at the infestation zone scale (0.90 in the *P. longicornis* zone defined post-sampling) than the average proportion at the individual trap scale (0.68). The same pattern was consistent whether considering just the *P. longicornis* zone or the *P. longicornis* + *P. megacephala* zone using post-sampling defined zones (Figure 3.5a). Yet, the proportion of *P. longicornis* individuals

in the *P. longicornis* + *P. megacephala* zone remained constant had the pre-sampling defined zones been used (Figure 3.5a). The proportion of *P. megacephala* in the *P. longicornis* + *P. megacephala* zone also remained constant across scales using pre-sampling defined zones, but *P. megacephala* contributed considerably fewer (<0.1) ants in this zone than *P. longicornis* (0.25–0.3) (Figure 3.5a & b).

Conversely to *P. longicornis*, when *P. megacephala* was present, the proportion of ants that it contributed was lower at the larger spatial scales (Figure 3.5b). The magnitude of the differences were considerable, for example *P. megacephala* contributed an average of 0.77 of all ants in the traps in which it occurred in, but only 0.2 of all ants in the zone that it occurred in (Figure 3.5b).

3.3.4 Native ant diversity indicators and the effect of scale and zone

Larger reporting scales naturally had more native ants collected and subsequently the number of ant species observed was larger (Figure 3.6a). However the magnitude of the difference between the zones changed with scale. At the trap scale there were significantly fewer native ant species collected in traps containing *P. longicornis* or *P. megacephala* using either the post ($F = 8.27$, $df = 3$, 128 , $p < 0.0001$) or pre-sampling defined zones ($F = 12.29$, $df = 3$, 128 , $p < 0.0001$). However, there was no statistical difference in average richness at the transect scale. At the zone scale there were considerably more native ant species collected in the *P. longicornis* zone than the *P. megacephala* zone or the native ants only zone (Figure 3.6a). This difference is no doubt because of the higher number of traps caused by the trap losses and changing boundaries (Table 3.1).

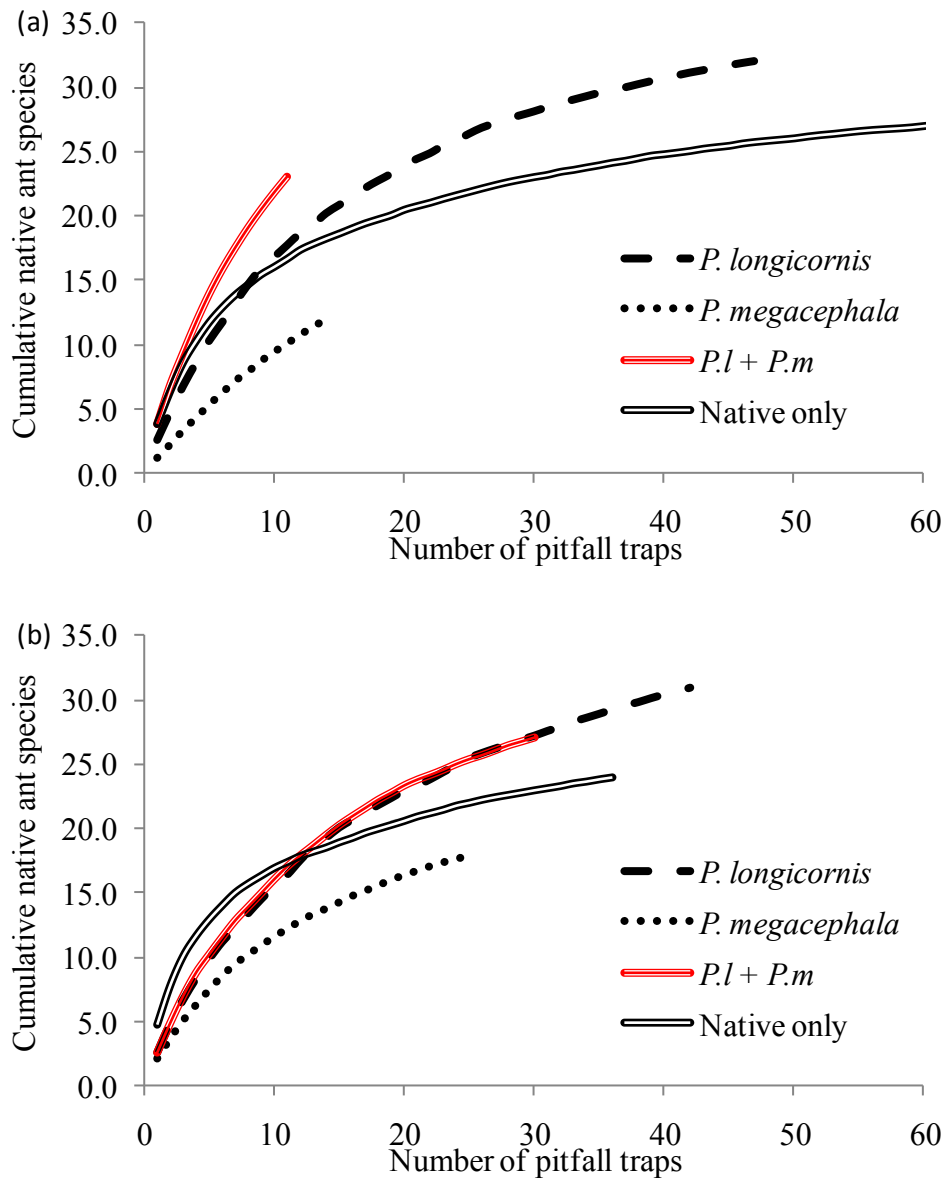


Figure 3.3. Species accumulation curves for native ants in pitfall traps in four zones at Kingfisher Bay, Fraser Island. The zones are defined (a) after sorting and identification of ants in traps and (b) prior to sampling.

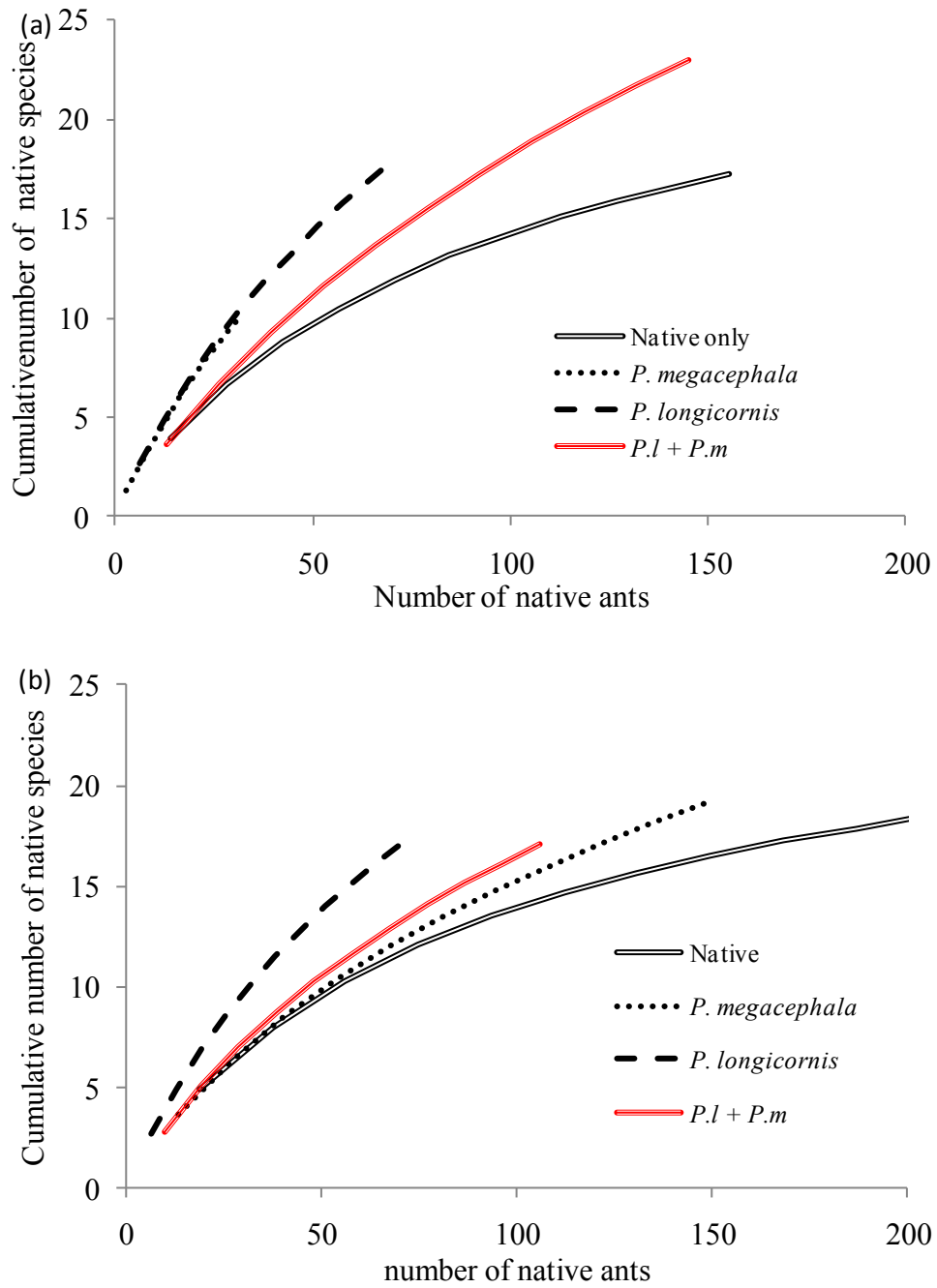


Figure 3.4. Cumulative ant species richness as a function of number of individual ants collected in pitfall traps at Kingfisher Bay Fraser Island. The zones are defined (a) after sorting and identification of ants in traps and (b) prior to sampling. Curves stop at 11 pitfall traps.

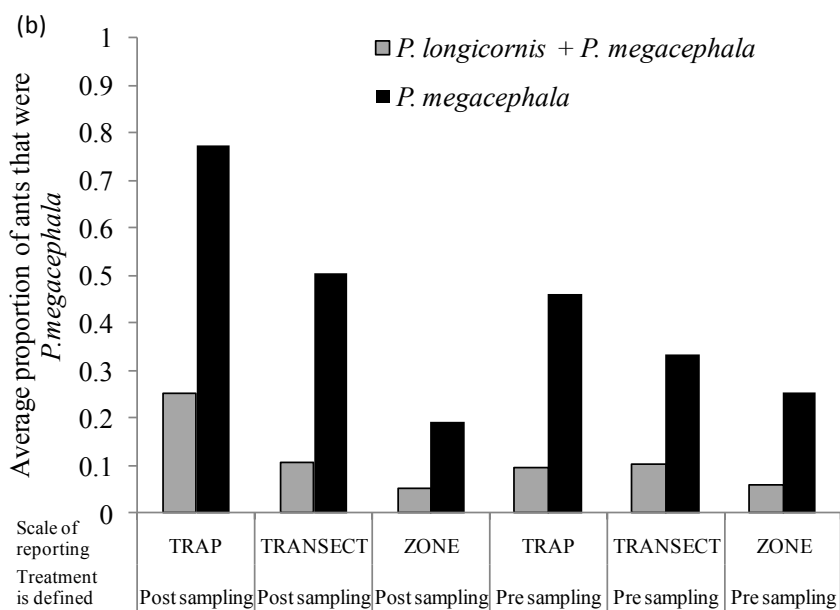
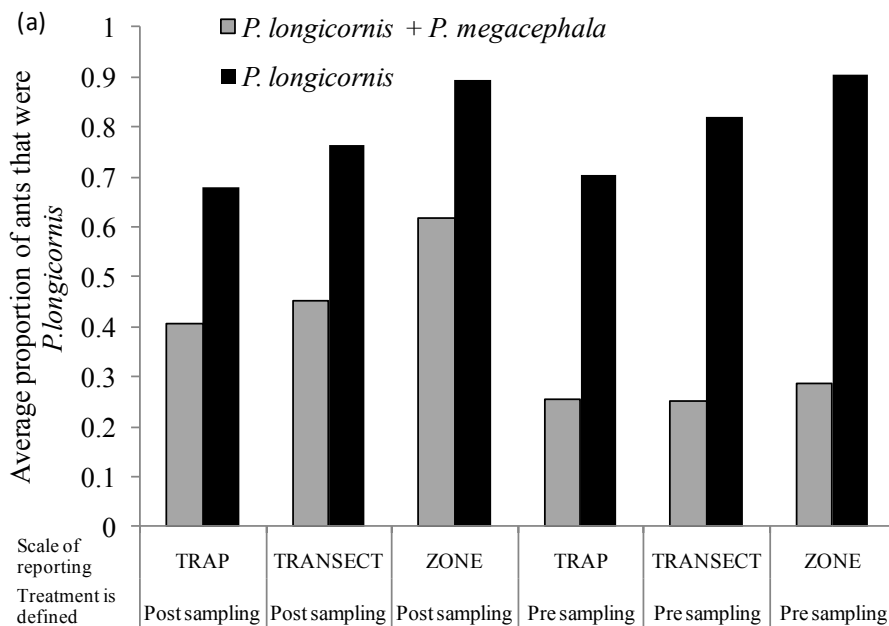


Figure 3.5. Proportion of ants in pitfall traps that were (a) *P. longicornis* or (b) *P. megacephala* at Kingfisher Bay, Fraser Island. Legend is the type of infestation zone as classified either pre or post-sampling. Proportion in traps is the average across all traps, proportion in transects is the average across all transects, proportion in zone is the total proportion of ants in the infested zone.

The abundances of native ants followed similar patterns to the species richness at the trap scale ($F_{\text{post}} = 11.07$, $df = 3, 129$, $p < 0.0001$; $F_{\text{pre}} = 11.22$, $df = 3, 129$, $p < 0.0001$) but there were fewer native ants collected in all invasive ant zones than native ant zones using either definition of zone (Figure 3.6b).

There was no statistical difference in the Simpson reciprocal diversity statistic at the trap or transect scales but diversity was at least 50% higher in the *P. longicornis* sites at the infestation zone scale and the pattern occurs across both definitions of sampling zone (Figure 3.6c). The native ant evenness was also constant across zones and scales (Figure 3.6d) but was significantly lower in the native ants only traps using pre-sampling defined zones ($F = 4.73$, $df = 3, 117$, $p < 0.005$).

On average there were significantly more ants (native + invasive combined) in traps containing *P. longicornis* than those containing *P. megacephala* using either the post ($F = 10.17$, $df = 3, 129$, $p < 0.0001$) or pre-sampling defined zones ($F = 14.28$, $df = 3, 128$, $p < 0.0001$). The same difference was significant at the transect scale using pre-sampling defined zones ($F = 5.6$, $df = 3, 12$, $p < 0.05$) and was apparent (Figure 3.7) but not as significant using post-sampling defined zones ($p = 0.08$). In both instances, the average number of all ants in traps in the *P. megacephala* area or the native ants area was not different.

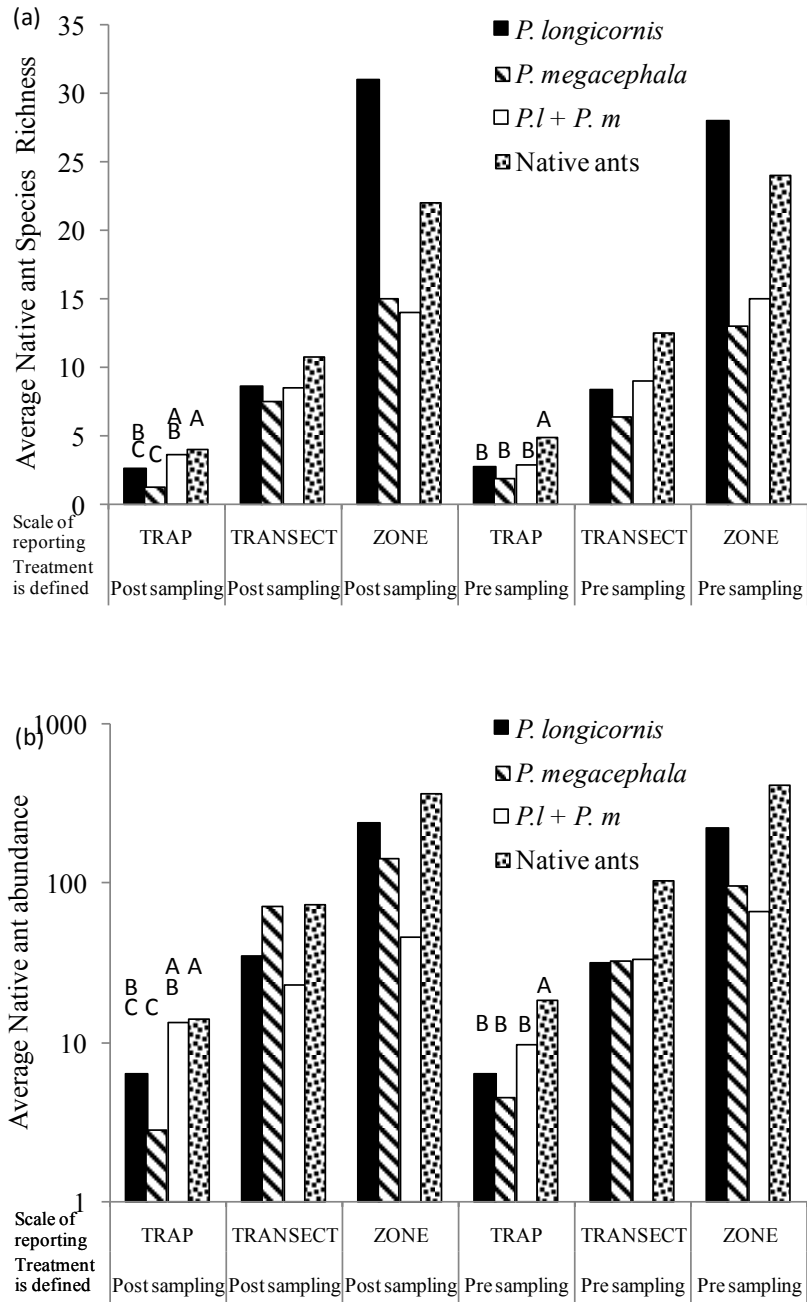


Figure 3.6. Average (a) Native ant species richness and (b) Native ant abundance in pitfall traps, transects or zones at Kingfisher Bay, Fraser Island. Trap scale is the average across all traps, transect scale is the average across all transects and zone scale pools all traps in the zone. Letters indicate groups of Honestly Significantly Different means.

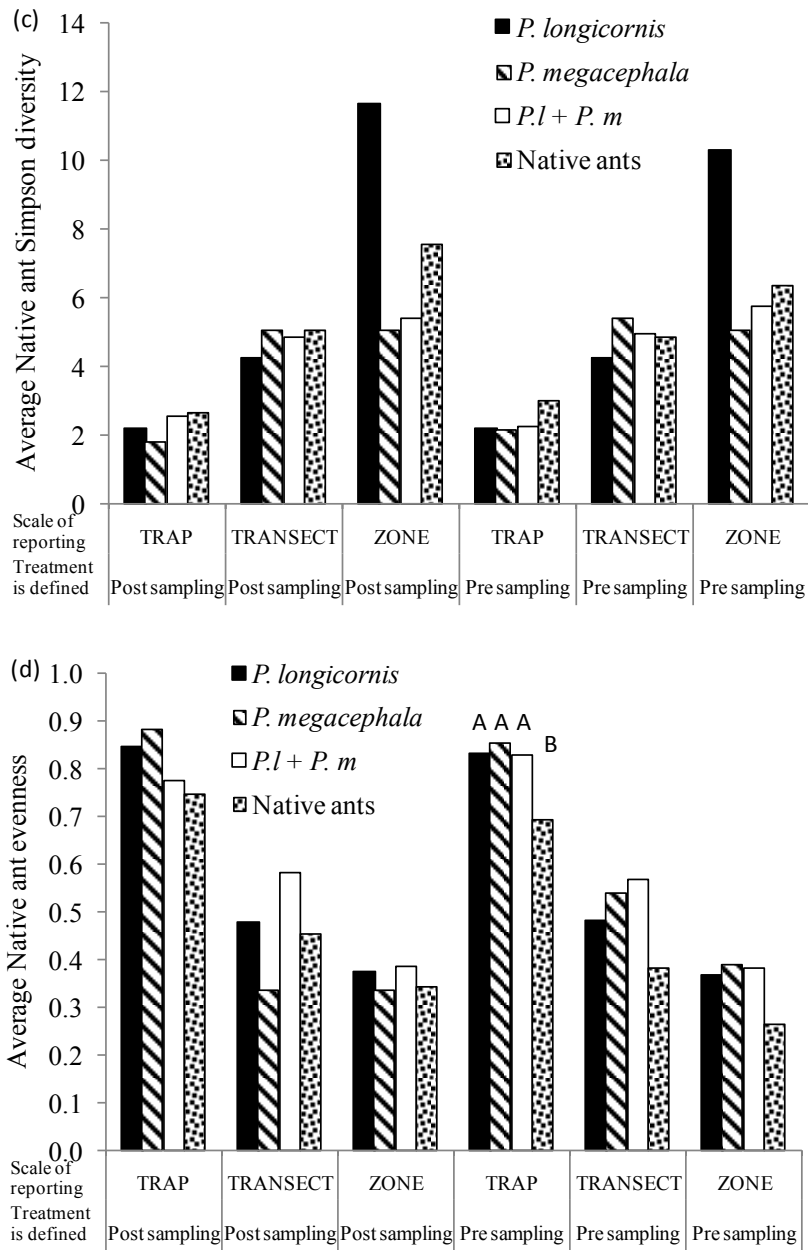


Figure 3.6 (cont.). Average (c) Native ant Simpson diversity and (d) Native ant evenness in pitfall traps, transects or zones at Kingfisher Bay, Fraser Island. Trap scale is the average across all traps, transect scale is the average across all transects and zone scale pools all traps in the zone. Letters indicate groups of Honestly Significantly Different means.

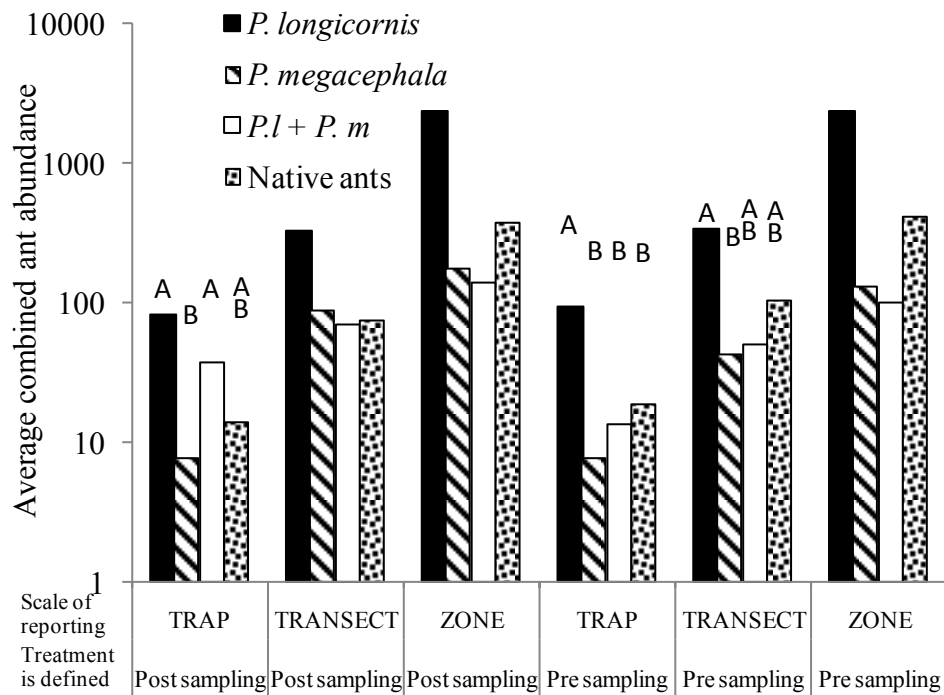


Figure 3.7. Combined ant (native + invasive) abundance in pitfall traps, transects or zones at Kingfisher Bay, Fraser Island. Trap scale is the average across all traps, transect scale is the average across all transects and zone scale pools all traps in the zone. Letters indicate groups of Tukey's Honestly Significantly Different means.

3.3.5 Relationships of invasive ant abundance and native ant biodiversity indicators

When using post-sampling defined invasion zones there were no significant rank correlations between invasive ant abundance and native ant abundance, species richness, diversity or evenness in pitfall traps in any of the invasion zones. However, the abundance of *P. megacephala* in pitfall traps in the pre-sampling defined *P. megacephala* zone was significantly positively related to the native ant evenness ($r_s = 0.69$, $n = 18$, $p < 0.005$), and significantly negatively related to native ant richness ($r_s = -0.63$, $n = 25$, $p < 0.001$) and abundance ($r_s = -0.68$, $n = 18$, $p < 0.0002$). There were no significant relationships with

native ant diversity indicators using pre-sampling defined zones and *P. longicornis* abundance or combined invader abundance.

3.3.6 Relationships with habitat

Potential significant differences were identified between the post-sampling defined zones in mean vegetation height ($H = 7.7$, $df = 3$, $p = 0.052$), percent bare ground ($H = 8.4$, $df = 3$, $p = 0.038$) and percentage litter cover ($H = 6.9$, $df = 3$, $p = 0.082$). Follow up analyses did not reveal any significantly different effects in any of the variables using a 0.05 family-wise error rate. However, using a 0.1 error rate, the *Pheidole megacephala* zone was significantly higher in leaf litter and significantly lower in bare ground than the native ant zone. The other two zones were intermediate and not different to any other zones on both these variables. Whilst multiple comparisons found no statistically significant differences in average height using a 0.1 family error rate, it was noted that the two *P. longicornis* zones tended to have higher average vegetation height (22 and 20.2 m) than the native (12.1 m) or *P. megacephala* zones (14.4 m).

The abundance of *Paratrechina longicornis* was significantly negatively related to the percentage leaf litter cover in the quadrats ($R_s = -0.33$, $n = 58$, $p < 0.02$), whilst *Rhytidoponera metallica* abundance showed a significant negative relationship with the mean height of trees in the transect ($R_s = -0.53$, $n = 17$, $p < 0.05$). Six other species including *Crematogaster laeviceps*, *Nylanderia vaga*, *Pheidole* A, *Pheidole* G, *Pheidole megacephala*, and *Rhytidoponera chalybea*, occurred in 20 or more traps but showed no significant relationships with the local scale habitat variables ($p > 0.05$).

3.4 Discussion

3.4.1 Sampling zones

The four zones used in this study were chosen because of known *a-priori* differences in invasive ant occurrence. The study then documented that there were also differences in the native ant community characteristics of the zones. However, this study has highlighted that the way the differences are reported and interpretations are dependent on the scale of interpretation and whether post survey information is used to redefine the boundaries of the zones. Hence, it is imperative to address the effects of zone definition and scale of reporting prior to considering the actual differences in native ant assemblages among infestation zones at Kingfisher Bay.

If the data had been analysed using the zone boundaries defined prior to sampling, the species turnover would have been more similar between infestation zones (Figure 3.3). This is because about half of the traps that would have been included did not contain any invasive ants (Table 3.1). Further highlighting the importance of correctly determining which data to include in the analyses, the proportion of invasive ants can be critically different, depending on whether calculated using pre- or post-sampling defined zones (Figure 3.5). The use of pre-sampling zones is appealing if the boundaries are clear and only the occasional non-edge trap is found to not have the invader present. This could be justified as simply a small patch randomly sampled from within the infestation and, hence, the indicators presented may appear unbiased. But in reality, the patch may not be an island, but a peninsular, and ants detected in nearby traps may not be just occasional foragers. On the other hand, it may appear that the boundaries used to determine the area pre-sampling were incorrect, in which

case post-sampling boundaries can be estimated and the indicators would again appear unbiased. So, the sampling and analytical decisions really need to be made in conjunction with the aims and indicators of the study in mind and knowledge of the species being studied. For example, in the drier sandy environs on Fraser Island, individual *P. megacephala* foragers do travel far from the nest (W Robinson Pers, Obs.) so their presence in a pitfall trap gives sound evidence of a colony in the immediate vicinity. On the other hand, *Linepithima humile* foragers have been observed up to 200 m from their nest (Holway 2005), so occasional foragers in traps may be expected in areas outside the infestation.

3.4.2 Indicators and scale of reporting

In comparative studies it is imperative is that the indicators used are as comparable as possible which means that a rigorous sampling effort is required. Yet, ant infestations are irregular in shape and size and often don't have a well-defined boundary (e.g. Krushelnycky et al. 2004, Holway 2005), so the boundaries of the area infested are often only estimates. To simply define an area as invaded or not may be to falsely apply a homogenous condition to a heterogeneous zone. Infestation boundaries and invader numbers vary in space and time (Holway et al. 2002a, Callan and Majer 2009) and some authors have used zones of invader density to assist in interpretation of impact (eg Vanderwoude et al. 2000, Callan and Majer 2009). Although these specific studies were inferring a gradient of impact that was appropriately documented because they used a grid style sampling strategy, the current study was designed to document differences between zones in a manner that allowed the results to be considered using a spatial sampling hierarchy. This sampling design still

allowed estimates of invasion success such as proportion and abundance of invaders whilst highlighting their spatial variability.

The proportion of all ants captured that were *P. longicornis* increased substantially as the scale of reporting increased (Figure 3.5). This effect was caused by several pitfall traps having many hundreds of individual *P. longicornis* collected with only a few native ants. With *Pheidole megacephala*, however, the opposite was true. *P. megacephala* occurred in low numbers generally, but native ant abundances in the (*P. megacephala*) pitfall traps were skewed (i.e. sometimes very high or very low). Therefore, reporting the proportion of all ants captured that are from the invasive species indicator alone is not a good measure of the magnitude of the exotic ant invasion.

The native ant indicators used to compare between the zones must also consider scale closely. In biodiversity studies in general, the more ants collected the more species are collected (Delabie et al. 2000, Dorazio et al. 2006). Accordingly, in this study, the richness and abundance behaved similarly at all scales (Figure 3.6). But both responses are also related to scale because average native ant species richness and abundances were significantly lower in invaded zones in individual pitfall traps but not different to uninvaded zones when looking at the transect scale (Figure 3.6). This occurs because there are fewer native ants per species in the invaded zones (Figure 3.4).

Therefore, the most appropriate way to detect differences in species richness between different zones without inserting a bias is to use species turnover, which calculates the average number of species for a large number of permutations of various trap numbers from the raw data. In this study, *P. longicornis* and *P. megacephala* both had lower native ant

species richness per pitfall trap, but the native species turnover was clearly lower in the *P. megacephala* zone (Figure 3.3) turning over 10 native species in 11 traps compared to the average of 16 species in 11 traps in the native zone. Similarly, the most appropriate way to detect differences in native ant abundances is to consider cumulative species average abundance (Figure 3.4), which clearly shows a reduced number of native ants present in the zones invaded by *P. megacephala* and *P. longicornis* at Kingfisher Bay.

In general, tramp ants are very successful at establishing in areas that have low native species richness (e.g. Greenslade 1971, Reimer 1994, Collingwood et al. 1997). This doesn't appear to be the case at Kingfisher Bay if the data are not interpreted correctly. In the joint invasion zone average species richness per trap could be misleading if interpreted alone because there were 23 native species observed in just 11 pitfall traps where both invaders were present, 12 different native ant species observed in the 14 traps where *P. megacephala* was the sole invader, and 32 native species in the 47 traps where *P. longicornis* was the invader. Only after using species turnover to compensate for the different sampling intensities was it found that there was actually low species richness in both invader zones (Figure 3.3). The inclusion of species turnover and abundance (Figure 3.4) revealed a substantially weaker native ant community only in the *P. megacephala* zone.

In summary, it is only after integrating the results of the different indicators and cumulative native species curves that it becomes apparent that the *P. megacephala* invasion is associated with substantially fewer native ants (fewer native ant species than any of the other zones). On the other hand, *P. longicornis* occurs in a species rich zone that has more native ants than the *P. megacephala* zone but still fewer than the native ants zone.

3.4.3 Proportion of invasive ants in the infested zone

Invasive species can reach the high population densities that allow them to be competitively superior (Morrison 2000) but this was certainly not the case for *P. megacephala* at Kingfisher Bay. *P. megacephala* made up less than 25% of ants in the zone where it was the sole invader and less than 25% of ants where it occurred with *P. longicornis*. This is considerably fewer than reported in any other Australian study (see Table 1.2). However when considering the abundances of *P. megacephala* only in traps where it occurred without *P. longicornis*, then it made up almost 80% of individuals (Figure 3.4), which is closer to the proportions published by other studies (see Table 1.2). This huge discrepancy (25% or 80%) is a function of the low native ant abundances in *P. megacephala* traps and reveals just how carefully results from published studies should be interpreted. For example, the 89% of individuals reported by Heterick (1997) was from 1775 *P. megacephala* individuals from nine pitfall traps placed in each of two sampling plots. If only one of the traps had been randomly placed near a nest the 89% proportion is not extraordinary. In such cases, a measure of evenness of the distribution of the invader would help interpretation. For example, a diversity or evenness index could be calculated for traps containing the invasive species with high values suggesting more patchy distributions and lower values representing more even invasions. In this study, the Simpson diversity for *P. megacephala* and *P. longicornis* within their respective traps were 9.6 and 6.6 (both reasonably high), suggesting patchy distributions. In traps where they both occurred, the diversity is still patchy (7.5 and 4.0) but more even than when solely occurring.

3.4.4 Native ant diversity values in the *P. megacephala* infested zone

A common justification for stating that *P. megacephala* has an impact on native ants is to compare the overall ant numbers or biomass in invaded zones with uninvaded zones. For example, *P. megacephala* biomass in infested sites was up to 18 times greater than that of native ants in uninfested sites (Callan and Majer 2009), and *P. megacephala* had 37 to 110 times the abundance of all native ants combined at uninfested sites (Hoffmann et al. 1999). Such comparisons are not possible in this study because of the differences in sampling effort among the zones. However, the average number of native ants per pitfall traps revealed that the *P. megacephala* and *P. longicornis* zones both had considerably fewer native ants than the native or joint invader zones (Figure 3.5b), but neither were different in carrying capacity to the native zone in total ant carrying capacity (Figure 3.6). In other words, in this study there was no evidence of increased ant biomass or abundance in infested and uninfested zones, so neither species could be described as achieving dominance. This has been reported occasionally in the literature, with no significant difference in total ant abundance reported between *P. megacephala* infested and uninfested sites in St Mary state Forest (Vanderwoude et al. 2000). Similarly, even after 150 years since arrival in Madeira *P. megacephala* and *L. humile* were deemed to have had little impact on native ant abundances (Wetterer et al. 2006).

Whilst there was no overall increase in total ant numbers in the *P. megacephala* zones, there was a definite association of both taxa with reduced native ant richness and abundance. This was particularly obvious for *P. megacephala*. However, because this study is observational and post-invasion, cause and effect are not considered. Still, there is obvious potential for impact on native ant assemblages by *P. megacephala* on Fraser Island and this requires

further investigation. Zones invaded by *P. megacephala* at Kingfisher Bay Resort and Village had lower native ant biodiversity value (as indicated by the lower species turnover) than those invaded by *P. longicornis* or nearby native ant zones.

3.4.5 Native ant diversity values in the *P. longicornis* infested zone

Paratrechina longicornis are the numerically dominant taxa where they occur at Kingfisher Bay Resort and Village. When they are the only tramp ant present, they average more than two thirds of ants in traps and 90% of ants in the infested area (Figure 3.3). *P. longicornis* infested zones average more ants per trap (Figure 3.5a) and accumulate more species than native ant zones or *P. megacephala* infested zones (Figure 3.3), but *P. longicornis* does not merely add to the existing ant community at Kingfisher Bay because there are fewer native ant species per trap recorded when it occurs (Figure 3.6a).

Whilst there were more than 30 native species recorded in the *P. longicornis* zone, there was no relationship between *P. longicornis* abundance and native ant species richness at the trap scale. This is in contrast to the results of Andersen (1993) who also found high *P. longicornis* abundance (up to 46% of ants) but a negative relationship with native species richness. A major difference between that study and the current one is the absence of the behaviourally aggressive *Iridomyrmex* around Kingfisher Bay. *P. longicornis* are known to be able to be displaced in competitive interactions at baits by aggressive taxa (Banks and Williams 1989, Stanley and Robinson 2007). On the other hand, it has been shown to be strongly favoured by disturbance or open habitats and extremely dominant when there are few aggressive taxa with which to compete (Farnsworth 1993, Wetterer et al. 1999). The dry

Casuarina dominated habitats around Kingfisher Bay, coupled with naturally low numbers of aggressive native taxa appear to suit *P. longicornis* well.

P. longicornis dominated already impoverished ant assemblages through exploitative competition in the Galapagos Islands (Meier 1994) and the Biosphere II project in the Arizona Desert (Wetterer et al. 1999), and was the numerically dominant taxon in disturbed mining revegetation sites in Northern Australia (Andersen 1993). This ability to exploit available resources more than likely enables *P. longicornis* to occasionally coexist with dominant native ants (Andersen 1993, Reichel and Andersen 1996) and other invasive species (Meier 1994).

3.4.6 Native ant diversity values in the joint *P. longicornis* and *P. megacephala* infested zone

There are examples demonstrating that the success of invasive ants may be facilitated by other invaders and vice versa (Holway et al. 2002a). However, this is usually based only on observational data and there are often extraneous factors influencing both invaders. For example, *Paratrechina longicornis* showed positive correlations with increasing *Solenopsis invicta* populations, probably because of being favoured by increasing urbanisation in Gainesville, Florida (Wojcik 1994). Nevertheless, the results in the current study do not suggest both taxa are flourishing, with *P. longicornis* obviously more successful at Kingfisher Bay than *P. megacephala* (Figure 3.5).

When *P. longicornis* occur with *P. megacephala*, the former species make up twice as many individuals on a trap by trap basis and more than ten times as many individuals in the

infested area as a whole (Figure 4.4). In this study, the densities when co-occurring were considerably lower than when only one was present (Figure 3.1). These two species have been recorded occurring together on three of the Florida Keys where both reached high densities on two Keys (Wetterer and O'Hara 2002), but not on a third Key. Nevertheless Wetterer & O'Hara (2002) still determined that *P. megacephala* was a dominant species and posed more of a threat to native species than *P. longicornis*. The two species are widespread in the French and Venezuelan Islands of the Caribbean but never occur on the same island (Jaffe and Lattke 1994).

The competitive ability of *P. longicornis* may be underestimated in Australia. Certainly it is the numerically dominant ant at Kingfisher Bay and may be well-suited by conditions there. It totally dominated all ants in disturbed areas at Kingfisher Bay (Stanley and Robinson 2007) and in this study it occurred in much greater numbers than *P. megacephala* when both occurred in undisturbed habitats (Figure 3.5). This may be in part because it is so abundant in the disturbed habitats and has a greater foraging range than *P. megacephala*. Alternatively, it may be that it is actually dominant over *P. megacephala* at Kingfisher Bay. All ants can be disadvantaged by abiotic factors, and in those instances, even *P. megacephala* can be displaced by other taxa. For example, they may have been displaced by *Solenopsis geminata* on some Florida Keys (Wetterer and O'Hara 2002) and *Linepithma humile* in parts of Hawaii (Passera 1994). *P. longicornis* is so fast and agile that Wheeler (1908) considered it would be able to hold its own against the fire ants, *Solenopsis invicta*. On the other hand, *P. longicornis* may be subordinate to *P. megacephala* but still captured more at Kingfisher Bay because of greater probability of capture in pitfall traps (because of greater foraging distances and speed). *P. longicornis* were seen to be subordinate and

displaced on baits by *Wasmannia auropunctata*, yet still made up to 43% of ants on cacti in the Galapagos Islands (Meier 1994).

There many possible reasons why *P. longicornis* infestations had higher native ant biodiversity values than the *P. megacephala* zones. *P. megacephala* may be a weaker competitor with native ants, perhaps being unable to invade areas with higher biotic resistance, or; *P. longicornis* may be a superior invader able to invade species rich habitats. Other possibilities include; *P. megacephala* may be a superior invader, able to displace more native ant species, or; *P. longicornis* may be a dominant taxon, able to remove subordinate taxa and thereby opening up interstitial spaces in the ecosystem allowing greater native ant diversity. None of these postulations can be directly answered because the surveys were performed post-invasion and therefore cause and effect cannot be determined. However, this study allows a much more detailed investigation of the characteristics of the invaded and native ant zones than most post-invasion studies because it was designed in a way that allowed multi-scalar comparisons of native ant biodiversity and took the effort to redefine invasion zones post-sampling.

The shared invasive ant zone in this study had more species on average in individual traps, but fewer species at the zone scale (Figure 4.5a). This is important because it may be the pool of species in the area that influences the susceptibility of the area to invasions. For example, there was on average about 9–12 ant species in all four transect types but very few species per trap when only *P. megacephala* was present (Figure 3.2a). In other words, the abundance of the native species present in these traps must also be low and this effect may be missed if only considering the results using one scale of reporting.

On a trap-by-trap basis in this study, there were the same number of native ants occurring when there were no invaders present as when both invaders were present, seven times more native ants occurring in native only traps than when *P. megacephala* was present and twice as many when *P. longicornis* was present (Figure 3.2b). At the zone scale, the native ants were 1.5×, 2.5× and 8× more abundant in the uninvaded zone than in the zones with *P. longicornis*, *P. megacephala* and *P. longicornis* + *P. megacephala* respectively (Figure 3.2b). The reason for this difference cannot be determined by this study. It may be the reduction in native ant numbers that allows the invaders to be present (by filling the niche) or vice versa (by displacing native ants). The data from the previous chapter may supply a clue. One of the Mixed Forest with Cypress sites sampled in Chapter 2 (MFC202) was within the KBRV lease and only about 300 m from the nearest site of this study. MFC202 had 39 and 40 species collected in the 2004 surveys and a predicted native ant richness approaching 100 (Figure 2.3). The sites surveyed in this chapter are of similar size and have more pitfall traps collected, yet are predicted to have ant species richness generally lower than 30 (Figure 3.4). Some of the difference may be because of the different vegetation assemblages and the litter not being sampled in this study, but also because all the current study sites, while not being undisturbed *per se*, do adjoin built up areas. So they may be thought of as disturbed by having proximity to known disturbed areas or having a lower regional pool of species from which to draw. This could explain the lower native ant species richness of these sites generally. Indeed disturbance has regularly been associated with both *P. longicornis* and *P. megacephala* infestations (e.g. Majer 1985a, Heterick 1997, Hoffmann 1998, Wetterer et al. 1999, Heterick et al. 2000, Wetterer and Wetterer 2004).

3.5 Conclusions

- *Results from surveys of sites infested by native ants can be very different when reported at different scales.*
- *When there is a difference in the sampling effort between zones in a comparative study then the results need to include trap based and turnover based, rather than transect or zone (whole of infestation) based, indicators.*
- *Indicators such as proportion of invader abundance or biomass are severely influenced by scale and should use average trap proportions if used at all.*
- *Paratrechina longicornis were the numerically abundant and locally dominant ant taxa at Kingfisher Bay when they occurred.*
- *When both invasive species occurred, P. longicornis was considerably more abundant than P. megacephala.*
- *Native ant species richness and abundance was lower in zones invaded by P. longicornis and/or P. megacephala at Kingfisher Bay.*
- *Pheidole megacephala was associated with very low native ant species richness and abundance.*
- *Zones invaded by P. megacephala had lower native ant species turnover than those invaded by P. longicornis.*
- *The cause of the low native ant species is not entered into and there is a clear need to understand seasonal fluctuations in exotic ant colony boundaries and the role of disturbance.*

Chapter 4: The role of disturbance in the localised spread of *Pheidole megacephala*.

4.1 Introduction

Once established, invasive ants are almost impossible to eradicate (Holway et al. 2002a) and a fundamental management strategy for control is to limit their dispersal (Krushelnycky et al. 2004). Whilst long distance dispersion is often human mediated (Suarez et al. 2001), local dispersion is generally related to resource availability and the biotic or abiotic components of the ecosystem (Holway 1998b, Human et al. 1998, Holway et al. 2002b, Walters and Mackay 2003, Walters and Mackay 2004, Krushelnycky et al. 2005, DiGirolamo and Fox 2006, Menke and Holway 2006). The majority of invasive ant species spread locally by budding, i.e. new queens walking just a few metres from the existing nest (Hölldobler and Wilson 1990, Passera 1994, Holway 1998b, McGlynn 1999b, Suarez et al. 2001, Holway et al. 2002a) and interactions at this scale with the environment and other biota may be critical for the success of the budding colony. Therefore, management that disturbs or affects the local environmental factors around an infestation may also prove critical in promoting or hindering colony budding and local dispersion.

Disturbance involving reduced vegetation cover changes the local microclimate and can promote the dispersal of exotic fauna and flora in general (Trombulak and Frissell 2000) and should favour ants suited to drier, hotter conditions (Andersen 1991, York 2000, Hoffmann

and Andersen 2003). Disturbance to soil and vegetation generally leads to less ant species diversity (Burbidge et al. 1992, Hoffmann et al. 2000, York 2000, Hoffmann and Andersen 2003) and is favourable to opportunistic ant species (Majer 1985a, Andersen 1990, Woinarski et al. 2002). But if dominant or aggressive ant taxa are present and favoured by the changed abiotic conditions in newly disturbed areas, they may dominate the newly depauperate ant fauna (e.g. Andersen 1991, Gibb and Hochuli 2003, Schnell and Dangerfield 2003). When the disturbance reduces dominant native taxa or when there are few native dominant taxa present, some forms of disturbance can allow accelerated access for some of the world's worst invasive ant species (e.g. Ward 1987, Majer 1994, Stiles and Jones 1998, Holway et al. 2002a).

Linear disturbances into vegetation such as clearing vegetation for roads or power lines are known to provide transportation routes for dominant ant fauna like *Solenopsis invicta* (Stiles and Jones 1998) and *Iridomyrmex purpureus* (Gibb and Hochuli 2003). Yet, like much invasive ant research, studies into the effects of vegetation clearing by power line routes, roads, fire trails or track formation are usually *post hoc* and post disturbance. Studies of invasions in progress, which sample across several years, may help to predict the spread and effects of invasive species (Sanders et al. 2001) and invasion ecology in general would benefit from research that uses experiments or long-term monitoring (Trombulak and Frissell 2000, Holway et al. 2002a, Hoffmann and Parr 2008).

One of Australia's worst invasive species, the African Big-headed ant, *Pheidole megacephala* is favoured by disturbance in general, although it is also recognised as being moisture limited (e.g. Tryon 1912, Greenslade 1971, Fowler et al. 1994, Hoffmann 1998, Hoffmann and Hohenhaus 1998, Hoffmann et al. 1999, Heterick et al. 2000, May and

Heterick 2000, Wilson 2003) and may be restricted by competitive exclusion in species rich faunas (Greenslade 1972, Majer 1985a; Chapter 3). Thus, disturbance by vegetation clearance creates an interesting dilemma for *P. megacephala*: can the reduced biotic resistance be used to promote the spread of the colony when faced with increased stress from environmental factors? Factors that affect the spread of *P. megacephala* into native vegetation are of serious concern on Fraser Island because the local ant assemblages do not contain behaviourally dominant taxa like *Iridomyrmex* (Chapter 2) and a *P. megacephala* invasion in native bushland near Kingfisher Bay Resort and Village was associated with very low native ant biodiversity values (Chapter 3).

This chapter uses annual sampling through a 5-year study period to investigate how the local spread of *P. megacephala* is influenced by management interventions that disturb habitat on Fraser Island in subtropical Australia. Specifically, the study looks at various boundaries of a large *P. megacephala* infestation and how they vary annually without interventions in comparison with boundaries that are influenced by managed vegetation clearing by fire and road/track formation.

4.2 Methods

4.2.1 Study site

The study was conducted immediately adjacent to Dilli Village on Fraser Island, located about 290 km N of Brisbane in South eastern Queensland (See section 3.3 for further details). Dilli Village is located 400 m from the beach on the Eastern side of the island about 22 km from the southern tip (Hook Point). It was created as a camp for sand mining staff in

the mid-1970s and is approximately 1.5 km from the nearest sand mining operations. *Pheidole megacephala* was probably introduced when the village was constructed and is common in and around the buildings but also in the native bushland and along the edges of most tracks around the village. The surrounding vegetation is predominantly coastal *Acacia* shrubland, dominated by *Acacia concurrens* with occasional *Banksia aemula* and *Eucalyptus* spp. as the major overstorey species.

4.2.2 Field sampling

Boundaries of a *P. megacephala* infestation were mapped annually to describe changes in the infestation boundaries before and after several disturbance types including fire, linear clearing for roads, walking tracks or wildlife exclusion zones (Figure 4.1, Table 4.1).

P. megacephala are dominant and monopolise resources when present, so are easy to find using baits. Annual surveys using peanut butter on bamboo kebab sticks were conducted between mid-September and mid-October from 2004 to 2009. There were six different surveys carried out, although not all of the surveys were conducted each year (Table 4.1).

Baits were generally positioned in the mid-afternoon, checked for ants before sunset (after about 1.5 hours), after dark (after about 4.5 hours) and again the following morning (after about 15 hours). In some surveys the baits were only inspected twice, which was still enough to locate *P. megacephala* when present because 95% of the time the initial detection was on the first inspection and only <0.5% on the third inspection of the bait. Baits are occasionally listed as missing because they may have been not set, lost or disturbed by external agents such as small mammals, dingoes or goannas.

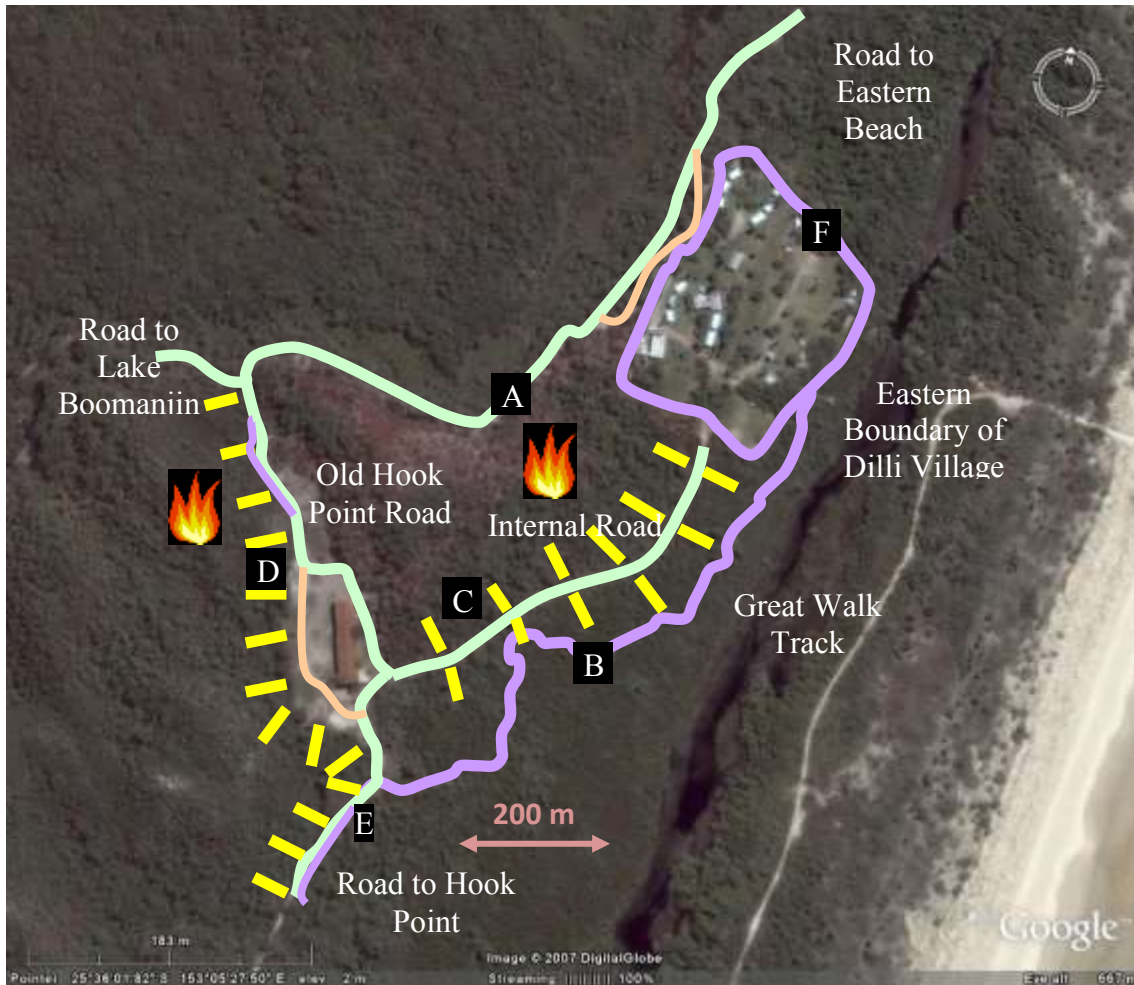


Figure 4.1. Location of bait surveys used to monitor boundaries of *Pheidole megacephala* infestation in disturbed and natural habitats around Dilli Village, Fraser Island. Letters match descriptions in Table 4.1.

Table 4.1. Description of bait surveys used to monitor the presence of *Pheidole megacephala* in disturbed and natural habitats around Dilli Village, Fraser Island. Note that survey E was conducted at a different spatial scale in 2005.

Survey	Survey ID (Figure 4.1)	Survey Year						Intervention	Intervention Date	Distance between lines	Baits per line	Monitoring of <i>P. megacephala</i> infestation is relevant to
		2004	2005	2006	2007	2008	2009					
External Road	A	✓	✓	✓	✓	✓	✓	nil (at extremes)	August 2005 April 2009	20 m	4 = each side of road + 2 m into bush off each side of road	Linear spread along existing road without intervention
Great Walk Track	B	✓	✓	✓	✓	✓	✓	Track cut through native bushland	May 2004	10 m	4 = each side of track + 2 m into bush off each side of track	Linear spread along track after initial intervention. Effect of natural vegetation regrowth
Internal road from Dilli Village	C	✓	✓	✓	✓	✓	✓	Management controlled burn on western side	August 2005 April 2009	5 m	2 = 1 at ground level + 1 on vegetation at 1.3 m	Natural and fire affected spread into native vegetation
Beyond the Shed	D			✓	✓	✓		Track widening Management controlled burn	April 2006 May 2008	10 m	1 on ground	Natural and fire affected spread into native vegetation and along an existing track
Road to Hook Point	E		✓	✓	✓	✓	✓	Track widened to become a fire break	April 2006	10 m	4 = each side of road + 2 m into bush off each side of road	Linear spread along track after intervention
Perimeter Fence	F	✓	✓	✓	✓	✓	✓	Dingo exclusion fence installed with fire break, cut through native bushland in parts	April 2004	5-15 m	3 = 1 next to fence + outer edge of fire break + 2 m into bush	Linear spread along fence after initial intervention Managed as a fire break by mowing

Survey A. The existing road to Lake Boomanjin [control for linear movements]

Lines of baits were placed every 20 m along the road from the Eastern beach to Lake Boomanjin from the first entrance to Dilli Village to 80 m past the Hook Point Road junction. Each line of baits included baits placed on each side of the road and another bait 2 m into the forest off each side. Advance or retreat of the infestation at either end of this transect was deemed to be natural spread/contraction without intervention. Baits between about 140 m and 380 m were exposed to management burns in August 2005 and April 2009.

Survey B. The Great Walk track [effects of linear vegetation clearing I]

The Dilli Village to Hook Point Road section of the Fraser Island Great Walk track was created in May 2004 by clearing a 1.5 m swathe through the coastal dune vegetation. It was the unexpected creation of this track that prompted this entire study as by July 2004 *P. megacephala* appeared to be colonising the track from near the Dilli Village end (W. Robinson pers. obs). This southern end of the track is seldom used as most walkers start their expedition on a northern trajectory from Dilli Village, and the internal road which runs almost parallel offers a lower impact option for the few walkers that arrive from Hook Point. There has been no maintenance of the track since it was installed and it is possible that the annual surveys for this research were the only use it received during this time. In 2009, the track was barely distinguishable in some parts and there was considerable leaf litter on the track for its entire length. There are no pre-track data, so this survey assumes the infestation encroached linearly and was not already in the bushland before the vegetation clearing occurred, although

even if this assumption was violated the data still allow a unique temporal record of infestation dynamics in a cleared and naturally regenerated area. A line of four baits was placed along the Great Walk track every 10 m from Dilli Village to the junction of the track and the Hook Point Road/Jabiru fire break. Each line of four baits included a bait placed on each side of the track, and another bait 2 m into the vegetation each side of these.

Survey F. Dingo exclusion fence [effects of linear vegetation clearing II]

An exclusion fence was constructed around Dilli Village in April 2004 to exclude large vertebrates. A cleared area about 4 m wide immediately outside the wire is regularly mown (at least once per annum) to also act as a fire break except for a section along the western boundary of the fence where a pre-existing driveway acts as the fire break. In this study, the lines of baits were aligned with posts on the dingo exclusion fence. Lines of 2–3 baits were therefore approximately 10 m apart, but occasionally slightly closer or further apart. On each bait line, a bait was positioned on the cleared area just outside the fence post and another on the outside of the mown area. In the surveys of 2005 to 2008, a bait was also positioned 2 m further away, into the native vegetation outside the cleared area. The main difference of this study to the Great Walk track is that this fire break receives regular mowing and there is no regrowth of the vegetation above grass height and it has a negligible litter layer.

Survey E. Hook Point Road [clearing of vegetation by track widening]

The Hook Point Road was surveyed in 2005 as part of a large scale search for *P. megacephala* in the old sand mining area with bait lines placed 40 m apart. A new

survey commenced in 2006, after the old road was widened on the east side only to act as a firebreak, with the bait lines 10 m apart. On each line, a bait was placed on each side of the track and another bait placed 2 m into the vegetation off each side. Whilst the road is only 10 or so metres across, the eastern (widened) side of the track is the downhill side of a sand dune and tends to support a moister habitat (Coastal *Acacia*) than the higher and more exposed western side (Coastal *Banksia*).

Survey D. Native vegetation beyond Dilli Village Shed [the effects of fire I]

This survey consisted of 13 transects placed 30 m apart along the old sand mining road side verge. The road has been closed to traffic for several years and was widened to form a fire break in April 2006. The first bait on the first four transects of this study overlap with some baits on survey A (Lake Boomanjin Road Survey) and this survey started in 2006 when *P.megacephala* were first observed here. The first baits on transects 10–13 also overlap with survey E (Hook Point Road survey). To compensate for a corner, an extra transect (7A) was placed in between transects 7 and 8, giving a total of 14 transects. At each transect a bait was placed next to the road and another 4 to 7 baits placed perpendicular to the road at 10m intervals. The fire break made the road about 10 m wider between transects 2 and 3 and their second baits were therefore also in a de-vegetated area. Transects 1 to 8 were burnt in a controlled burn in May 2008. The spread of *P. megacephala* along the roadside verge laterally (*between* transects) is a measure of spread along an existing road, whilst the spread between baits within transects is a measure of spread into native bushland with and without fire.

Survey C. Native vegetation within Dilli Village lease [the effects of fire II]

A transect was placed every 50 m on each side of the internal road from Dilli Village to the machinery shed. The road is closed to the public so has only about 25 vehicle uses per week. For each transect, a bait was placed every 5m up to 25 m into the native vegetation perpendicular to the road. Baits were placed at ground level and on the vegetation at 1.3 m. Vegetation in all transects on the western side of the road was subjected to controlled burns in August 2005 and April 2009. The spread of *P. megacephala* between baits within a transect is a measure of spread into native bushland with and without fire. Surveys were conducted from 2005 to 2009 but the arboreal survey was not conducted in 2009.

4.2.3 Ant identification

Pheidole megacephala are very easy to recognise (see Plate 3) from morphology, high levels of recruitment and timidity when the bait or nearby habitat is disturbed. Native ants were identified to species when recognised otherwise to genus. Ants were therefore identified *in situ* where possible or when the observer was in doubt a specimen was collected and later identified.



Plate 3. *Pheidole megacephala* on a peanut butter bait

4.2.4 Data analysis

The data for each bait point in each year were converted to presence and absence of *P. megacephala* and/or native ants. The distribution of *P. megacephala* along the bait lines are interpreted via schematic diagrams that display sequential annual distributions on all baits. For the studies looking at the advance and retreat of *P. megacephala* in native bushland and the effects of fire, the maximum distance of *P. megacephala* along each transect away from the roadside verge each year was calculated. The difference in this distance between years was calculated for each transect and tested against the null hypothesis of no average change in the distribution between the two years. The transect closest to Dilli Village in survey C could not be

used because the ants were commonly at the extent of the transect and advance was therefore not measurable. Similarly, any transect that had no record of *P. megacephala* in the previous year was excluded from the next year's analysis. The effect of the three management fires was tested against a hypothesis of no change in the distribution between burnt and unburnt transects. The data were not normally distributed being constrained to 5 m or 10 m measurements. Therefore, the annual comparisons were tested with a Wilcoxon Signed Rank test and the between fire comparisons made with a Wilcoxon Rank Sum test.

4.3 Results

Survey A. The existing road to Lake Boomanjin [control for linear movements]

P. megacephala advanced away from Dilli Village along the road towards Eastern Beach by about 60 m over the three years between 2004 and 2007 (Figure 4.2). There was also an initial advance in the infestation at the Lake Boomanjin end of the transect after the fire in 2005, but this was followed by a similar sized retreat in 2006 and it continued to oscillate by about 40 m each year. The infestation was predominantly on the eastern side of the road in 2004 with only five baits recording *P. megacephala* on the western side, but this had increased to 12 points by 2006 (Figure 4.2). Although *P. megacephala* monopolised fewer baits in 2008 than 2004, the extent along the road had increased from 340 m in 2004 to about 480 m in 2008 (Figure 4.2).

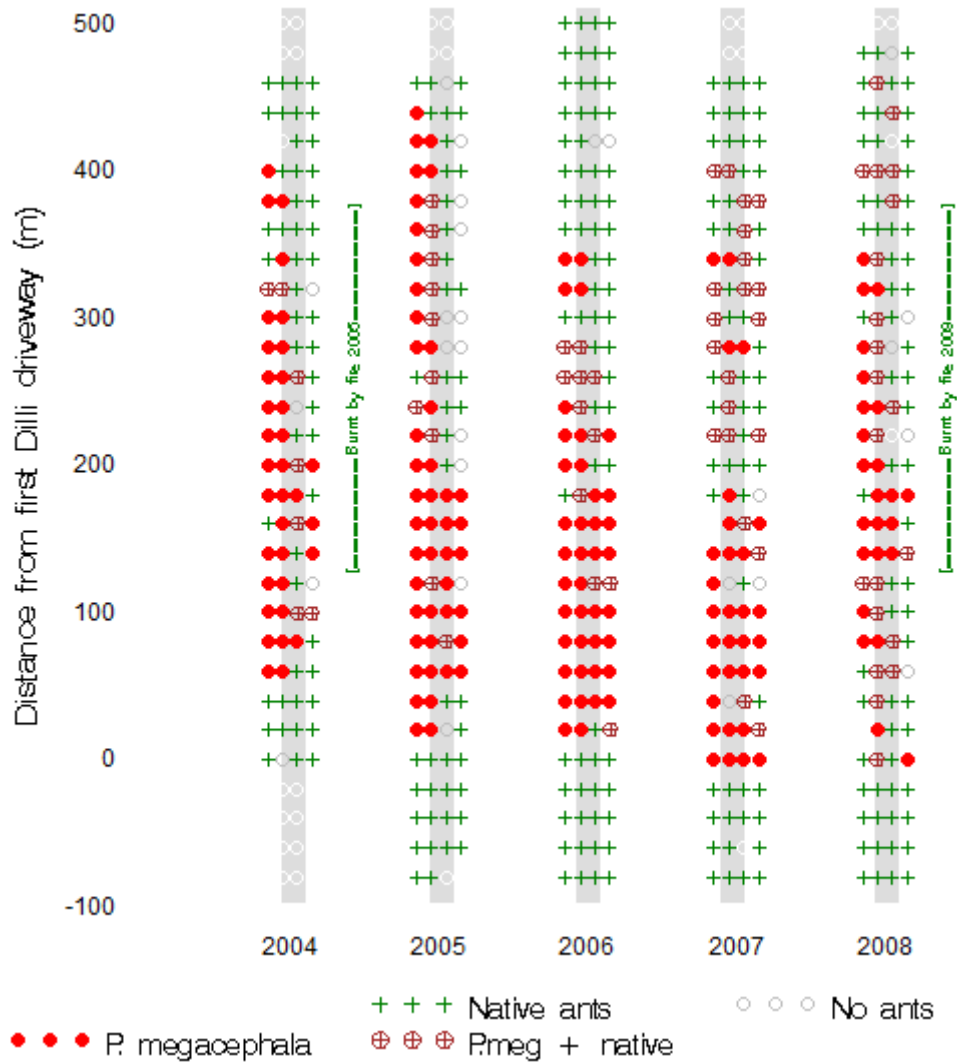


Figure 4.2. Distribution of *Pheidole megacephala* on peanut butter baits along the road from eastern beach to Lake Boomanjin near Dilli Village, Fraser Island. The grey line represents the road, the middle two points are either edge of the road, and the outside points were positioned 2 m into the adjacent bush. White or blank points are where the bait was lost or not set.

Survey B. The Great Walk track [effects of linear vegetation clearing I]

There is evidence of an early competitive invasion along the track by *P. megacephala* followed by retreat and displacement by native species (Figure 4.3). In September 2004 the first 100 m of track from Dilli Village was dominated by *P. megacephala* and no native ants were observed. The next 100 m and the first 100 m from the other end generally had both *P. megacephala* and native ants present (Figure 4.3). By 2005 *P. megacephala* had monopolised most of these competitive points but the infestation retreated significantly towards both ends of the track in each successive year since (Figure 4.3). By September 2009, the infestation was largely restricted to 40 m from each end of the track, with *P. megacephala* observed only occasionally on other baits within the first 100 m. There was no obvious trend between the points 2 m into the bushland compared to those on the track (Figure 4.3).

Survey F. Dingo exclusion fence [effects of linear vegetation clearing II]

These data are much clearer than the other surveys as there is only occasional overlap between the native species and the *P. megacephala* zones (Figure 4.4). The data suggest an early competitive invasion along the dingo fence by *P. megacephala* after the clearing for the fence. The infestation moved about 80 m along the eastern boundary of the fence between 2004 and 2007 and moved back about 20 m from 2007 to 2009 (Figure 4.4). A similar but less defined increase and decrease occurred on the western side. There is no discernible trend between the points on the firebreak and the points that were 2 m into the bush.

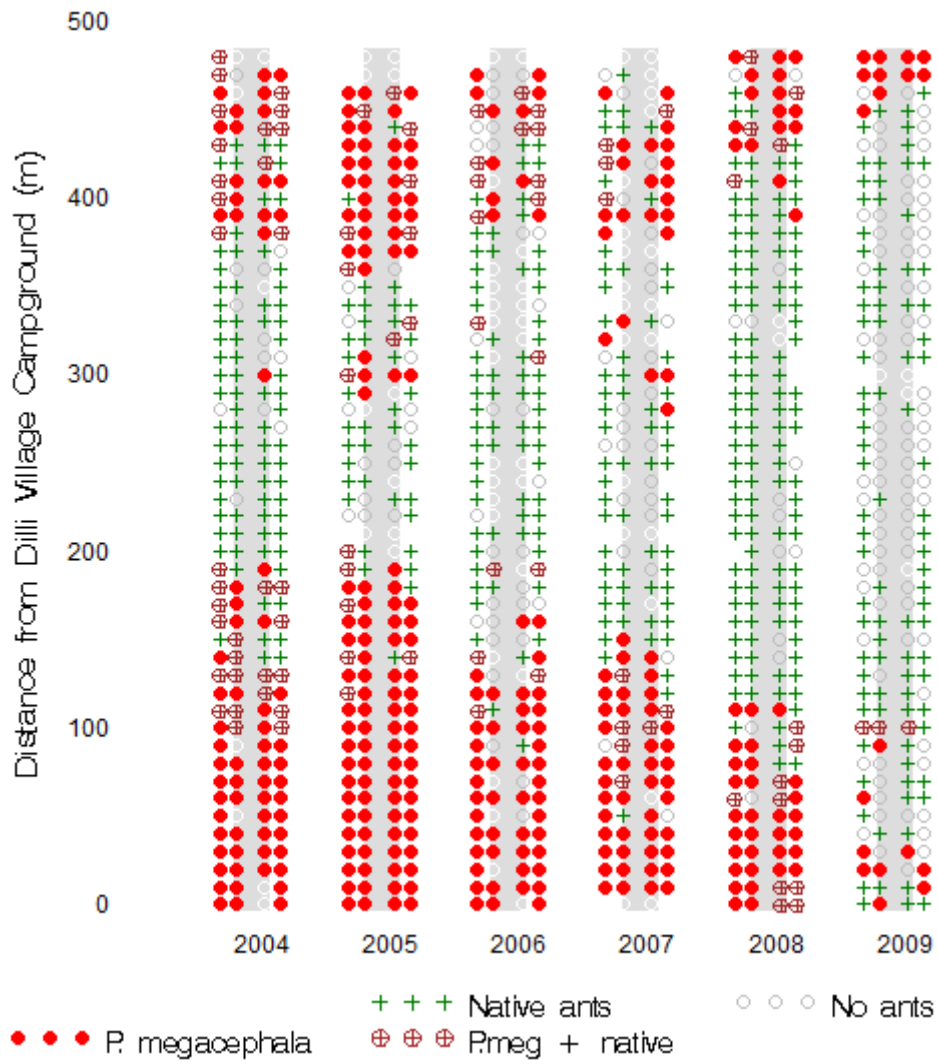


Figure 4.3. Distribution of *Pheidole megacephala* on peanut butter baits along the Great Walk Track near Dilli Village, Fraser Island. The grey line represents the track, the middle two points are either edge of the track, and the outside points were positioned 2 m into the adjacent bush. White or blank points are where the bait was lost or not set.

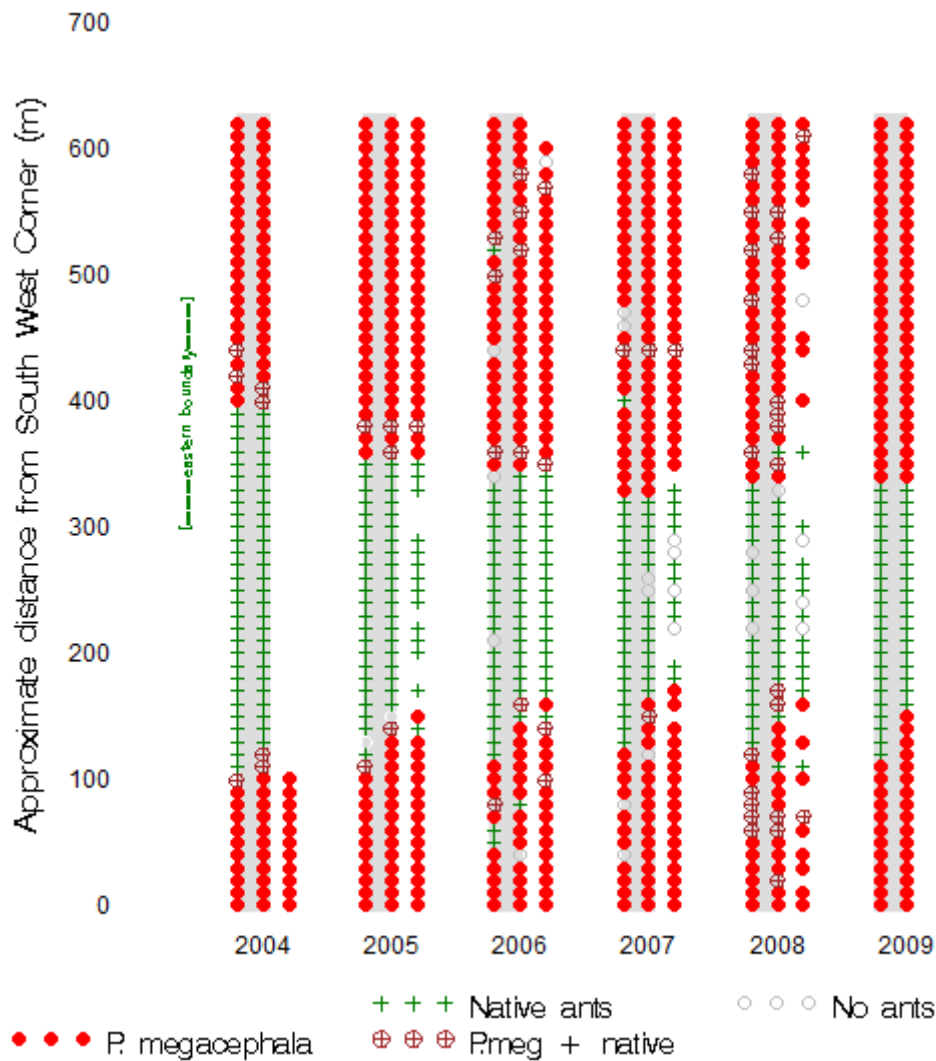


Figure 4.4. Distribution of *Pheidole megacephala* on peanut butter baits around the dingo exclusion fence surrounding Dilli Village, Fraser Island. The grey line represents the cleared area and the other point is positioned 2m into the adjacent bush. White or blank points are where the bait was lost or not set. The point at the top of the graph is next to the point at the bottom.

Survey E. Hook Point Road [clearing of vegetation by track widening]

Two of the four points at 80 m along the road had only native ants in 2005 but were monopolised by *P. megacephala* in later years (Figure 4.5). There was no noteworthy spread of *P. megacephala* along the Hook Point road from 2006 to 2009 (Figure 4.5).

It isn't known whether this advance occurred before or after the road widening in 2006, but *P. megacephala* were on both the cleared and uncleared sides of the road in 2006. Overall, there has been no apparent substantial advance in the distribution of *P. megacephala* along the roadway since 2006 and the pattern is the same on the cleared and uncleared sides of the road verge (Figure 4.5).

Survey D. Native vegetation beyond Dilli Village Shed [the effects of fire I]

The first baits on transects 11, 12 and 13 coincide with the baits at 30, 60 and 90m from the Hook Point Road surveys (Figure 4.5). Hence, *P. megacephala* were present at the roadside along all but the final transect in each year and had still not spread to the final transect by 2009.

On average, *P. megacephala* did not significantly increase or decrease in the spread into the bushland along the 13 transects between 2006 and 2007 or 2008 (Table 4.2). Between 2007 and 2008, *P. megacephala* advanced 10 m in all four unburnt transects but varied between advancing 10 m (3 transects) and retreating 20 m (3 transects) in the burnt area (Figure 4.6). This difference between burnt and unburnt transects was almost significant using a p-value of 0.05, ($p = 0.052$; Table 4.2). All of the burnt transects where *P. megacephala* advanced in 2008 were where it had retreated to the roadside in the 2007 survey. On the other hand, *P. megacephala* retreated in four of the five burnt transects where it had been recorded in the native bushland in 2007 (Figure 4.6).

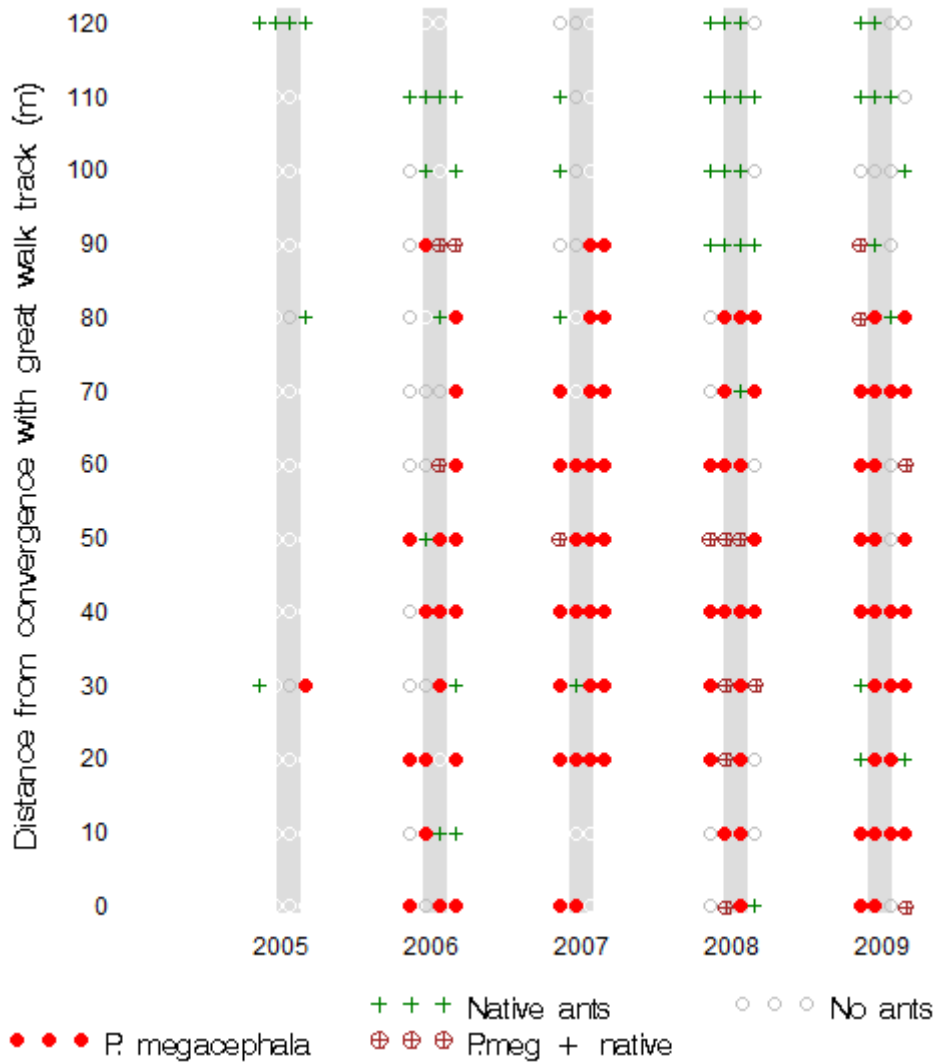


Figure 4.5. Distribution of *Pheidole megacephala* on peanut butter baits along the Hook Point Road from Dilli Village, Fraser Island. The grey line represents the road and the other points are positioned 2 m into the adjacent vegetation. White or blank points are where the bait was lost or not set. The leftmost two points in each line were subject to disturbance by the widening of the road in 2006.

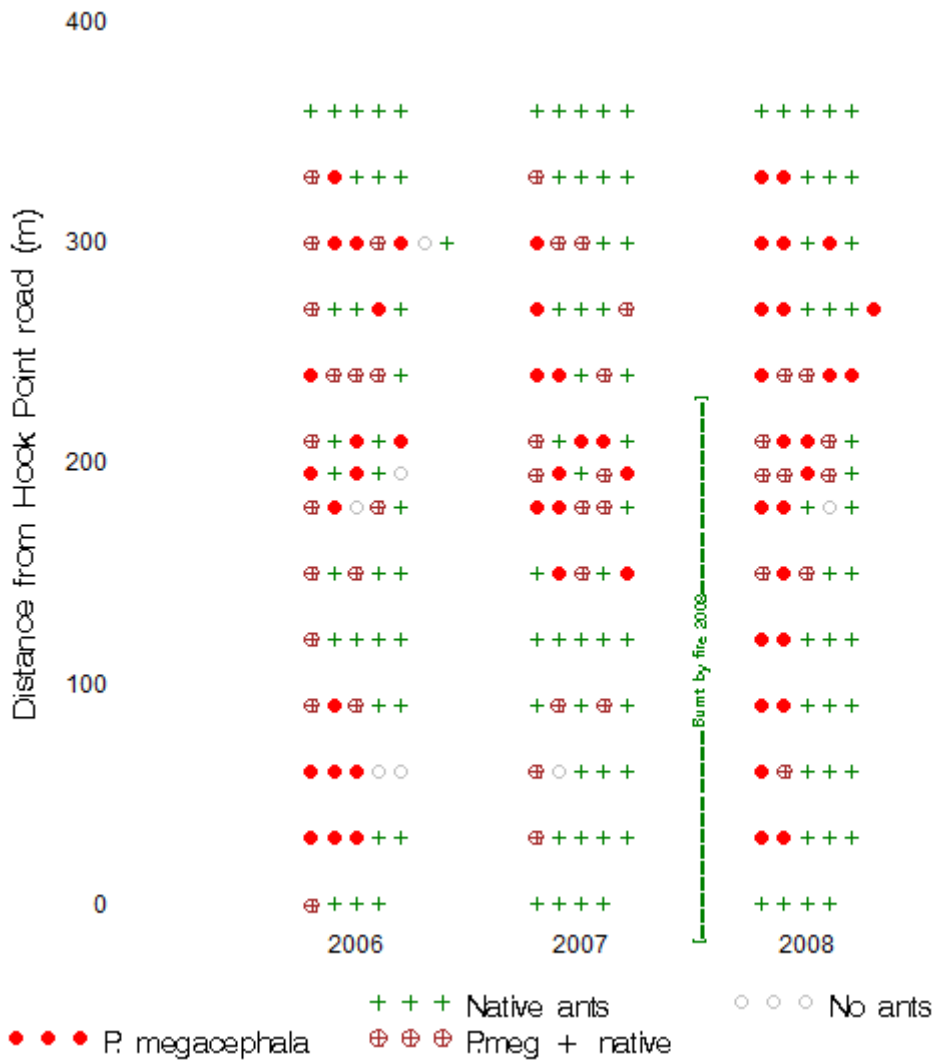


Figure 4.6. Distribution of *Pheidole megacephala* on baits in native bushland in survey D at Dilli Village, Fraser Island, between 2006 and 2008. White or blank points are where the bait was lost or not set. The leftmost points in each line are adjacent to the road and all baits within each line are 10m apart.

Table 4.2. Results from Wilcoxon tests to determine significance of advance or retreat of *Pheidole megacephala* infestation into native bushland in survey D at Dilli Village, Fraser Island, between 2006 and 2008.

Comparison years	Median advance (m)	Hypothesis	Wilcoxon T	P-value
2006 to 2007	0	No average advance/retreat	-3.5	0.805
2006 to 2008	0	No average advance/retreat	-4.5	0.793
2007 to 2008	10	No average advance/retreat	-1.5	0.836
2007 to 2008	0 Burnt, 10 Unburnt	No difference in spread between Burnt Vs Unburnt transects	40	0.052

Survey C. Native vegetation within Dilli Village lease [the effects of fire II]

There was no significant overall advance or retreat of the *P. megacephala* invasion in survey C in any given year (Table 4.3). However in the four burnt transects in 2005 where it had only been recorded at the roadside edge in the previous year, *P. megacephala* advanced 5 m, 10 m, 20 m and 20 m whilst in the other burnt transect the infestation remained at 20 m before and after the fire. In the unburnt transects that year *P. megacephala* advanced 5 m in one transect and retreated 10 m and 15 m in the other two. In two of the burnt transects in the 2009 fire, *P. megacephala* were not recorded before or after the burn. In the lone transect where it was recorded at the roadside in 2008, *P. megacephala* advanced 20 m after the fire, whilst in the two burnt transects where it was recorded into the vegetation in 2008 it retreated completely to the roadside verge (by 10 m and 20 m) after the 2009 fire.

Table 4.3. Results from Wilcoxon tests to determine significance of advance or retreat of *Pheidole megacephala* infestation into native bushland in survey C at Dilli Village, Fraser Island between 2006 and 2008.

Survey	Median advance (m)	Comparison years	Hypothesis	Wilcoxon T	N	P-value
Ground	2.5	2004 to 2005	No average spread/retreat	5.5	8	0.42188
Ground	2.5	2005 to 2006	No average spread/retreat	2	9	0.84375
Ground	-2.5	2006 to 2007	No average spread/retreat	-7.5	9	0.0625
Ground	0	2007 to 2008	No average spread/retreat	-2.5	9	0.5
Ground	0	2008 to 2009	No average spread/retreat	-4	9	0.375
Ground	-5	2004 to 2009	No average spread/retreat	-6	8	0.25
Arboreal	0	2004 to 2005	No average spread/retreat	3	8	0.25
Arboreal	0	2005 to 2006	No average spread/retreat	-0.5	9	1
Arboreal	0	2006 to 2007	No average spread/retreat	-0.5	9	1
Arboreal	0	2007 to 2008	No average spread/retreat	-1.5	9	0.875
Ground	10 Burnt, -10 Unburnt	2004 to 2005	Burnt Vs Unburnt spread	7.5	3,5	0.097
Ground	0 Burnt, -2.5 Unburnt	2008 to 2009	Burnt Vs Unburnt spread	18	4,5	0.701
Ground	0 Burnt, -17.5 Unburnt	2004 to 2009	Burnt Vs Unburnt spread	8.5	3,5	0.167
Arboreal	0 Burnt, 0 Unburnt	2004 to 2005	Burnt Vs Unburnt spread	15	3,5	0.696

4.4 Discussion

The presence and absence data can be interpreted as indicating occurrence and dominance of *P. megacephala*. Presence on baits indicates occurrence which identifies when and where the extremes of the infestation expanded or contracted whilst the monopolisation of each bait (exclusion of native species) identifies dominance. The surveys that had no additional management interventions from the previous survey all showed regular variation in the *P. megacephala* occurrence and dominance.

Changes in P. megacephala infestation boundaries and dominance without intervention

The added value of using multiple repeat visits rather than just a snapshot or even a single return visit are highlighted by the detection of the variability in the infestation boundaries. The infestation along the external road from Eastern Beach to Lake

Boomanjin was 100 m longer after 4 years, but featured only 22 monopolised baits (Figure 4.2). If this survey had looked only the right hand side of the road and sampled in 2004 and 2009, the conclusion may have been that that infestation extended 280 m further in 2009 than 2004. The value of a longitudinal study is highlighted when the changes are looked at on a year to year basis and between the different sides of the road. At the western end of this survey (further from Dilli Village driveway) the boundary was 60 m further along at the end but it also contracted by 100 m between 2005 and 2006, advancing 60 m in each of the next two years (Figure 4.2). But in those years that it contracted there were more than 40 monopolised baits compared to only 18 in 2009.

Both the other surveys that can be treated as controls (without intervention) showed significant average contraction during the study. The infestation in the native bushland transects (survey C) that were never burnt during the study (on the eastern side of the road) contracted by an average of 17.5 m across the 5 years (Table 4.3), and the linear transect along the Great Walk track showed a contraction of over 300 m (Figure 4.3). However had the Great Walk survey been performed only between 2004 and 2005 when the data showed a significant 50% increase in bait monopolisations then the conclusions would be very different. By 2009 the *P. megacephala* monopolised baits on the Great Walk track had decreased from over 100 in 2005 to just 18 baits (Figure 4.3). Similarly the *P. megacephala* advance of 10 m in native bushland transects in survey C between 2004 and 2005 may have raised concerns but the infestation actually retreated an average of 17.5 m in non-intervention native bushland transects between 2004 and 2009 (Table 4.3).

Invasive ant infestation boundaries vary annually between seasons and within years (Sanders et al. 2001). The added variability caused by the seasonal component of the variation was moderated in this study by always sampling at the same time of year. However, the prevailing conditions and recent climatic history may have been major contributing factors to the annual variation described here. The observed inter-annual variation and natural expansion or contraction in the surveys without intervention make it difficult to infer the effects of the management interventions in the fire and clearing surveys.

Changes in P. megacephala infestation boundaries and dominance after mechanical vegetation clearing

The advance of a species along a transect does not reflect the true rate of spread of the species in general (Sanders et al. 2001) but does allow a broad interpretation of the potential effects of vegetation clearing. The effect of (linear) clearing of native vegetation at Dilli Village varied between the different surveys. There was an increase in the range and dominance of *P. megacephala* along the great walk track and the fire break around the Dilli campground after clearing. Yet when the Hook Point Road was widened in 2006, *P. megacephala* did not show a similar rapid spread. In the Great Walk study there was a significant contraction of the spread after 2006 whilst the Dilli fire break infestation boundary remained stable. These results are contrary to expectations. *P. megacephala* nest close to the surface (Broekhuysen 1948) and are thought to be vulnerable to desiccation (Greenslade 1971, Majer 1985a, Hoffmann et al. 1999) so they should be better suited to the shaded Great Walk track habitat than the hotter, open fire break. The occurrence of *P. megacephala* was associated with

increased leaf litter at another site on Fraser Island (Chapter 3), so why not the Great Walk track? Greenslade (1971, 1972) and Majer (1985a) also noted that *P. megacephala* may not be able to invade areas with strong biotic resistance. This resistance may simply be by behaviourally dominant native ant species (Hoffmann et al. 1999), however, there are few Dominant ant taxa on Fraser Island (see Chapter 2). The only *Iridomyrmex* species encountered on the great walk were the occasional *I. bicknelli* colonies and one *I. rubriceps* colony that was not in the vicinity of the *P. megacephala* infestation (W. Robinson, pers. obs). Neither of these taxa are considered typical of the behaviourally Dominant Dolichoderinae (Alan Andersen, pers. comm.). Given the general lack of dominant taxa in Fraser Island and the Great Walk track in particular, it seems unlikely that the taxa encountered there can outcompete *P. megacephala* and other abiotic factors could be causing its apparent retreat there. Perhaps the role of desiccation as a limiting factor has been over-stated, particularly given that even in dry climates, *P. megacephala* are well known to forage 24 hours a day when conditions are right (Broekhuysen 1948, Carnegie 1960, Greenslade 1971; W. Robinson, Pers. Obs.) as demonstrated by the data collected for this chapter. Future research needs to look at the role of biotic resistance and insolation or soil moisture as limiting factors in the local distribution and spread of *P. megacephala*.

Changes in P. megacephala infestation boundaries and dominance after vegetation clearing by burning

There was 3 to 5 months between the fires and the surveys and there are limited data points so the results from the surveys should be treated cautiously. Furthermore there

were only three fires carried out during the research, so the use of multiple transects within single fires in a statistical analysis is intended as a guide and not definitive. Nevertheless, the results do complement the literature. Across the seven transects where *P. megacephala* were only observed at the edge (first bait) in the year before the fire (in surveys C and D) they were observed to advance in all seven transects the following survey (Table 4.3; Figure 4.6). After eradicating *P. megacephala* from pineapple fields, new populations were able to recolonise from perimeter populations within a week (Reimer and Beardsley Jr 1990). In survey D (native vegetation beyond the Dilli Village leasehold) in 2008, *P. megacephala* had advanced 10 m into the vegetation in three of the four transects where they were at the transect edge (0 m mark) in 2007 (before the fire). But at the same time they had advanced 10 m in transect 12, the only unburnt transect where the invaders were at the edge of the vegetation the year before (Figure 4.6). The lack of replication and scale of resolution make it difficult to interpret anymore from the fire effects.

Fire has been mentioned as a possible tool to control BHA in Australia (Hoffmann 1998). Fire can favour *Iridomyrmex* (Andersen 1991) and litter biomass and soil moisture levels are lower in unburnt areas (York 2000). Fire can itself impact the other ants, arthropod, vertebrate and vascular plant types present (York 2000) and could therefore be a case of the cure being more severe than the disease. Anecdotally however, the results from these surveys suggest that fire as a management tool for *P. megacephala* will not work unless the perimeter populations are eradicated first.

The transects either side of the Dilli Village internal road provide some indication of the ineffectiveness of fire on its own as a management control for *P. megacephala*.

Between 2004 and 2009, the *P. megacephala* infestation in the unburnt Eastern side transects contracted an average of 17.5 m but in the burnt Western side transects were at the same distance into the bushland in 2009 as 2004 (Table 4.3).

It is difficult to recommend the use of fire as a control measure for *Pheidole megacephala* on Fraser Island, because: (1) there is only a limited pool of dominant native taxa to benefit from a reduction in vegetation (Chapter 2) and; (2) *P. megacephala* were consistently shown to advance after fire in this chapter (Table 4.2 and 4.3).

Naturally, the advance after fire may also be related to reduced biotic resistance. A better understanding of the role biotic resistance is an important next step in planning future management of the *P. megacephala* infestation at Dilli Village. We know however that biotic resistance from native ants varies regionally (Holway et al. 2002a) and therefore a good starting point would be to document which native ants occur around Dilli Village.



Plate 4. *Rhytidoponera metallica* on peanut butter baits at Dilli Village.

4.5 Conclusions

- *Annual variation in P. megacephala infestation boundaries were documented in a longitudinal survey.*
- *The documented retreat and advances of the boundaries show that snapshot surveys of invasive ant infestations have very limited use compared to longitudinal surveys.*
- *Return once surveys are shown to have the potential to give misleading interpretations of invasion extent, even without management interventions.*
- *Effects of clearing by mechanical means had varying effects*
 - *There was a significant expansion then contraction of the P. megacephala infestation along a cleared walking path that was allowed to regrow*
 - *There was a significant expansion then stabilization of the P. megacephala infestation along a cleared and regularly managed linear fire break.*
- *Effects of fire on P. megacephala spread was not directly discernible from these data*
 - *Support for the suggestion that fire reduces native ant and arthropod resistance allowing rapid invasion from edge populations.*
- *The role of disturbance alone is difficult to interpret and is almost certainly site specific and dependent on prevailing biotic and abiotic conditions.*
- *The role of biotic resistance and the impacts of native ants on P. megacephala invasions are required.*
- *Species list of native ants occurring in this infestation is required.*

Chapter 5: Native ants and longitudinal changes in a *Pheidole megacephala* invasion in native bushland on Fraser Island

5.1 Introduction

The invasion ecology literature is dominated by post-hoc and post-invasion surveys that leave most results confounded by pre-invasion variation. This lack of pre-invasion data means the existing faunal assemblages that are reported as different after the invasion or in the different zones may actually have already been different anyway (Sanders et al. 2003). In other words, because of their design, many studies cannot determine whether the invader is the cause or the effect (Holway et al. 2002a). Studies that can document the local ant assemblages in an area before and after an invasion are extremely rare in the invasive ant literature and consequently there is a strong demand for such research (Holway et al. 2002a). The ethical problems associated with performing true experiments involving introducing exotic ants to new areas prohibit many true experimental designs (Holway 1998b, Holway et al. 2002a), however, monitoring local ant assemblages before and after invasion without manipulating the invader gives extra weight to the evidence of invader impacts (Hoffmann and Parr 2008). When the invasive ants *spread* their boundaries, return visits to previously surveyed invaded and uninvaded sites can allow inference of the ability of the invader to displace native species (Morrison 2002, Hoffmann and Parr 2008). For example, a study looking at the effects of *Pheidole megacephala* in Northern Australia documented differences in native ant assemblages between

invaded and uninvaded areas (Hoffmann et al. 1999). However, it was a repeat survey nine years later that first revealed that the differences in native ant assemblages were more than likely associated with the invasion (Hoffmann and Parr 2008).

This repeat visit approach, however, also assumes that external forces aren't facilitating the invasion spread and it cannot be certain whether the invader is the cause or the consequence of any observed changes in the native ant community. What happened in the gap between return surveys may have provided valuable information about factors influencing the spread and the impact of the invader. Furthermore, a once only return visit cannot detect range contractions and expansions, only one or the other or neither. Therefore, longitudinal (regular repeat visit) studies, have a potentially greater advantage over snapshot or return surveys of being able to quantify temporal changes in the impacts of the invasion of interest (Sanders et al. 2001, Sanders et al. 2003).

Dynamic equilibrium between the invader and other ants can occur over time (e.g. Haskins and Haskins 1965, Passera 1994, Morrison 2002, Wetterer and Wetterer 2004), so short-term impacts of invasive ant species may not accurately predict the long-term consequences (Morrison 2002). The distribution of invasive ants in an infested area can vary from year to year and season to season (Hoffmann 1998, Hoffmann et al. 1999, Sanders et al. 2001; see previous chapter) and part of the equilibrium process can be the contraction of an infestation boundary (Wetterer and Wetterer 2004). Monitoring that has more frequent sampling can cover range expansions *and* contractions, as well as monitoring external factors influencing the invasion that can be missing in large-gap return studies. Therefore, so called

longitudinal studies could be a valuable and relatively unexploited source of information in invasive ant research.

This study uses pitfall trapping data over a four-year period to investigate the relationships of *Pheidole megacephala* and native ants on Fraser Island in South East Queensland. It gives a comprehensive list of native Australian ants that can co-exist with *P. megacephala*, documents some of the drawbacks associated with making inference by using zones of impact at a single point in time, and takes advantage of the additional information derived when range contraction and expansion occur.

5.2 Methods

5.2.1 Study site

The study was conducted immediately adjacent to Dilli Village on Fraser Island, located about 290 km north of Brisbane in south-east Queensland (see Chapter 4 for a more detailed description).

5.2.2 Field sampling

Six transects on each side of the internal road from the campground to the machinery shed, spaced 50 m apart were established, starting 20 m from the Dilli Campground. These transects correspond with survey C in Chapter 4, Figure 4.1, but pitfall trapping was carried out at independent times to bait surveys and there is no trap at the roadside. Along each transect, pitfall traps were positioned every 5 m from the road into the native bush. A further three ‘control’ transects 30 m apart were located in native bushland approximately 100 m from the last sand track transect in what was

initially thought to be a non-*Pheidole megacephala* infested area. Pitfall traps were plastic vials 42 mm in diameter and half filled with a mixture containing 70% ethanol and 3% glycol. To pre-empt a proposed management fire, all traps were opened for two days and nights in July 2005 and then for four days and nights in the last week of September in 2005, 2006 and 2007 and the first week of October in 2008. September is the driest month of the year and sampling at the same time moderates seasonal variation in boundary changes (Hoffmann 1998). In some surveys, up to 9 traps were lost to disturbance by vertebrates and if more than two of these were from the same transect then that transect was re-sampled the following week. Otherwise there are occasional missing samples in the data set.

5.2.3 Ant Identification

All ants in all samples were identified following Andersen (2000) and voucher specimens are lodged at the Tropical Ecology Research Centre at CSIRO in Darwin.

5.2.4 Data analysis

Spatial scale of the infestation

The spatial distribution of *P. megacephala* for each sampling date is presented schematically and the proportion of traps where it was detected compared.

Relationship with native ant abundance and diversity

The proportion of ants that were *P. megacephala* in traps containing *P. megacephala* on each date was calculated and differences between dates compared using a Kruskal-Wallis test for non-parametric data. ANOVA and Scheffe' multiple comparisons on

the ranks of the proportions, pooled across all dates, was used when follow up analysis was required. The native ant species richness, Simpson's reciprocal diversity, evenness and abundance of native ants per trap were compared between traps with and without *P. megacephala* and year of sampling, using the data only from the annual Spring surveys (i.e. excluding the July 2005 data) employing a mixed model analysis that was able to treat trap sampling points as subjects in a repeated measures design. Log transformations were performed where necessary to correct for violations of the assumption of normality.

Native ant species turnover between traps with and without *P. megacephala* was calculated using curves documenting average species accumulation per unit effort (pitfall trap) and per cumulative native ant abundance (as described in Chapter 2).

The relationship between *P. megacephala* abundance and the four native ant indicators was investigated using Spearman's rank correlation for all dates including July 2005. For these analyses, all 75 traps were included as independent observations. The combined probabilities (Sokal and Rohlf 1981) from the five rank correlation tests (one test for each date) for each native ant variable were calculated to determine whether multiple correlations in the same direction on the same hypothesis were chance events or statistically significant.

Changes in biodiversity when the infestation boundary changed

Pitfall traps in locations where *P. megacephala* had appeared or disappeared between successive years of sampling were identified for each year excluding the initial 2005 July sample. The change in native ant species richness, Simpson's reciprocal

diversity, evenness and abundance of native ants per trap was tested for significance in these traps between years using Wilcoxon's signed rank test.

Native species and their interactions with P. megacephala

The frequency of occurrence of native ant species was compared between traps with and without *P. megacephala*. A generalised linear model using a logistic link was fitted for the presence and absence of native ant species in traps whilst including date as a repeated measure and the presence/absence of *P. megacephala* as a fixed factor. An unstructured covariance model was found to be the most appropriate for the repeated measure and fitted using generalized estimating equations (Liang and Zeger 1986). Many taxa occurred in numbers too low for an adequate model fit, so species that occurred only in traps when *P. megacephala* was either present or absent are also documented without formal statistical analysis.

5.3 Results

Infestation boundaries and intensity

The *Pheidole megacephala* infestation in native bushland at Dilli Village expanded then contracted between July 2005 and October 2008 (Figure 5.1). The ants remained abundant in transects at each end, uncommon in transects in the middle of the area, and were less prominent in transects 2 and 5 in 2008. There was a tendency for an increase in *P. megacephala* distribution and abundance in the three control transects during the course of the study (Figure 5.1). Only 36% of traps had *P. megacephala* in October 2008 compared to 48% in July 2005, 57 % in September 2005 and 2006 and

44% in September 2007. Native species richness generally increased throughout the study, regardless of where the traps were located (Figure 5.1b).

In July 2005, *P. megacephala* made up an average of 75% of ants in traps where they occurred. This decreased to 51% of ants in October 2008 (Figure 5.2). The change in proportion was statistically significantly different ($\chi^2 = 12.3$, $df = 4$, $p < 0.05$) but the follow-up analysis suggested that only the July 2005 and October 2008 proportions were significantly different. Only eight of the 75 traps had *P. megacephala* on every sampling occasion and these traps also showed a marked decline in proportion of ants that were *P. megacephala* through time ($F = 6.08$, $df = 4, 35$, $p < 0.001$) dropping from an average of 98% in July 2005 to 77% in October 2008.

In July 2005, 20% of traps containing *P. megacephala* contained no native ants and this proportion gradually declined over time (14% in Sep 2005, 8% in Sep 2006, 3% in Sep 2007). In October 2008 all *P. megacephala* traps had native ants present.

Native ant abundance and diversity in and out of the infestation

P. megacephala and native ant abundances generally increased annually through the study (Figure 5.3). The difference in the average number of native ants between pitfall traps with and without *P. megacephala* was dependent on the date ($F = 4.90$, $df = 3, 207$, $p < 0.005$). Although there was a tendency for more native ants in non-*P. megacephala* traps earlier and vice-versa later (Figure 5.3), the follow up analysis found that the effect was not statistically significant after correction for type I error.

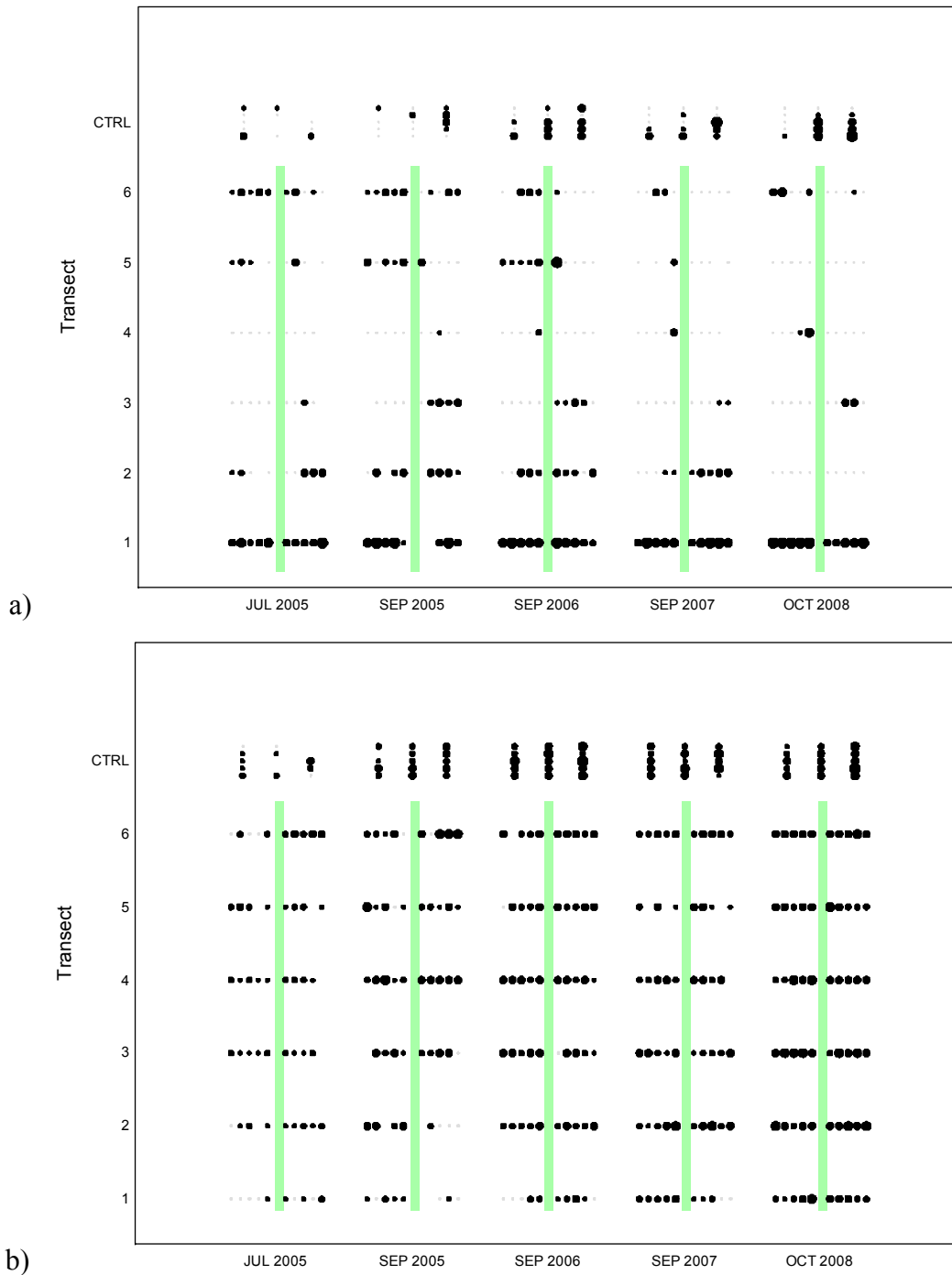


Figure 5.1. Schematic representation of a) *Pheidole megacephala* infestation and b) native ant species richness in pitfall traps at Dilli Village between 2005 and 2008. Vertical lines represent the internal road between Dilli Village campground and machinery shed. Black dots range from smallest a) (1 or 2 ants) up to largest (> 50 ants per pitfall trap) and b) 1, 2-3, 4-6, 7-10 or > 10 species per trap. Grey points are where no a) *P. megacephala* or b) native ants were recorded.

The average number of native ant species was higher in all traps in 2008 than in earlier years ($F = 10.07$, $df = 3$, 207 , $p < 0.0001$; Figure 5.4). Native ant species richness was slightly higher in non-*P. megacephala* traps in three of the four years (Figure 5.4) but not significantly different overall ($F = 0.34$, $df = 1$, 42 , $p = 0.57$).

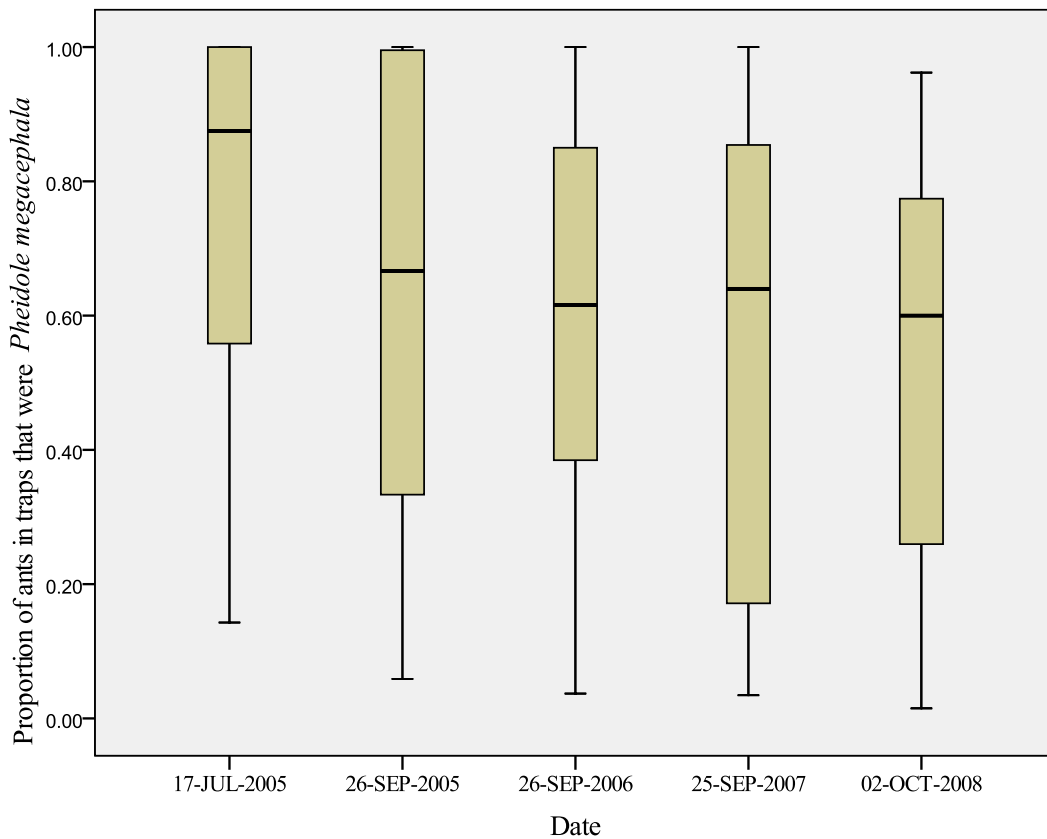


Figure 5.2. Proportion of ants that were *Pheidole megacephala* in pitfall traps at Dilli Village between 2005 and 2008. Only traps that contained *P. megacephala* are included. Box includes median and inter-quartile range, whiskers extend to extremes.

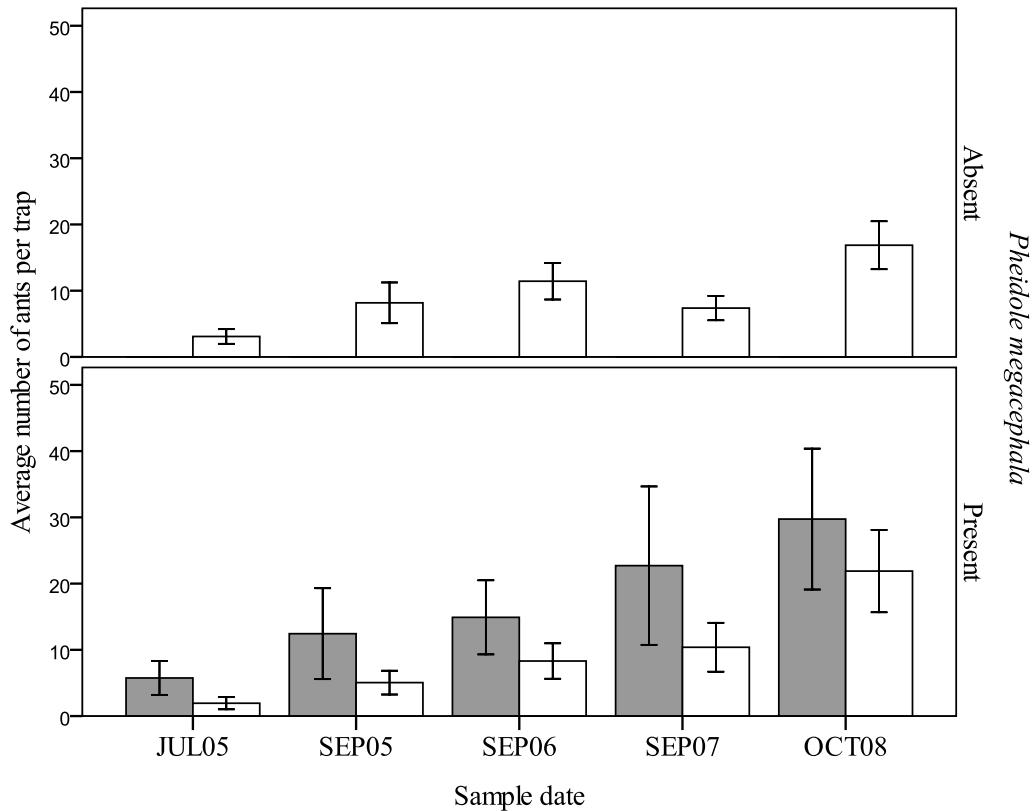


Figure 5.3. Average number of ants collected in pitfall traps with and without *Pheidole megacephala* near Dilli Village, Fraser Island. Grey bars are *P. megacephala* abundance and hollow bars are native ant abundance. The July 2005 data were not included in the mixed model analysis.

The average native ant Simpson's Diversity (reciprocal) index per trap was not significantly different among dates ($F = 2.37$, $df = 1, 40$, $p = 0.13$) or between traps with and without *P. megacephala* ($F = 2.38$, $df = 3, 189$, $p = 0.07$). This may have been a reflection of the variability of the index in general as the native ant only traps were higher in diversity than *P. megacephala* traps in all but 2008 (Figure 5.5).

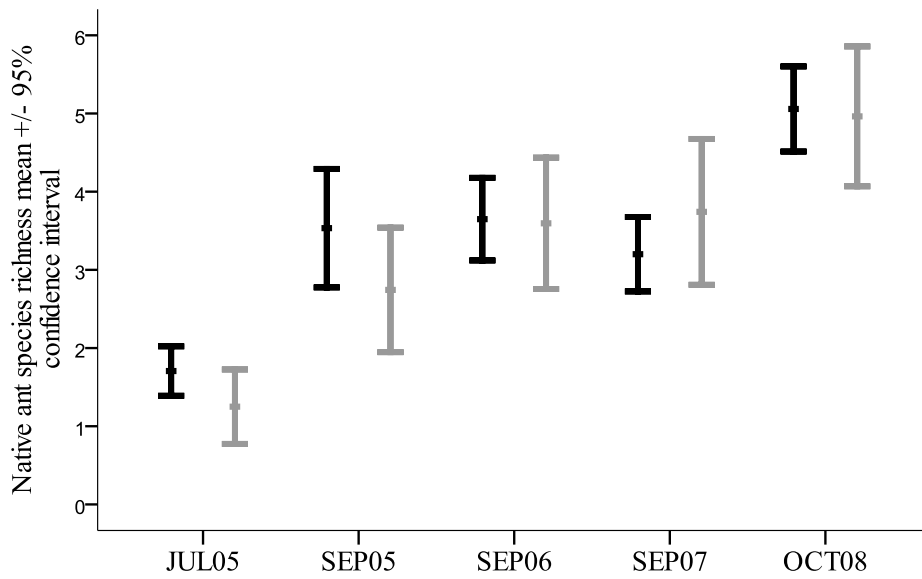


Figure 5.4. Native ant species richness (mean \pm 95% CI) in traps with (light bars) and without (dark bars) *Pheidole megacephala* during a 4-year study at Dilli Village, Fraser Island. The July 2005 data were not included in the mixed model analysis.

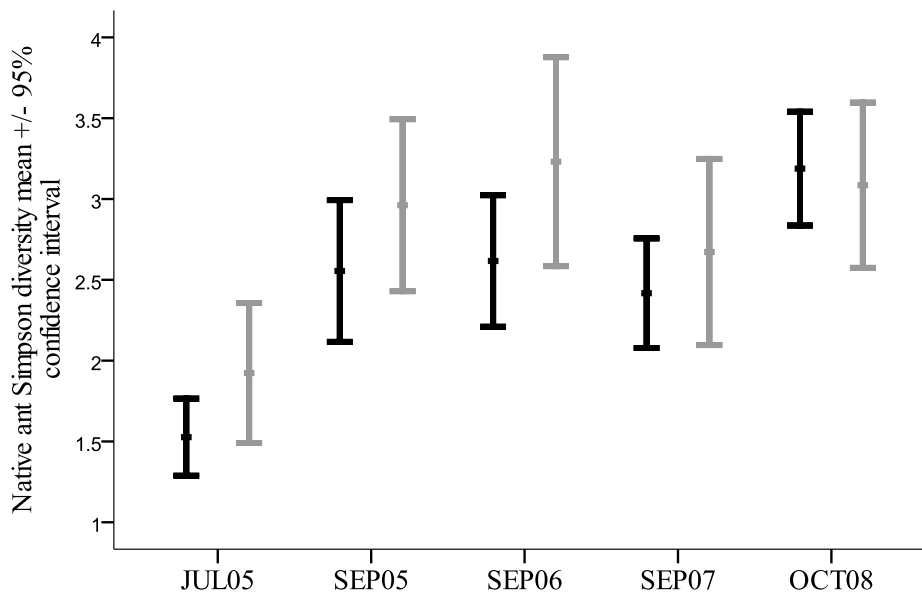


Figure 5.5. Native ant Simpsons diversity (mean \pm 95% CI) in traps with (light bars) and without (dark bars) *Pheidole megacephala* during a four year study at Dilli Village, Fraser Island. The July 2005 data were not included in the mixed model analysis.

The evenness of native ants in the samples was not affected by the presence of *P. megacephala*, but the date of the survey was significant ($F = 8.82$, $df = 3, 189$, $p < 0.0001$) (Figure 5.6). Multiple comparison using Scheffe's adjustment for type 1 error found that samples were significantly less even in all traps in 2008 than in traps with *P. megacephala* in September 2005 (Figure 5.6).

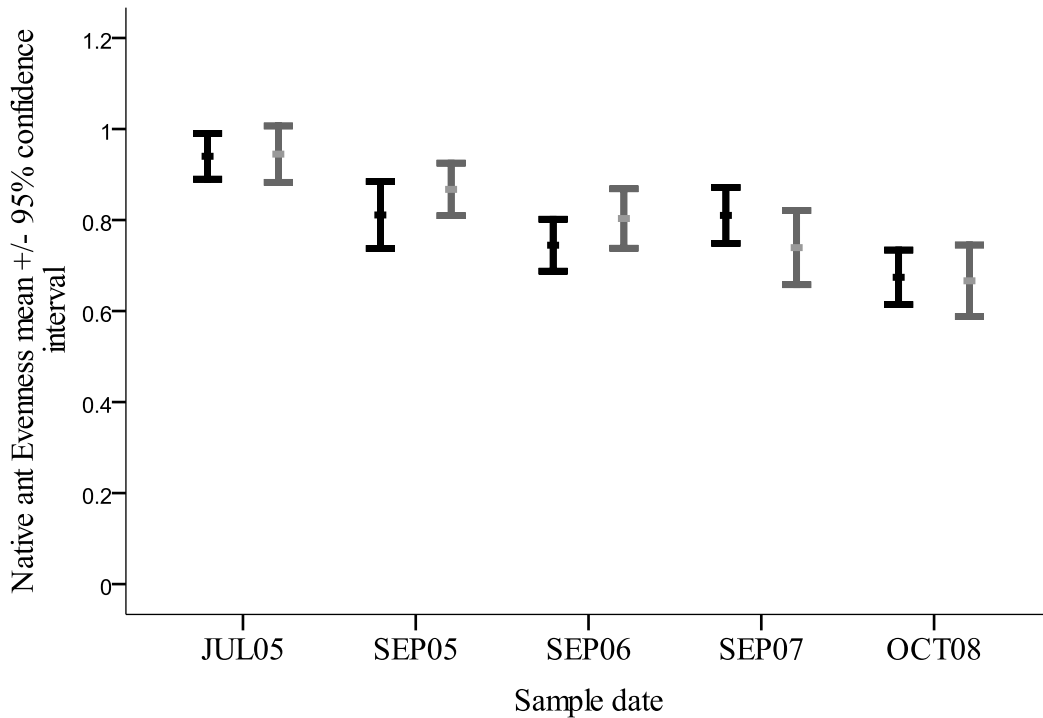


Figure 5.6. Native ant Evenness (mean \pm 95% CI) in traps with (light bars) and without (dark bars) *Pheidole megacephala* during 4-year study at Dilli Village, Fraser Island. The July 2005 data were not included in the mixed model analysis.

There was a tendency for more native ant species per pitfall trap in traps containing *P. megacephala* in 2005 to 2007 but the species accumulation per pitfall trap was almost identical in 2008 (Figure 5.7a). There were fewer ants of each native species on average in *P. megacephala* traps from 2005 to 2007, but in 2008 the number of ants per species were at their highest in traps with and without *P. megacephala*

(Figure 5.7b). This was probably a reflection of the greater number of ants in general in 2008 (Figure 5.3).

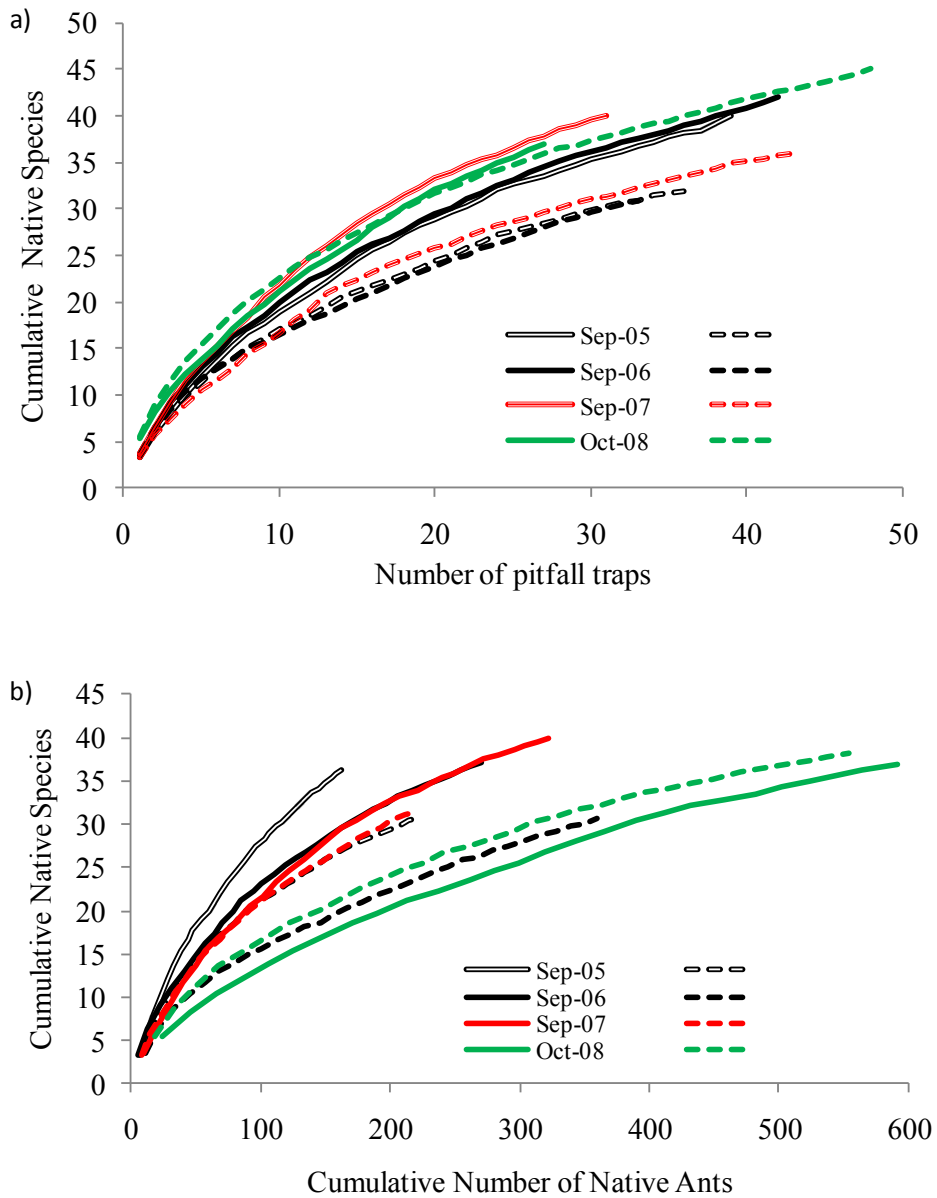


Figure 5.7. Average cumulative native ant species as a function of a) number of pitfall traps and b) number of ants collected in pitfall traps with (solid lines) and without (hatched lines) *P. megacephala* at Dilli Village, Fraser Island.

Native ant abundance and diversity relationship with P. megacephala

There was a tendency for *Pheidole megacephala* abundance in traps to be negatively correlated with the abundance, richness and diversity of native ants, but none of the relationships were statistically significant (Table 5.1). The evenness index of native ants was always positively related to abundance of *P. megacephala* and combined, the relationship was just significant ($-2\ln P = 19.6$, $df = 10$, $p < 0.05$) (Table 5.1).

Table 5.1. Spearman's rank correlation coefficients (r_s) and statistical significance for the relationship between the native ant index and abundance of *Pheidole megacephala* in individual pitfall traps across five sampling periods at Dilli Village, Fraser Island.

Date		Number of native ants	Native ant species richness	Simpson's Diversity index of native ants	Evenness of native ants
17-Jul-05	r_s	0.02	0.03	-0.20	0.35
	sig	0.930	0.890	0.402	0.146
	n	32	32	19	19
26-Sep-05	r_s	-0.10	-0.13	-0.17	0.27
	sig	0.536	0.416	0.368	0.152
	n	39	39	29	29
26-Sep-06	r_s	-0.26	-0.18	-0.03	0.25
	sig	0.099	0.254	0.852	0.142
	n	42	42	36	36
25-Sep-07	r_s	-0.33	-0.38	-0.27	0.17
	sig	0.069	0.036	0.158	0.391
	n	31	31	29	29
2-Oct-08	r_s	-0.36	-0.37	-0.21	0.39
	sig	0.067	0.059	0.291	0.045
	n	27	27	27	27
Combined probability		0.09	0.08	0.41	0.03

Changes in native ant indices when Pheidole megacephala appeared or disappeared from a sampling point in successive years

The total number of ants collected in the traps that had gained *P. megacephala* in successive years always increased (Figure 5.8a) although the number of native ants collected also increased in the same traps (Figure 5.8b). Traps that had lost *P. megacephala* from 2007 to 2008 contained significantly more native ants in 2008

(Figure 5.8b). The same trend occurred but was not significant between 2005 and 2006, but those traps losing *P. megacephala* between 2006 and 2007 contained significantly fewer native ants in 2007 (Figure 5.8b). Native ant species richness always increased in traps when *P. megacephala* were collected after being absent the previous year (Figure 5.8c) but the trend was not statistically significant. Native ant Simpson diversity and evenness showed great variation, with no consistency of responses to the appearance or disappearance of *P. megacephala*.

Native species and their interactions with P. megacephala

Across the entire study, 77 native ant taxa were collected (Table 5.2). Sixty five of the taxa had too few observations for the logistic model to fit and test the effect of *P. megacephala* on their probability of occurrence. Of these taxa, *Aphaenogaster longiceps*, *Pheidole* sp. D 'variabilis' and *Hypoconerops* sp. A never occurred when *P. megacephala* occurred, whilst *Cardiocondyla 'atalanta'*, *Eurhopalothrix* sp. A, *Plagiolepis* sp. A and *Tapinoma* sp. B 'minutum', occurred regularly in *P. megacephala* traps but never when *P. megacephala* were absent (Table 5.2). Of the 11 taxa that the full model could fit, only *Pheidole* sp.2 A 'variabilis' showed a definite relationship, occurring in significantly fewer traps when *P. megacephala* were present (Table 5.2).

Across all dates, there were 66 native ant species collected in traps containing *P. megacephala* and 62 in native only traps (Table 5.2).

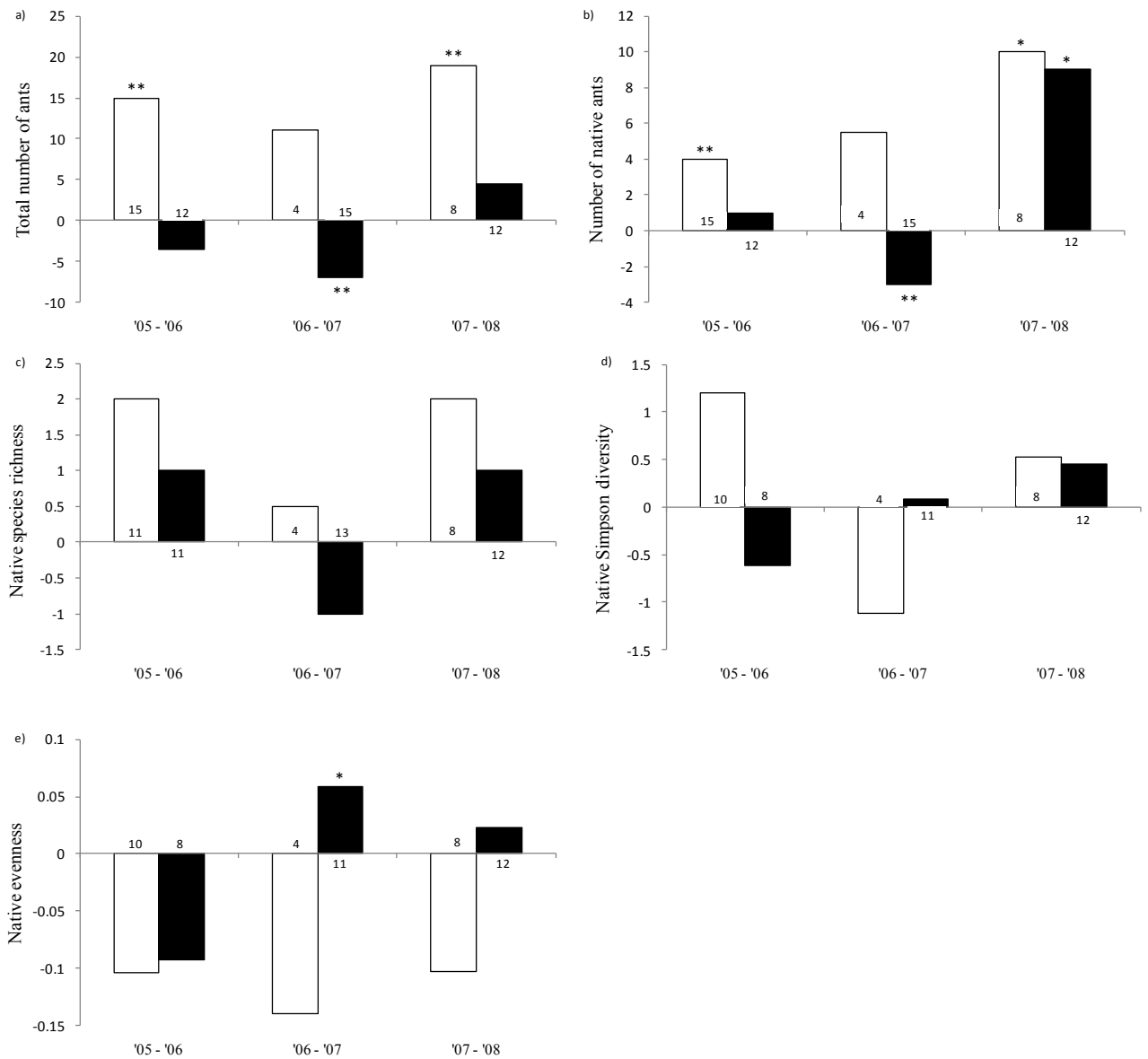


Figure 5.8. Median change per pitfall trap in (a) total ant abundance and native ant community attributes (b) native ant abundance, (c) native ant species richness, (d) native ant diversity (Simpson reciprocal diversity index) and (e) native ant evenness when *Pheidole megacephala* infestation spread (hollow bars) or retreated (solid bars) at Dilli Village, Fraser Island between 2005 and 2008. Sample sizes are shown adjacent to axis. Significant effects are shown by * $p < 0.10$, ** $p < 0.05$.

Table 5.2. Frequency of occurrence (% of pitfall traps) of native ants in traps with and without *Pheidole megacephala* across five sampling periods at Dilli Village, Fraser Island. Shading gradient is < 10%, 10–50% or > 50% of traps. P-values are for significant effect on likelihood of occurrence of the native taxa. Solid arrow indicates statistically significant relationship of *P. megacephala* with native taxa. Hollow arrows indicate possible relationship with native taxa not testable statistically. July 2005 data are not included in the generalised linear model.

Native ant species	without <i>P. megacephala</i>					with <i>P. megacephala</i>					Hypothesis test, P > Chi Square		
	Jul-05	Sep-05	Sep-06	Sep-07	Oct-08	Jul-05	Sep-05	Sep-06	Sep-07	Oct-08	BHA	Dates	Date*BHA
<i>Alderzia froggatti</i> (Forel)	3		3	10	2	5	2						
<i>Anochetus</i> sp. B (<i>graeffei</i> gp.)					8		2	3					
<i>Anonychomyrma</i> sp. A (<i>nitidiceps</i> gp.)		7				3							
<i>Aphaenogaster longiceps</i> (Smith)			3	5	10						↓		
<i>Bothroponera</i> sp. A			3	3	2	5	2	6					
<i>Bothroponera</i> sp. B (<i>porcata</i> gp.)									3	4			
<i>Brachyponera lutea</i> (Mayr)	3	7	6	8	6	3	3	9	11		.	0.245	.
<i>Carebara</i> sp. A		7			8		2	3	7				
<i>Camponotus</i> sp. A (<i>novaehollandiae</i> gp.)	3	3		3	8	8	2	3					
<i>Camponotus</i> sp. C (<i>discors</i> gp.)					2								
<i>Cardiocondyla atalanta</i>						8	5	9	7		↑		
<i>Cerapachys</i> sp. A (<i>singularis</i> gp.)					2								
<i>Cerapachys longitarsus</i>			3	3									
<i>Colobostruma biconvexa</i> Shattuck			6			3	5		3				
<i>Crematogaster</i> sp. C (<i>laeviceps</i> gp.)		3		8	4			2					
<i>Crematogaster</i> sp. F (<i>cornigera</i> gp.)			3										
<i>Crematogaster queenslandica</i> Forel				3		3	3		3				
<i>Dolichoderus dentatus</i>										4			
<i>Eurhopalothrix</i> sp. A								2	3	4	↑		
<i>Hypoponera</i> sp. A	3	7	3	3	2			2			↓		
<i>Hypoponera</i> sp. C	3			5	8			2	3				
<i>Hypoponera</i> sp. E				3		3	5			4			
<i>Iridomyrmex bicknelli</i> Emery		10	13	8	2		5	3	17	4			
<i>Iridomyrmex</i> sp. B (<i>pallidus</i> gp.)						6							
<i>Iridomyrmex</i> sp. C (<i>rufoniger</i> gp.)										4			
<i>Iridomyrmex rubriceps</i> Forel		3											
<i>Leptomyrmeis cnemidatus</i> Wheeler	12	10	3	8	15	13	13	9	7				
<i>Mayriella abstinens</i> Forel	3	3	13	5	13	3	3	6	22	4	0.835	0.077	0.273
<i>Mayriella ebbei</i>			3		4				3				
<i>Melophorus</i> sp. B (<i>bruneus</i> gp.)		7			4		3	7	3				
<i>Melophorus</i> sp. D (<i>njobergi</i> gp.)					4					4			
<i>Mesoponera australis</i> (Forel)		3	3	5	8		5	5	3	7	0.989	0.605	0.932
<i>Mesostruma browni</i> Taylor					2								
<i>Monomorium</i> sp. A (<i>laeve</i> gp.)		10	6	20	25		13	9	10	11	0.514	0.357	0.520
<i>Monomorium</i> sp. E (<i>nigrum</i> gp.)		7			10		15	16	17	7			
<i>Monomorium</i> sp. F (<i>nigrum</i> gp.)					4		10			4			
<i>Monomorium</i> sp. I (<i>laeve</i> gp.)				3									
<i>Myrmecia brevinoda</i> Forel	3	3	3		2	3	3	5	3	4			
<i>Myrmecia nigrocincta</i> Smith					4		3	7		7			
<i>Myrmecia fulviculis</i> Forel			6		2					4			
<i>Notoncus</i> sp. B (<i>enormis</i> gp.)					2				3				
<i>Ochetellus</i> sp. A (<i>glaber</i> gp.)					2					4			
<i>Ochetellus</i> sp. B				3									

Table 5.2 (cont.).

Native ant species	without <i>P. megacephala</i>					with <i>P. megacephala</i>					Hypothesis test, P > Chi Square		
	Jul-05	Sep-05	Sep-06	Sep-07	Oct-08	Jul-05	Sep-05	Sep-06	Sep-07	Oct-08	BHA	Dates	Date*BHA
<i>Odontomachus</i> sp. A (<i>turneri</i> gp.)	3	3	3	8	6		5	3	19	4	0.776	0.876	0.267
<i>Nylanderia</i> sp. A (<i>vaga</i> gp.)	12	43	38	38	58	22	36	38	53	56	0.715	0.125	0.727
<i>Paraparatrechina</i> sp. D (<i>minutula</i> gp.)		7		5	2			5	17	22			
<i>Paraparatrechina</i> sp. F (<i>minutula</i> gp.)		3	3			6	5	7	7	11			
<i>Pheidole</i> sp.1 A (<i>variabilis</i> gp.)	21	17	25	15	29	9	13	12	19	26	0.855	0.074	0.723
<i>Pheidole</i> sp.2 A (<i>variabilis</i> gp.)	6	27	47	23	40	3	3	3	14	11	0.0001 ↓	0.090	0.688
<i>Pheidole</i> sp. D (<i>variabilis</i> gp.)	6	7	3	3	10		3						
<i>Pheidole</i> sp. L (group C)			3	5	4					3			
<i>Plagiolepis</i> sp. A							3	7		37	↑		
<i>Polyrhachis ammon</i> (Fabricius)				3					3				
<i>Polyrhachis hookeri</i> Lowne				3	2		3		3	4			
<i>Polyrhachis australis</i> Mayr										7			
<i>Rhytidoponera</i> sp. A (<i>convexa</i> gp.)	35	33	41	33	58	19	21	39	55	56	0.675	0.001	0.505
<i>Rhytidoponera</i> sp. nr. <i>cristata</i>		7					5						
<i>Rhytidoponera chalybaea</i> Emery	29	27	31	18	23	3	3		3	4			
<i>Rhytidoponera metallica</i> (Smith)	21	40	44	40	52	9	26	18	29	37	0.879	0.286	0.884
<i>Rhytidoponera</i> sp. 2 nr. <i>victoriae</i>										7			
<i>Rhytidoponera</i> sp. nr. <i>metallica</i>			9	3	2		3	2					
<i>Rhytidoponera</i> sp. 1 nr. <i>victoriae</i>						3				3			
<i>Solenopsis</i> sp. A		23	34	13	40		8	13	24	78	0.988	0.000	0.012
<i>Stigmacros</i> sp. A (<i>aemula</i> gp.)	3	3					3	7					
<i>Stigmacros aciculata</i> McAreavey								7					
<i>Stigmacros</i> sp. C (<i>pusilla</i> gp.)		3	3					7	13	7			
<i>Stigmacros</i> sp. F (<i>rufa</i> gp.)				3		3							
<i>Stigmacros</i> sp. G (<i>flavinodis</i> gp.)		3				3	10	2	6				
<i>Strumigenys deuterus</i> Bolton			3	3	4	3	3	3	9	7			
<i>Strumigenys emmae</i> (Emery)							3						
<i>Tapinoma</i> sp. A (<i>minutum</i> gp.)										3			
<i>Tapinoma</i> sp. B (<i>minutum</i> gp.)						3	3	9	4	4	↑		
<i>Tapinoma</i> sp. C	3	13	13	8	2	6	5	7	13	15	0.487	0.742	0.407
<i>Technomyrmex sophiae</i>		3		3									
<i>Technomyrmex jocosus</i>							3						
<i>Tetramorium</i> sp. C (<i>striolatum</i> gp.)					2								
<i>Tetramorium</i> sp. D (<i>ornatum</i> gp.)					4			2	3				

5.4 Discussion

This study gives a list of 65 Australian native ant species that can co-exist with *Pheidole megacephala* and the first such list documenting the relationship through time. Several studies have noted the changes in infestation boundaries through time (e.g. Wetterer and Wetterer 2004, Hoffmann and Parr 2008; see previous chapter), but this study also documents the changes in the dominance (number of traps occurred in, number of traps occurred in without other species, proportion of all ants in traps) of a *P. megacephala* infestation through time.

The study has several limitations that need to be considered before discussing the results. It should be noted that there is some spatial confounding, as some trap locations were exposed to fire in between surveys (see previous chapter). These fires are treated as a random effect because they occur in locations with and without *P. megacephala*. Also, when interpreting native species relationships with *P. megacephala* occurrence (Table 5.2) the logistic regression models can only be fit when the taxa occurs in both zones on all four dates. It should be noted that 26 of the taxa only occur in one of the zones (infested area or not) and it would be reasonable to assume that some of these do have a significant relationship with *P. megacephala*, even though these can't be identified by this research.

The trend of more native ants in years that also yielded more *P. megacephala* (Figure 5.3) suggests that it may be favourable environmental conditions for pitfall trapping ants in general that is of major importance to ant abundance. Because annual native ant abundances and the changes in native ant abundances were independent of

P. megacephala presence (Figure 5.3) and abundance (Table 5.1) it seems that *P. megacephala* are merely additional biomass and possibly filling a vacant niche. The lack of differences in the native ant biodiversity indices with the presence of *P. megacephala* support this suggestion. The species turnover curves also showed that in this infestation, if there was any difference, it was that *P. megacephala* traps had more species and fewer individuals than native ant only traps. But, in 2008, there was practically no difference in native ant species and population sizes between the different trap types (Figure 5.7). All previous Australian studies of *P. megacaphala* infestations have found a negative relationship (see Table 1.2) with native ant species richness. Of the international literature, only Wetterer (2006) also found no significant effect on native ants from *P. megacephala* invasions.

Most studies that find a negative relationship are confounded by disturbance and by sampling post-invasion. The reduced native ant species richness in the *P. megacephala* infestation at St Mary's State Forest had the caveat of being in a 'long undisturbed open forest' (Vanderwoude et al. 2000). It is well known that once an invasive ant species like *P. megacephala* get a foothold they are extremely difficult to eradicate (e.g. Wheeler 1908, Krushelnycky et al. 2004), and inspection of Vanderwoude *et al.*'s (2000) site leaves no doubt that there were once significant dwellings there, albeit several decades ago (W. Robinson per. obs.). The Fraser Island ant fauna has low diversity and abundance of dominant native ant fauna like *Iridomyrmex* (see Chapter 2) and that was a characteristic of the *P. megacephala* infested site at St Mary State Forest (Vanderwoude et al. 2000). We know that sites that have lower species richness or reduced dominant taxa from disturbance are more

susceptible to invasion by *P. megacephala* (Majer 1985a, Heterick 1997, Samways et al. 1997) and Vanderwoude *et al*'s (2000) findings may well be documenting the lack of recovery of native species from the initial disturbance. The vegetation between Dilli Village and the Machinery shed was never cleared or disturbed during sand mining operations (John Sinclair pers. comm. 2006) and has only been subjected to low intensity autumn/winter management burns twice, both since 2005 (Ivan Thrash, pers. comm. 2008). In other words, the study sites here are unique because apart from the traps along the roadside edges, the study is in a never disturbed area. This supports a new suggestion that the biotic characteristics of an invaded site remain the same at least for a while. The results from this chapter agree with (2000) that *P. megacephala* can still invade undisturbed areas, accessing them from disturbed areas like campgrounds or roads. However, these results show that the native ants in the infested area, as indicated by average pitfall trap abundance, species richness, diversity and evenness may remain unaffected by the presence of *P. megacephala*.

Table 5.1 has provided some evidence contrary to the idea of the native ants remaining unaffected. In all of the spring samples there were less native ants, lower native ant species richness, lower Simpson's diversity, and greater evenness when there were more *P. megacephala* in the trap. This shows how difficult it can be to interpret the results and issues like sampling date and sampling scale need to be considered. Similarly confusing, Figure 5.2 shows that *P. megacephala* represented a lower proportion of ants in traps later in the study, but ambiguously we know *P. megacephala* occurred in fewer traps (Figure 5.1) and there were considerably fewer *P. megacephala* in traps later in the study (Figure 5.3).

These results demonstrate just how complex invasive ant infestation dynamics can be and further confirm that one off snapshot studies are of lesser value than longer term studies. It also provides support for the suggestion of differential impacts according to local environmental conditions (Greenslade 1972, Passera 1994, Heterick et al. 2000).

The September average rainfalls during this study were generally within 50 mm of the long-term average and on their own not unusual (Figure 5.9). However many of the normally wetter months (December-April) recorded lower than average precipitation during this study (Figure 5.9).

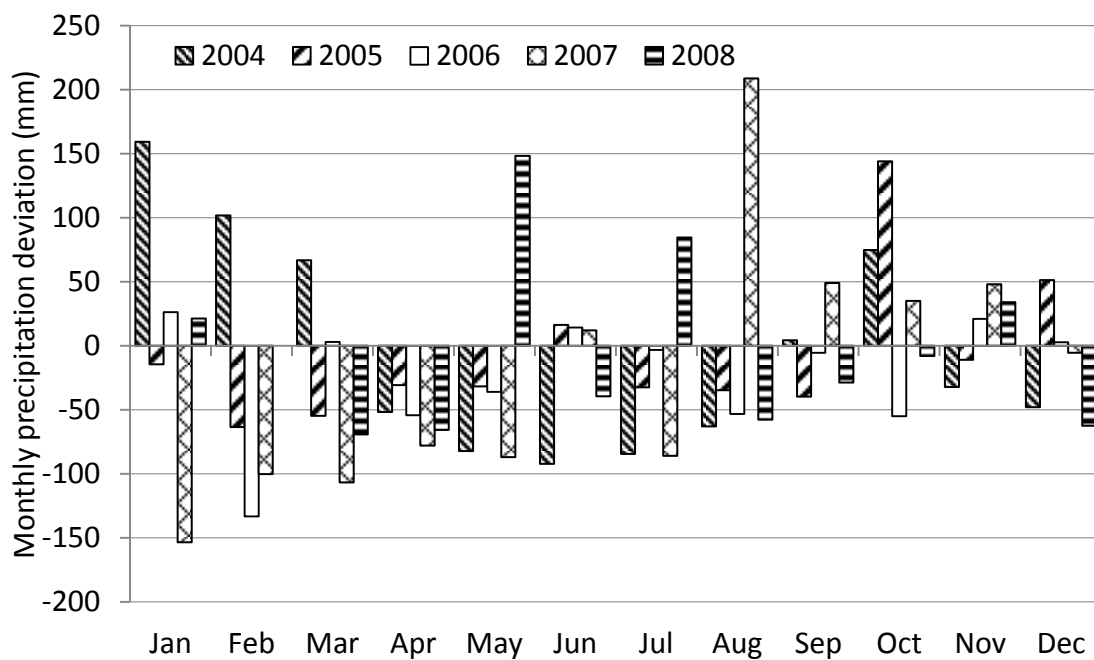


Figure 5.9. Deviation of monthly precipitation from long term average at Hervey Bay airport prior to and during this study. (source: <http://www.bom.gov.au> accessed 21/10/2012).

The long-term climate conditions during the study reveal a possible explanation for the overall decreasing impact of *P. megacephala* (increased native ants per trap, reduced traps *P. megacephala* occurred in and reduced proportion of *P. megacephala*

per trap) (Figure 5.10). Each year of the study had lower than average rainfall, with 2006 – 2008 all having at least 15% less precipitation than average, and 4 of the 5 years preceding the study period had at least 20% less than average precipitation (Figure 5.10).

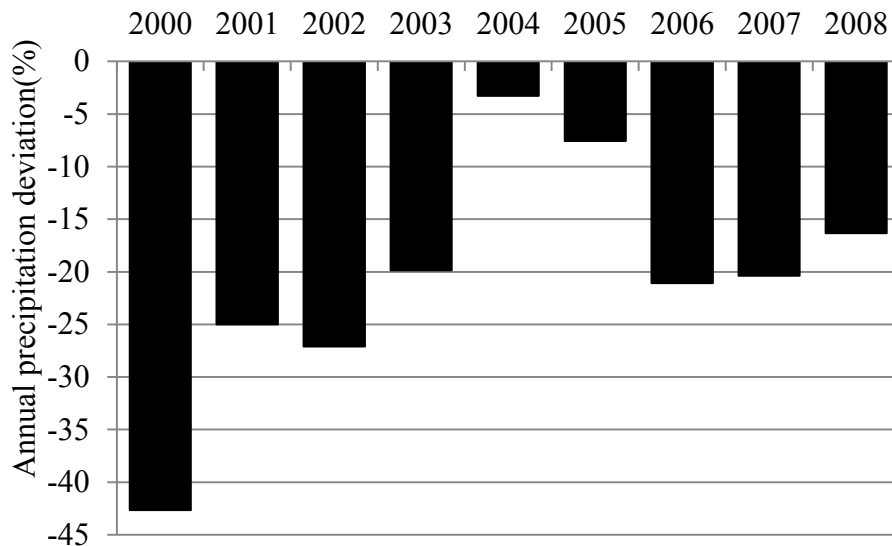


Figure 5.10. Percent deviation of annual precipitation from long term average at Hervey Bay airport prior to and during this study. (source: <http://www.bom.gov.au> accessed 21/10/2012).

In essence, the study was carried out during a drought and the reduced impact of *P. megacephala* may have been because they have lower tolerance to drier conditions. This aligns with the general findings of Greenslade (1971) and Hoffman (1999) where *P. megacephala* tend to be associated or restricted to moister habitats or drainage lines. This also assists in interpreting the decrease in distribution of *P. megacephala* along the great walk track in Chapter 4. The great walk track like all of Fraser Island is a sand dune environment, and because it follows high ground, drier conditions are exacerbated there as only the gullies remain moist. Therefore, to better understand the

interaction of *P. megacephala* and native ants, there is a need to better understand, macro and micro climatic effects. A start on addressing these factors using experiments begins in Chapter 6 and 7 of this thesis.

There were very few taxa if any that were definitely affected by *P. megacephala* or vice-versa. *Aphaenogaster longiceps* is the dominant taxa in terms of biomass on Fraser Island (Chapter 2) and it and *P. megacephala* were mutually exclusive in traps at Dilli Village. A similar segregation between *A. longiceps* and *Paratrechina longicornis* was recorded at Kingfisher Bay by Nicholls (2005). Without experiments it is difficult to interpret these observations but *A. longiceps* is not a behaviourally aggressive taxa (Alan Andersen pers. comm.) and it may be sub-ordinate to invasive taxa. At Kingfisher Bay it may well be that it is absent because of the disturbance to the soil when the resort was built.

Interestingly, many of the taxa that occur frequently throughout this study such as *Nylanderia* spp. and *Rhytidoponera* spp. are opportunistic species (Andersen 1990). Opportunistic species are commonly associated with disturbed sites and are particularly sensitive to competitive interactions such that their responses oppose those of Dominant Dolichoderinae (Hoffmann and Andersen 2003). The ant fauna in the undisturbed vegetation around Dilli Village have few dominant Dolichoderinae (Table 5.2) which is common for Fraser Island (see Chapter 2) therefore generally suitable for opportunistic species and subsequently susceptible to invasion by *P. megacephala*. Still, competition can occur at the edge of invaded areas (Holway 2005). At Mary State Forest *Iridomyrmex purpureus* are dominant on fire trails and BHA dominant in the vegetated areas either side of the fire trails (W Robinson, pers.

obs.). It is possible that these two groups co-exist by partitioning foraging times of the day. With the exception of Tryon's 1912 observations of 'extermination', there are no published data on direct interactions between *P. megacephala* and *Iridomyrmex* spp.

Whichever way the data are interpreted, there is little doubt that any impacts of *P. megacephala* on native ant fauna at Dilli Village is certainly less than other published papers in Australia. Converse to all previously published studies there was the same levels of native ant abundance, species richness, diversity and evenness in traps with and without *P. megacephala* and little change from year to year. It may be local environmental and species interactions that are important and these are the focus of the next two chapters.

5.5 Conclusions

- *This is the first research to publish a broad native ant species list documenting changes through time in a P. megacephala infestation.*
- *There was a very rich native ant fauna in pitfall traps containing P. megacephala.*
- *There was no difference in native ant biodiversity indicators including species turnover between traps with and without P. megacephala.*
- *P. megacephala invasions can be stochastic and results from snapshot studies need to be interpreted with caution.*
- *When there was no reduced native ant species list pre-invasion then there was no reduced native ant species list post-invasion.*
- *There is a need for experiments to probe the relationships between biotic resistance and environmental conditions/tolerances for P. megacephala.*

Chapter 6: The influence of abiotic factors on foraging competition by native ants with *Pheidole megacephala* on baits.

6.1 Introduction

Areas that are invaded by exotic ants almost always have lower overall ant species richness (Delabie et al. 1995, Holway 1998b, Suarez et al. 1998, Hoffmann et al. 1999, Kaspari 2000, Holway et al. 2002a, Le Breton et al. 2003, Sanders et al. 2003). In Australia, *Pheidole megacephala*, the African Big-Headed ant, is regularly associated with reduced native ant species richness but there are always some native ants that manage to remain despite the presence of *P. megacephala* (see Tables 1.2 and 5.3). These species may be able to persist because *P. megacephala* can be patchily distributed locally (Wilson 2003) and its numbers can fluctuate because of abiotic factors (Greenslade 1971, Heterick et al. 2000). For example, moisture is recognised as a limiting factor in the distribution of *P. megacephala* at the local scale (e.g. Tryon 1912, Greenslade 1971, Fowler et al. 1994, Hoffmann 1998, Hoffmann and Hohenhaus 1998, Hoffmann et al. 1999, Heterick et al. 2000, May and Heterick 2000, Wilson 2003). Abiotic factors and limits of tolerance in the invasive species have been shown to facilitate native ant coexistence for other introduced ants (Human et al. 1998, Holway et al. 2002b,

Walters and Mackay 2004, Krushelnycky et al. 2005, DiGirolamo and Fox 2006, Menke and Holway 2006).

An infestation of *P. megacephala* around Dilli Village on Fraser Island offers an interesting study area because it occurs across habitats ranging from heavily managed to never disturbed *Acacia* shrubland to dry open sand dunes. It also offers a study area where the native ant species richness is very high (see Chapter 5). The native ant fauna of Fraser Island has naturally low numbers of Dominant Dolichoderinae (see Chapter 2), which are Australia's most aggressive native ant taxa (Andersen 1990, Andersen and Patel 1994, Andersen 2000, Gibb and Hochuli 2003), but resources monopolised by *P. megacephala* at Dilli Village one day may be occupied by a native ant species the next day and vice versa (see Chapter 4). So it is of interest to determine the role of abiotic factors in the partitioning of foraging between native ants and *P. megacephala* on Fraser Island. Specifically, the relative effects of temperature and humidity on the presence and absence of *P. megacephala* and native ant species are examined, as well as the influence of temporal differences in foraging behaviour. The effect of these factors may influence the strength and nature of competition between *P. megacephala* and native ant species.

6.2 Methods

6.2.1 Study site description

The Dilli Village study area is described in Chapter 4. Records of ant occurrences on baits from previous baiting surveys (Chapter 4) were studied and four sites

were chosen within walking distance of Dilli Village. Two sites were open with no over-storey and two sites were shaded by naturally occurring *Acacia concurrens* approximately 3–5 m in height. One of each shading type was selected in an area near the advance front of the infestation where it was expected that native ants would compete for the baits. One open and one shaded site were also selected closer to the Dilli Village campground, where the infestation is older and it was expected *P. megacephala* would be the dominant taxa (Table 6.1).

Table 6.1. Site descriptions for study of foraging times of *P. megacephala* near Dilli Village, Fraser Island.

Site	Selection Criteria	Characteristics	Easting Northing
A	Open area near invasion front where competition with native ants was expected	Open sand, less than 10 % grass cover	E153.5.36 S25.36.119
B	Vegetated area near invasion front where competition with native ants was expected	<i>Acacia</i> shrubland < 5m height. Approximately 90% vegetation cover	E153.5.404 S25.36.14
C	Vegetated area in established infestation where no competition with native ants was expected	<i>Acacia</i> shrubland < 5m height. Approximately 90% vegetation cover	E153 5.497 S25.36.004
D	Open area in established infestation where no competition with native ants was expected	Open managed lawn area, more than 90 % grass cover	E153.5.526 S25.35.965

6.2.2 Field methods

At each site eight bait stations were positioned approximately 5 m apart. At each bait station, two petrie dishes were located approximately 40 cm apart. To modify small scale temperature and humidity, one petrie dish was randomly allocated to be shaded and one left open to the atmosphere. The shaded petrie dish had a

double layer of black 70% shade cloth (30 cm × 30 cm) positioned about 10 cm above the dish held in place by four bamboo stakes. The dishes were baited with a half a teaspoon mix of tuna in spring water and pilchard-based cat food. The dishes and initial baits were placed between 4:45 and 5:15 PM on Sunday 10th December 2006.

The species and estimated number of ants on each dish were recorded on 23 occasions during the next 48 hours. Generally there was 1–2 hours between observations during the day and three hours between observations during the night. When the bait was missing or had been substantially reduced it was replaced during the observation round. Most taxa were familiar from collections during previous baiting trials, however, when a species was not instantly recognisable a sample was taken and later identified following the Ants of Northern Australia (Andersen 2000). The temperature and relative humidity were recorded on a shaded and an unshaded dish in a control (unbaited) station during all but the first observation round.

To separate the effect of dish location from the effect of the shade cloth, the dishes stayed in place for the entire study, but all the shading apparatus were swapped at each bait station at 9 PM on Monday 11th December 2006.

6.2.3 Statistical analysis

The relationship between temperature and humidity was quantified using analysis of covariance (ANCOVA) that included a comparison of the slopes of the regression line between the zone and shade combinations. The mean difference in

temperature and humidity between shaded and unshaded baits was tested using a paired t test for each of the four sites.

Patterns in the foraging behaviour were investigated by plotting the abundance of *P. megacephala* and the common native ant species against time. The relationship of *P. megacephala* abundance when occurring (i.e. no zero abundances are included) to temperature and humidity was tested using rank correlations. Non-parametric analysis of covariance (Stokes et al. 2001) was used to compare *P. megacephala* forager abundance between the sites and zones. This required a Cochran-Mantel-Haenzell (CMH) test between the residuals from a multiple regression of the ranks of *P. megacephala* abundance against the ranks of temperature and relative humidity, pooled across all zones. To follow up significant CMH statistics, Scheffé multiple comparisons test between the zones and sites was performed on the same residuals.

To interpret the relationship between the effects of the vegetation cover, the effect of the shade cloth and the interaction of native ants and *P. megacephala*, tables documenting the presence or absence of *P. megacephala* and the common native ant species for every observation during the study are presented.

6.3 Results

Temperature and humidity in open and shaded sites and the effect of the shade cloth

Temperature and relative humidity were strong negatively linearly related ($R^2 = 0.87$, $df = 1, 162$, $p < 0.0001$), although the slope of the relationship was dependent on whether the points were in the shade or not ($F=15.8$, $df = 1, 162$, $p < 0.0001$). Shaded dishes tended to be slightly more humid at higher temperatures and slightly less humid at lower temperatures. There were consistent patterns across all sites of higher temperatures and lower humidity during the daytime (Figure 6.1).

The effect of the shade cloth on the environmental variables was dependent on the time of day, with no discernible effect during the night (Figure 6.1). Across the entire 48-hour sampling period the relative humidity was significantly higher by an average of 2.1–2.5 % and the temperature was significantly lower by an average of 3.3–3.6 °C on the shaded dish in the open sites A and D (Table 6.2). Both variables were similar whether shaded or not during the night so the daytime effect was approximately 5% for humidity and 7°C for temperature (Figure 6.1). In the *Acacia* sites the trends were in the same direction but were not statistically significant, except temperature in site B which was 2.2 degrees lower under the shade cloth (Table 6.2).

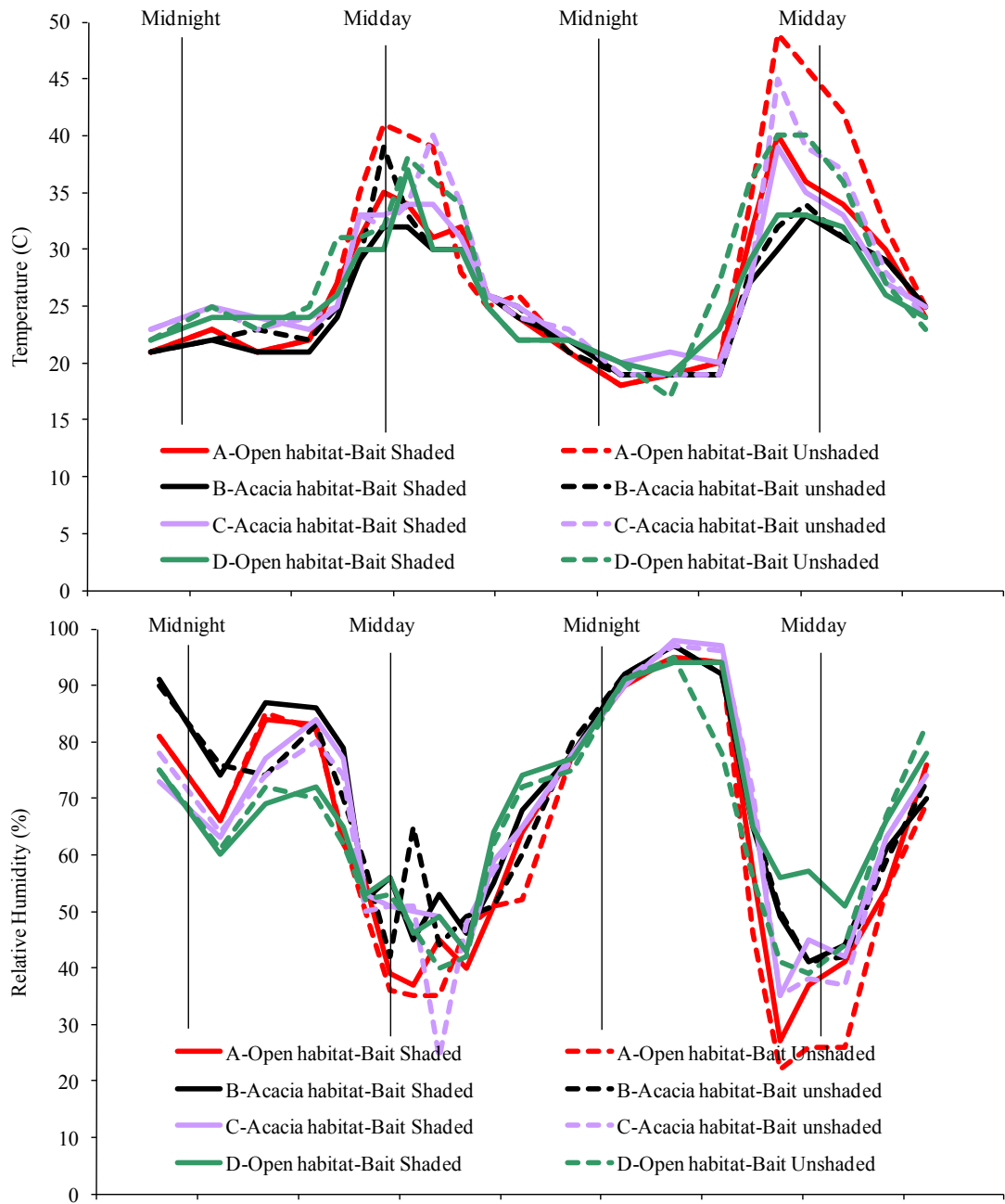


Figure 6.1. Temperature and relative humidity at ground level at four sites during the baiting trial for *Pheidole megacephala* at Dilli Village, Fraser Island.

Table 6.2. Mean difference (Shaded–Unshaded) in temperature (°C) and relative humidity (%) in each site during the baiting trial for *Pheidole megacephala* at Dilli Village, Fraser Island. The paired t test statistic (t) is for the null hypothesis that the average difference is 0.

Site	Parameter	Mean	Stddev	t	sig.
A–Open	Relativehumidity	3.27	5.52	2.84	< 0.01
B–Acacia	Relativehumidity	1.23	7.09	0.83	0.4154
C–Acacia	Relativehumidity	1.82	5.91	1.48	0.1542
D–Open	Relativehumidity	3.55	6.22	2.73	< 0.02
A–Open	Temperature	–2.45	3.78	–3.12	< 0.005
B–Acacia	Temperature	–0.73	1.58	–2.21	< 0.05
C–Acacia	Temperature	–0.82	2.30	–1.70	0.1023
D–Open	Temperature	–2.14	2.85	–3.59	< 0.005

P. megacephala foraging in relation to temperature and humidity

Pheidole megacephala were observed at least once on all petrie dishes except one of the bait stations in site B. In the open sites A and D, the number of *P. megacephala* tended to follow relative humidity down with the higher temperatures of the daytime and up again in the evenings (Figure 6.2). Abundances tended to be more evenly distributed throughout the day and night in the *Acacia* shrubland sites B and C (Figure 6.2). *P. megacephala* numbers in sites A, C and D all showed significant negative rank correlations with temperature and positive rank correlations with humidity, yet the opposite was found in site B (Table 6.3).

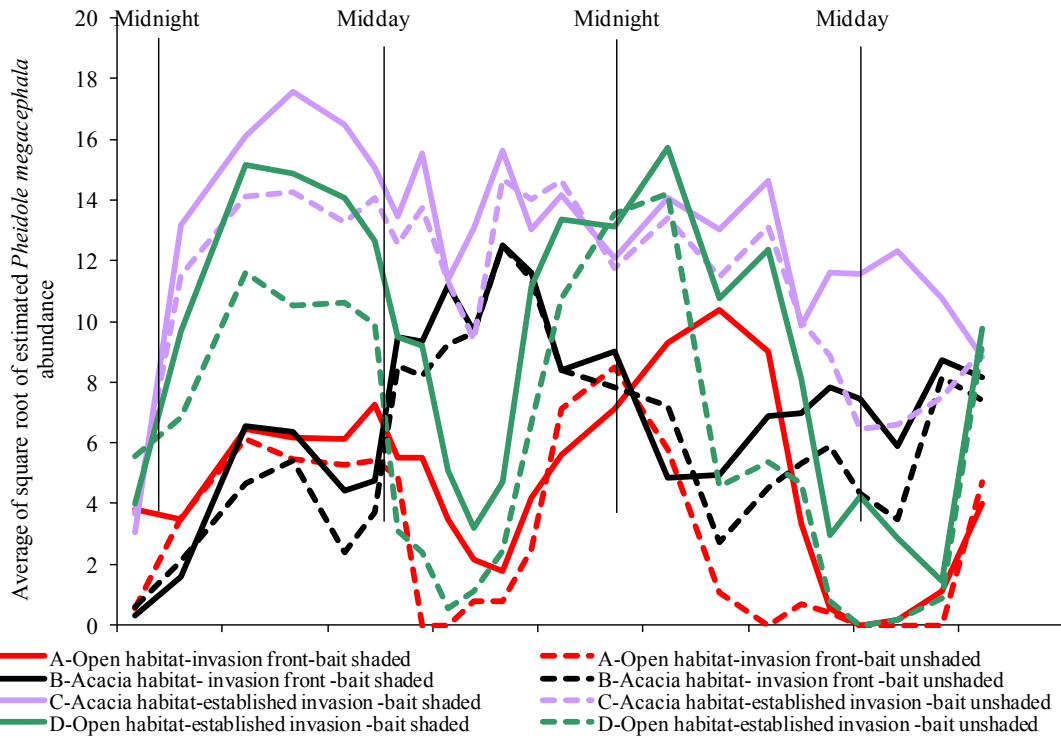


Figure 6.2. Average estimated *Pheidole megacephala* abundances on baited petrie dishes at four sites Dilli Village, Fraser Island.

Table 6.3. Rank correlations (r_s) of average *Pheidole megacephala* abundance with temperature and relative humidity on baits in different shade and location zones at Dilli Village, Fraser Island. * = $p < 0.05$, ** = $p < 0.005$, *** = $p < 0.0001$.

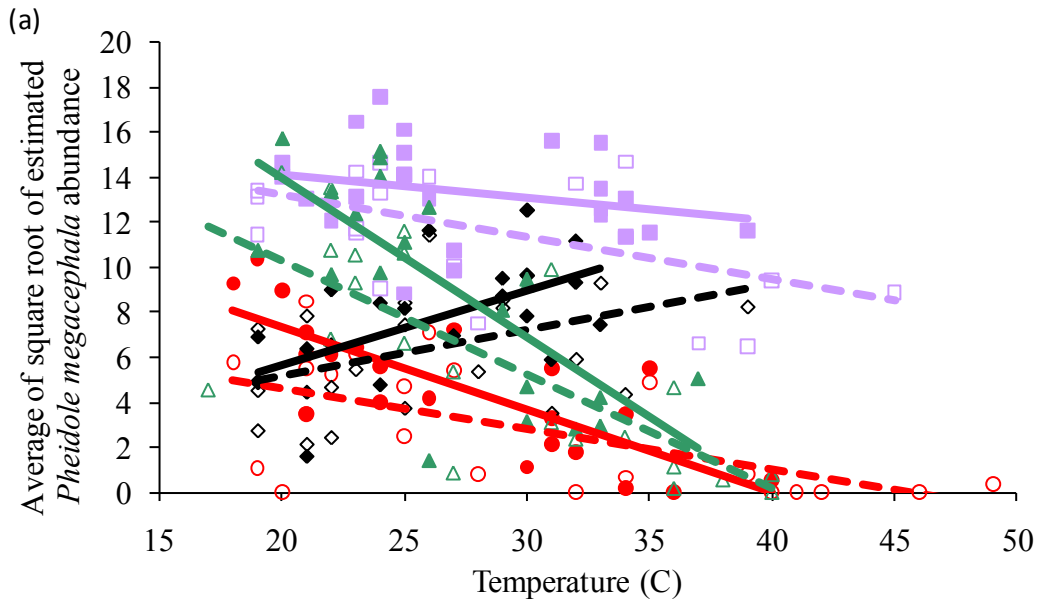
Site	Habitat	Location	Zone	Relative humidity R_s	Temperature R_s
A	Open	Invasion front	Shaded	0.787 ***	-0.785 ***
A	Open	Invasion front	Unshaded	0.478 *	-0.548 *
B	Acacia	Invasion front	Shaded	-0.596 **	0.563 *
B	Acacia	Invasion front	Unshaded	-0.425 *	0.367
C	Acacia	Invasion established	Shaded	0.237	-0.372
C	Acacia	Invasion established	Unshaded	0.316	-0.406
D	Open	Invasion established	Shaded	0.614 **	-0.753 ***
D	Open	Invasion established	Unshaded	0.727 ***	-0.767 ***

Pheidole megacephala numbers in the two open sites (A and D) approached zero in the middle of the day (Figure 6.2) which corresponded to around 40° C and 20 % humidity, yet numbers were still high in the vegetated sites (B and C) at the same times and environmental values (Figure 6.3).

Pheidole megacephala abundance was significantly different between sites, but the difference depended on the zone (CMH = 394.37, df = 7, p < 0.0001). Abundances were only statistically significantly higher on shaded than unshaded baits in the open site in the Dilli campground area, site D (Table 6.4). The *Acacia* shrubland sites generally had higher *P. megacephala* abundances, although the shaded bait in the Dilli campground had more *P. megacephala* than the unshaded bait in the *Acacia* at site B (Table 6.4).

Table 6.4. Comparison of average *Pheidole megacephala* abundances on baits after a non-parametric ANCOVA partitioned the effects of temperature and relative humidity. Vertical lines join zones that are not significantly different after Scheffé correction to maintain family-wise error rate at 0.05.

Site	Treatment	Effect
C- <i>Acacia</i> habitat-established invasion	Shaded	Most abundant
C- <i>Acacia</i> habitat-established invasion	Unshaded	
D-Open habitat-established invasion	Shaded	
B- <i>Acacia</i> habitat invasion front	Shaded	
B- <i>Acacia</i> habitat invasion front	Unshaded	
D-Open habitat-established invasion	Unshaded	
A-Open habitat invasion front	Shaded	Least abundant
A-Open habitat invasion front	Unshaded	



● A-open shaded ○ A-open unshaded ◆ B-Acacia shaded ◇ B-Acacia unshaded
 ■ C-Acacia shaded □ C-Acacia unshaded ▲ D-open shaded △ D-open unshaded

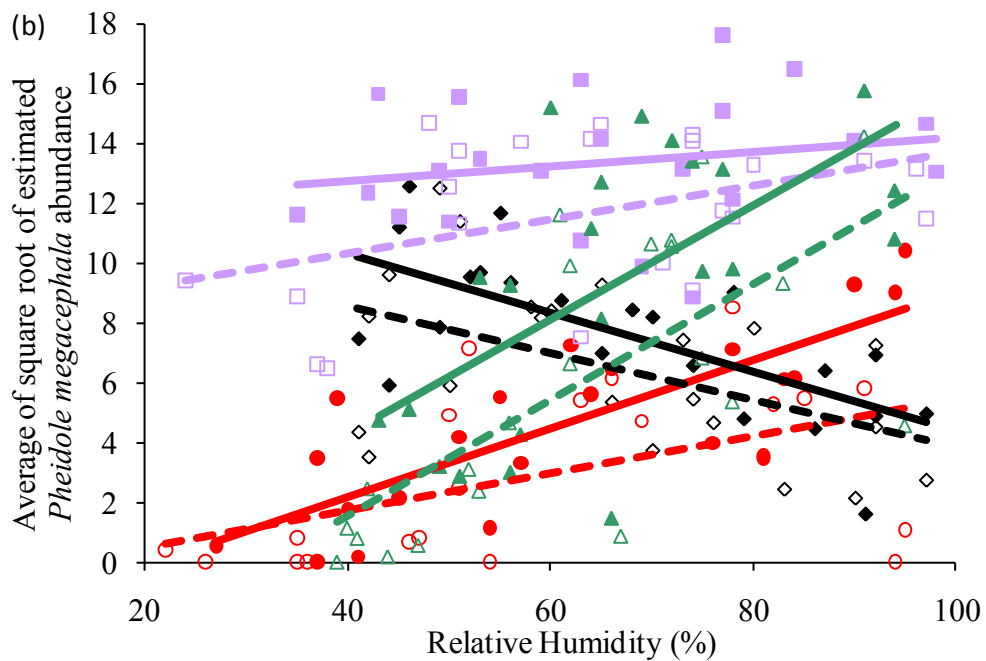


Figure 6.3. Relationship between *Pheidole megacephala* foraging activity on baits and (a) temperature and (b) relative humidity in four habitats on Fraser Island.

Native ant species occurring on the baits

Fifteen native species were observed on the baits during the study. The two sites nearer the invasion front (A and B) had more native ant species (9 and 12 native species) occurring on petrie dishes than the two older sites (3 and 5 native species) (Table 6.5). Many species occurred on only a few dishes and only *Camponotus novaehollandiae*, *Iridomyrmex bicknelli*, *Monomorium sydneyense* and *Nylanderia vaga* occurred on ten or more dishes in total (Table 6.5). *I. bicknelli*, *M. sydneyense* and *Melophorus* sp. were more numerous in the open sites, while *N. vaga* favoured the vegetated areas (Table 6.5).

Monomorium sydneyense foraged on the baits only during the middle of the day in all the sites they occurred in (Figure 6.4). *Iridomyrmex bicknelli* foraged around the clock in the open site (A) except in the early hours of the second morning (when temperature was lowest and relative humidity was highest) and only late in the afternoon on the other two sites it occurred in (Figure 6.4).

Interactions of native species with Pheidole megacephala at baits

Site A. Open habitat at the invasion front

Pheidole megacephala, *Monomorium sydneyense* and *Iridomyrmex bicknelli* all occurred at least once at every bait station in site A. *P. megacephala* appeared to have dominance at stations 1,2, 3, 7 and 8 and *I. bicknelli* dominated baits 4,5, and 6 (Table 6.6). *P. megacephala* were able to access all of the *I. bicknelli* baits during the second night but were displaced on these baits by *I. bicknelli* or *M. sydneyense* by about 9AM the next morning. On the baits where *P. megacephala* appeared to be dominant,

M. sydneyense were still able to occupy the baits during the higher temperatures in the middle of both days (Table 6.6). Overall, *P. megacephala* featured in 54% of shaded and 37% of unshaded dish observations, and at every bait station where *P. megacephala* appeared to be dominant it was displaced on the unshaded petrie dish before the shaded dish (Table 6.6).

Table 6.5. Number (n=16) of baits in each site where native ant species occurred near Dilli Village, Fraser Island. *indicates that this species only occurred on a bait that was never visited by *Pheidole megacephala*.

Species	Site			
	A–Open habitat–near invasion front	B– <i>Acacia</i> habitat–near invasion front	C– <i>Acacia</i> habitat–in established invasion	D–Open habitat–in established invasion
<i>Pheidole megacephala</i>	16	14	16	16
<i>Camponotus novaehollandiae</i>	6	6	1	1
<i>Crematogaster</i> sp.	1	1		
<i>Iridomyrmex bicknelli</i>	12	2*		3
<i>Iridomyrmex pallidus</i>	1			
<i>Iridomyrmex rubriceps</i>	1			
<i>Mayriella</i> sp.		1		
<i>Melophorus</i> sp.	3			2
<i>Monomorium sydneyense</i>	14	5		14
<i>Myrmecia nigrocincta</i>		1*		
<i>Pheidole</i> sp.		3		
<i>Ochetellus</i> sp.	2	5		
<i>Odontomachus</i> sp.		1	1	
<i>Nylanderia vaga</i>		12	2	
<i>Rhytidoponera convexa</i>	1	3		3
<i>Technomyrmex</i> sp.		2		

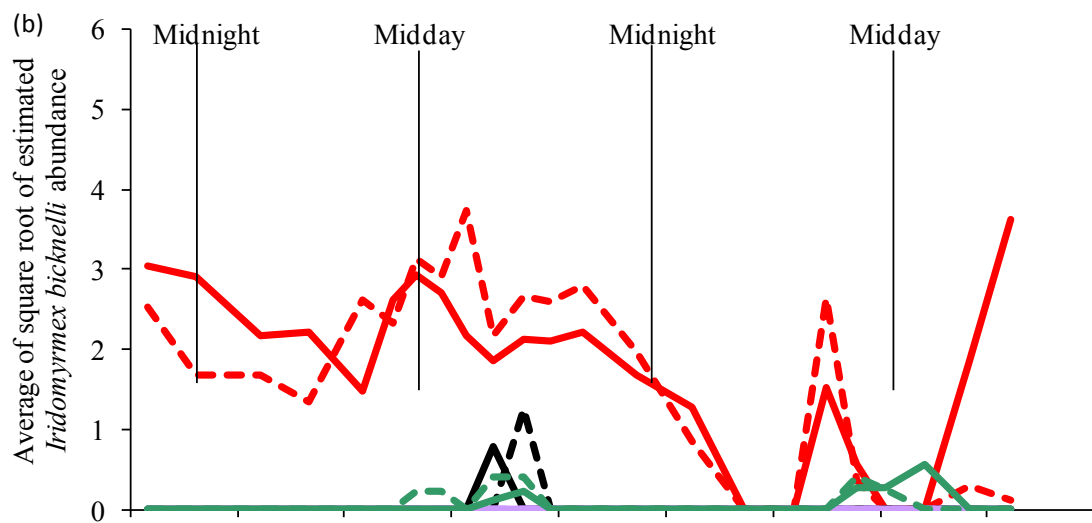
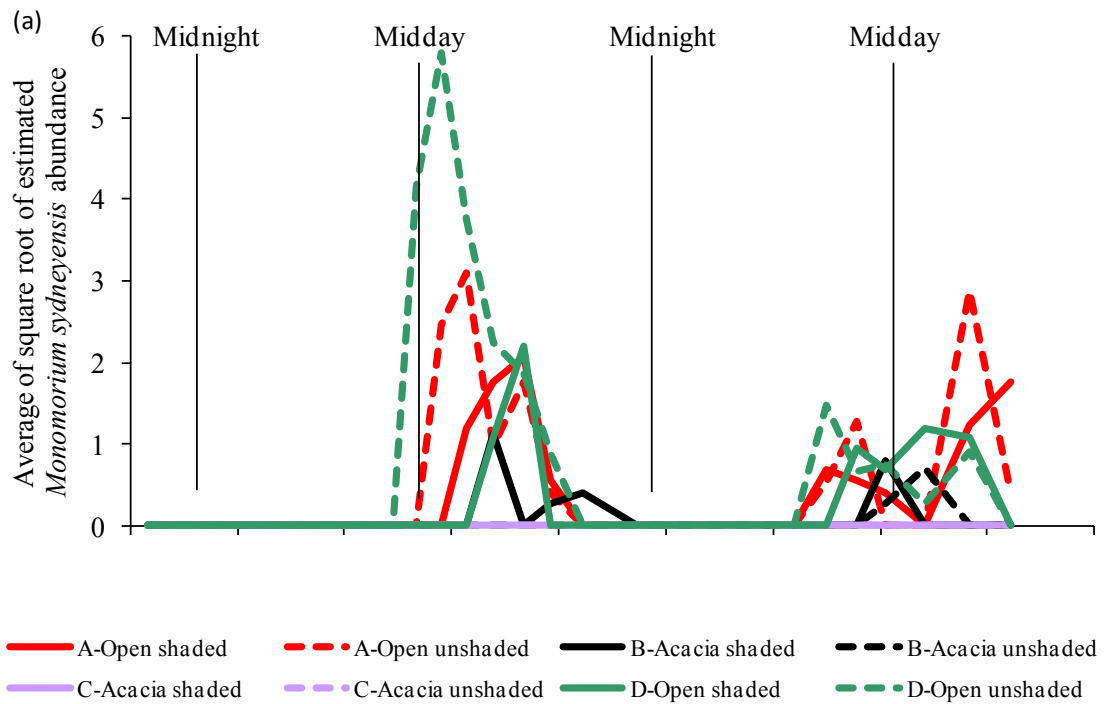


Figure 6.4. Average of estimated (a) *Monomorium sydneyense* and (b) *Iridomyrmex bicknelli* abundances on baited petrie dishes at four sites near Dilli Village, Fraser Island. Averages are across all eight stations at the site although the ants may not have occurred on all dishes.

Site B. Coastal *Acacia* habitat near the invasion front

The shade cloth may have had a marginal effect as *P. megacephala* featured in 76% of shaded and 70% of unshaded dish observations. *Nyanderia vaga* and *P. megacephala* were observed sharing four of the baits on several occasions, but *N. vaga* were displaced by *P. megacephala* on eight of the baits (Table 6.7). *M. sydneyense* and *Ochetellus* sp. tended to occur only in the middle of the day whilst *N. vaga* and *P. megacephala* occurred day and night. The bait station that had no *P. megacephala* recorded was intermittently attended on more than one occasion by *I. bicknelli*, *M. sydneyense*, *N. vaga*, *Ochetellus* sp., *Camponotus novaehollandiae*, *Rhytidoponera chalybea*, a native *Pheidole* sp. and once by a *Myrmecia nigrocincta*.

Site C. Coastal *Acacia* habitat near the oldest part of the invasion

The shade cloth had no effect on occurrence of *P. megacephala*, as they featured in 96% of shaded and 94% of unshaded dish observations (Table 6.8). This site was almost exclusively *P. megacephala*, except one bait where *Nyanderia vaga* occasionally occurred and a solitary *Odontomachus* forager occurred once. There were occasional unattended baits when the dish was intermittently exposed to the sunlight through a gap in the vegetation (W. Robinson pers. obs.).

Site D. Open habitat near the oldest part of the invasion

Pheidole megacephala occurred more frequently in shaded (87%) than unshaded (65%) dish observations. *M. sydneyense* occurred at every bait station at least once and every unshaded dish at least once (Table 6.9). Where *M. sydneyense* was able to displace *P. megacephala* from both dishes at a station, it always accessed the unshaded dish first (Table 6.9). *M. sydneyense* only accessed the baits during the daytime hours and the baits it attended during the day were always occupied by *P. megacephala* when the temperatures reduced after about 4 PM (Table 6.9). *I. bicknelli* competed with *M. sydneyense* at two bait stations during daylight hours.

Table 6.6. Presence of *Pheidole megacephala* (B), *Monomorium sydneyense* (M), *Iridomyrmex bicknelli* (I) and *Ochetellus* sp. (O) on baits in site A, open habitat near the invasion front at Dilli Village. Temperature shades are lightest 11–20, 21–30, 31–40, to darkest 41–50 °C. Relative humidity shades are lightest 21–40, 41–60, 61–80, to darkest 81–100 %.

		17:40	20:20	00:00	02:40	05:40	07:20	08:40	10:05	11:30	13:00	14:40	16:15	18:00	21:00	00:05	03:00	05:50	07:40	09:20	11:00	13:10	15:40	18:00
Temperature	Shaded	21	23	21	22	27	31	35	34	31	32	26	24	21	18	19	20	31	40	36	34	30	24	
	Unshaded	21	23	21	22	27	35	41	40	39	28	25	26	21	18	19	20	34	49	46	42	32	25	
1	Shaded	B	B	B	B	B	B		B	IM	M	M	B	B	B	B	B	B	BI	I			BM	B
1	Unshaded		B	B	B	B	B	B	M	M	M	M	B	B	B	B	B		BM				M	B
2	Shaded	B	B	B	B	B	B	B	B	B	M	M	M	B	B	B	B	B	B		M		M	M
2	Unshaded	B	B	B	B	B	B	BI	I	I	I	B	B	B	B	B	B		M				IM	B
3	Shaded	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B			B	B	B
3	Unshaded		B	B	B	B	B	B	IM	I	I	I	B	B	B	B	B		B	B			IM	B
4	Shaded	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	B	B	B	IM				M
4	Unshaded	I	I	I	I	I	I	I	I	I	I	I	I	I	I	B	B		I				M	BM
5	Shaded	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	B	B	BI				BM	I
5	Unshaded	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	B		I	M				O
6	Shaded	I	I		B	I	I	I	I	IM	I	I	I	I	I	I	B	B	I	M			I	I
6	Unshaded	I				I	I	I	I	I	IM	I	I	I	I	I	B		I	I			M	IM
7	Shaded	B	B	B	B	B	B	B	B	B	BM	M	B	B	B	B	B	B	BI				I	I
7	Unshaded	I	B	B	B	B	B	BI	I	M	M	I	I	B	B	B			I	M			M	B
8	Shaded	B	B			B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	O	O	BI	B
8	Unshaded		B	B	B	B	B	B	M	M	B	M	M	B	B	B			M	M			M	B
Relative humidity	Shaded	81	66	84	83	62	55	39	37	45	40	51	64	78	90	95	94	57	27	37	41	54	76	
	Unshaded	81	66	85	82	63	50	36	35	35	47	51	52	78	91	95	94	46	22	26	26	54	69	

Table 6.7. Presence of *Pheidole megacephala* (B), *Monomorium sydneyense* (M), *Iridomyrmex bicknelli* (I), *Nylanderia vaga* (N), and *Ochetellus* sp. (O) on baits in site B, *Acacia* habitat near the invasion front at Dilli Village. Temperature shades are lightest 11–20, 21–30, 31–40, to darkest 41–50 °C. Relative humidity shades are lightest 21–40, 41–60, 61–80, to darkest 81–100 %.

		17:40	20:20	00:00	02:40	05:40	07:20	08:40	10:05	11:30	13:00	14:40	16:15	18:00	21:00	00:05	03:00	05:50	07:40	09:20	11:00	13:10	15:40	18:00	
Temperature	Shaded	21	22	21	21	24	29	32	32	30	30	26	24	22	19	19	19	27	30	33	31	29	25		
	Unshaded	21	22	23	22	25	29	39	33	30	30	26	25	21	19	19	19	28	32	34	31	29	25		
1	Shaded	B	N	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	
1	Unshaded			B	B		N	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	
2	Shaded		B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	
2	Unshaded	B	B	B	B	N	N	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	
3	Shaded	B	N	N	BN		B	B	B	B	B	B	BN	B	B	BN	B	BN	BN	BN	B	B	B	B	
3	Unshaded			N	B	B	B	BN	B	B	B	B	B	B	N		N	N	N	N	B	B	B	B	
4	Shaded		N	N	N	N		B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	
4	Unshaded		B	B	N	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B		B	B	B	
5	Shaded		B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	BM	B	B	B
5	Unshaded	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	M	B	B
6	Shaded			B	B	B	N	N	B	B	M	B	B	B	B	B	B	B	B	B	B	B	B	B	B
6	Unshaded		B	B	B	B	B	B	B	B	B	B	B	B	B	B		B	B	B	O	B	B	B	B
7	Shaded			N	B	BN	B	BN	B	B	B	B	B	B	B	ON	N	B	B	B	B	B	B	B	B
7	Unshaded				B		B	B	B	B	B	B	B	B	O				BN	O	M	M	B		
8	Shaded		N				N			N	I		M	MN		ON	N		N	O	O	O	O	O	O
8	Unshaded		N	N		N	N			O		I	O		N			N	N	O		O	O	O	O
Relative humidity	Shaded	91	74	87	86	79	52	56	45	53	46	55	68	78	92	97	92	65	49	41	44	61	70		
	Unshaded	90	76	74	83	70	58	42	65	44	49	51	60	80	92	97	92	66	50	41	42	59	73		

Table 6.8. Presence of *Pheidole megacephala* (B), and *Nylanderia vaga* (N) on baits in site C, *Acacia* habitat in the established invasion area at Dilli Village. Temperature shades are lightest 11–20, 21–30, 31–40, to darkest 41–50 °C. Relative humidity shades are lightest 21–40, 41–60, 61–80, to darkest 81–100 %.

		17:40	20:20	00:00	02:40	05:40	07:20	08:40	10:05	11:30	13:00	14:40	16:15	18:00	21:00	00:05	03:00	05:50	07:40	09:20	11:00	13:10	15:40	18:00
Temperature	Shaded	23	25	24	23	25	33	33	34	34	31	26	25	22	20	21	20	27	39	35	33	27	25	
	Unshaded	23	25	23	24	25	33	32	34	40	34	26	24	23	19	19	19	27	45	39	37	28	24	
1	Shaded	N	B	B	B	N	B	B	B	B	B	B	B	B	B	B	B	BN	B	B	B	B	B	
1	Unshaded	N			N	B	B	B	B	B	B	B	B	B	B		BN	B		B	B	B	B	
2	Shaded	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	
2	Unshaded	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	
3	Shaded		B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	
3	Unshaded	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B			B	B	
4	Shaded		B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	
4	Unshaded	B	B	B	B	B	B	B	B		B	B	B	B	B	B	B	B	B	B	B	B	B	
5	Shaded	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	
5	Unshaded	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	
6	Shaded			B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	
6	Unshaded	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	
7	Shaded	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	
7	Unshaded	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	
8	Shaded		B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	
8	Unshaded	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	
Relative humidity	Shaded	73	63	77	84	77	53	51	50	49	43	59	65	78	90	98	97	69	35	45	42	63	74	
	Unshaded	78	64	74	80	74	50	51	51	24	48	57	65	77	91	97	96	71	35	38	37	63	74	

Table 6.9. Presence of *Pheidole megacephala* (B), *Monomorium sydneyense* (M) and *Iridomyrmex bicknelli* (I) on baits in site D, open habitat in the established invasion area at Dilli Village. Temperature shades are lightest 11–20, 21–30, 31–40, to darkest 41–50 °C. Relative humidity shades are lightest 21–40, 41–60, 61–80, to darkest 81–100 %.

		17:40	20:20	00:00	02:40	05:40	07:20	08:40	10:05	11:30	13:00	14:40	16:15	18:00	21:00	00:05	03:00	05:50	07:40	09:20	11:00	13:10	15:40	18:00
Temperature	Shaded	22	24	24	24	26	30	30	37	30	30	25	22	22	20	19	23	29	33	33	32	26	24	
	Unshaded	22	25	23	25	31	31	32	38	36	34	25	22	22	20	17	27	36	40	40	36	27	23	
1	Shaded	B	B	B	B	B	B	B	B	B	M	B	B	B	B	B	B	B	B	B	B	B	B	
1	Unshaded	B	B	B	B	B	B	M	M	M	M	B	B	B	B	B	B	B	B	B		B	B	
2	Shaded	B	B	B	B	B	B	B	B		M	B	B	B	B	B	B	B	M	M	M	M	B	
2	Unshaded	B	B	B	B	B	M	M	M	M	M	B	B	B	B	B	B	M				M	B	
3	Shaded	B	B	B	B	B	B	B	B	BM	BM	B	B	B	B	B	B	B	B	B	B	B	B	
3	Unshaded	B	B	B	B	B	B	B		M	M	B	B	B	B	B	B	B	B	B		M	B	
4	Shaded	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B		BM	M	B	
4	Unshaded	B	B	B	B	B	M	M	M	M	B	B	B	B	B	B	B	M				M	B	
5	Shaded	B	B	B	B	B	B	B		M	M	B	B	B	B	B	B	B	B	M	M	M	BM	B
5	Unshaded	B	B	B	B	B	M	M	M	M	M	M	B	B	B			B						B
6	Shaded	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B
6	Unshaded	B	B	B	B	B	M	M	M	BIM	BM	B	B	B	B	B	B	B	B	M	M			B
7	Shaded	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B
7	Unshaded	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	M	M	BM	B	B
8	Shaded	B	B	B	B	B	B	B	B	IM	I	B	B	B	B	B	B	B	B	I	I	I	B	B
8	Unshaded	B	B	B	B	B	IM	IM	M	IM	I	B	B	B	B				I	I				B
Relative humidity	Shaded	75	60	69	72	65	53	56	46	49	43	64	74	77	91	94	94	65	56	57	51	66	78	
	Unshaded	75	61	72	70	62	52	53	47	40	42	62	72	75	91	95	78	56	41	39	44	67	83	

6.4 Discussion

This study was carried out in a warm period of the year and the results agree with the previous finding that *P. megacephala* partition foraging and nest activity according to the climate of the local region (Broekhuysen 1948, Carnegie 1960, Greenslade 1972). In particular, they were absent from baits in the hottest part of the day. There is no doubt that *P. megacephala* prefer the shaded habitats for foraging. They were always on shaded baits longer during the daytime in the open sites and foraged around the clock in the *Acacia* sites.

The most successful of the native ants in getting to the baits were *Iridomyrmex bicknelli* and *Monomorium sydneyensis*. In the open site A there was a temperature differential of about 6°C between shaded and unshaded baits and this was enough to allow partitioning between *P. megacephala* and *I. bicknelli* on the baits (Table 6.6). The data generally agree with Hoffmann *et al's* (1999) suggestion that *P. megacephala* could forage on bare open areas during the cool parts of the day, to avoid other aggressive native taxa. The question that can't be answered is whether *P. megacephala* or *I. bicknelli* are the dominant taxa. In the other open site (D), the temperatures on the baits were slightly cooler and *P. megacephala* were able to stay on most shaded baits during the daytime (Table 6.9). This suggests that when they are numerically dominant they stay on the baits and the other taxa access the bait when *P. megacephala* leave. There is strong evidence that *M. sydneyense* and *I. bicknelli* are dominated by *P. megacephala* because there were ten occasions when *P. megacephala* abandoned the bait and were not immediately replaced by a native species, and on four of these occasions *P. megacephala* were the first taxa back on the bait when the temperature cooled (Table 6.9).

The experiment was designed to determine if *P. megacephala* foraging times would be the same in zones with and without competition from native ants. However there were slight temperature differences between sites and differences can't be attributed to competition alone. In both open sites *P. megacephala* always left the unshaded bait first, perhaps from competition perhaps from environmental limits. I suggest the latter is more likely because on the second day of the trial, *P. megacephala* were not observed on any of the open area baits after 9:20 AM, were seldom replaced by native taxa, and, these baits were left unattended by any ants. Nevertheless the results show how it is possible for some native ant species and *P. megacephala* to co-exist.

This study did not find lower tolerance limits for temperature but found an upper tolerance of about 40°C and a minimum relative humidity tolerance of about 20 %. Temperature and humidity need to be considered together however because there were definite differences in *P. megacephala* tolerance between shaded and unshaded habitats. *P. megacephala* were still active in site C, an *Acacia* habitat with little competition at an observed temperature of 45°C (Table 6.8). That temperature was recorded on a control bait station and it could be that that particular station was exposed to sunlight through a gap in the canopy at that time. Regardless, *P. megacephala* were consistently observed foraging when temperatures were approaching 40°C in the *Acacia* habitat and regularly abandoning baits in open sites when temperatures approached 35°C. It seems that their competitiveness is reduced when approaching environmental tolerances.

In this study *P. megacephala* were generally equally active in *Acacia* habitats between 20 and 35°C but in open habitats more active between 20 and 25°C (Figure (6.3)). These values are generally comparable with South Africa where the greatest activity was between and 24

and 29°C (Carnegie 1960). The foraging during the night observed in the dry area here also is in agreement with observations in the Solomon islands where *P. megacephala* were described as mainly but not exclusively nocturnal (Greenslade 1972).

Pheidole megacephala abundances were only statistically significantly higher on shaded than unshaded baits in the Dilli Campground area, Site D. In other words when the infestation occurs in a naturally shaded area like an *Acacia* habitat the ants forage freely. This would suggest that vegetation that offers more shade and moister conditions can be more readily invaded by *P. megacephala* than open areas. However the results from the open habitats show that *P. megacephala* will forage at cooler times of the day when invading hotter drier areas and hence can still invade or at least cross drier habitats readily. A comparison here is the Argentine Ant, which has some similarities to *P. megacephala* and has been much better studied. *L. humile* are like *P. megacephala* in that they do not nest deeply underground and are also moisture restricted (Holway 2005). But *L. humile* can occur in drier regions where fragmented by irrigation or urban runoff, or in coastal areas where fog can ameliorate the summer drought (Holway 2005). *P. megacephala* were observed in small numbers in irrigated areas that were around Howard Springs near Darwin, (Hoffmann et al. 1999). Although moisture limited, *L. humile* may have a higher desiccation tolerance than *P. megacephala*. In xeric environments, with low ground level cover and higher ground level insolation, *L. humile* are less active and therefore the native ants are less affected (Holway et al. 2002b).

This research shows that *P. megacephala* can monopolise baits in a site that has high native species richness (See Chapter 5), but that some native species can outcompete it when it approaches abiotic tolerances. *P. megacephala* were extremely dominant in the shaded

Acacia site close to Dilli Village (Site C) where temperature and humidity extremes were moderated (Table 6.8). Interestingly, this site is close to and has similar vegetation cover to the regenerated Great Walk track (Chapter 4) where, contrary to intuition, the infestation has retreated as vegetation cover has increased during the last 5 years. This raises the question about temporal changes in dominance as the sub-tropical climate of Fraser Island experiences seasonal changes in temperature and humidity. Perhaps the humidity in the dry season restricts the infestation spread along the Great Walk track. The understanding of how biotic and abiotic factors interact with *P. megacephala* invasions and their spread certainly requires a lot more research and a large scale experiment would be an ideal approach.

6.5 Conclusions

- *Pheidole megacephala* foraged 24 hours a day in native vegetation areas on Fraser Island.
- *P. megacephala* rarely foraged above 40°C or below 20% relative humidity in open areas.
- At least 12 native ant species occurred in the vicinity but most were sub-ordinate to *P. megacephala* on baits.
- *Iridomyrmex bicknelli*, *Monomorium sydneyense* and *Nylanderia vaga* were regularly observed at bait stations but partitioned foraging to avoid *P. megacephala*.
- *Iridomyrmex bicknelli* and *Monomorium sydneyense* were able to displace *Pheidole megacephala* on baits when the invader reached the limits of temperature and humidity tolerance.
- Experiments to understand the role of biotic and abiotic factors allowing *P. megacephala* invasion in species rich areas are required.

Chapter 7: The role of biotic resistance in a *Pheidole megacephala* invasion in undisturbed native bushland on Fraser Island

7.1 Introduction

Areas that are invaded by exotic ants have reduced biodiversity of invertebrates in general and almost always have lower overall ant species richness (Delabie et al. 1995, Holway et al. 1998, Suarez et al. 1998, Hoffmann et al. 1999, Kaspari 2000, Holway et al. 2002b, Le Breton et al. 2003, Sanders et al. 2003). In some instances the lower richness may contribute to the susceptibility of invasion in the first place (Collingwood et al. 1997), and in some cases the invasion may be causing the lower richness (Holway *et al.* 2002a). The latter case is of great concern but there have been only a few studies documenting (using experiments or well-designed observational studies) where it has actually been documented (e.g. Holway *et al.* 2002a).

P. megacephala, is widespread in coastal regions of Eastern, Northern and Western Australia and has been consistently associated with reduced native ant species richness and abundance (e.g. Chapter 3; Heterick 1997, Samways et al. 1997, Hoffmann et al. 1999, May and Heterick 2000, Hoffmann and Parr 2008, Callan and Majer 2009). Yet, as well as they have been studied, there have been no well-designed experiments investigating *Pheidole megacephala* invasions and almost all published research on this invader is

confounded by disturbance. Hoffman and Parr (2008) performed a repeat visit survey documenting changes in a *P. megacephala* infestation and native ant assemblages but even this study is purely observational and required an act of faith to infer cause and effect in the observed changes between visits.

P. megacephala are known from at least six locations on Fraser Island with four of the infestations restricted to the vicinity of developed areas and still in their infancy. However two of the infestations, one at Dilli Village (Chapter 5) and one near the northern access track to Lake Wabby cover several hectares. Given the consistent relationship of *P. megacephala* with reduced biodiversity values in the literature and the lack of behaviourally dominant native ants in undisturbed vegetation on Fraser Island (Chapter 2), this invader may seriously threaten invertebrate biodiversity in natural vegetation on Fraser Island.

The *P. megacephala* infestation near Lake Wabby occurs in the exposed dune vegetation, but stops at the boundary of a vegetation change to dry woodland. The infestation may stop because temperature and humidity changes are limiting (see Chapter 6) or because of a change in the native ant community, i.e. the biotic resistance by native ants. The invasion offered a chance to use experimental design to manipulate the environmental and biotic variables influencing a *P. megacephala* invasion on Fraser Island.

The study aimed to elucidate the roles of environmental variables (namely temperature and humidity) and biotic resistance (competition with native fauna) in the invasion of native vegetation areas by *Pheidole megacephala* near Lake Wabby on Fraser Island. The experiment was a partial failure because cyclones hit Fraser Island during two of the four

sampling periods and the efficacy of the treatment zones was minimal. However, because the experimental design was good and included multiple samples at permanent sampling points, the data were able to be used to further investigate the relationships between native ant biodiversity and *P. megacephala* on Fraser Island. The results complement the findings of Chapter 5 from Dilli Village.

7.2 Methods

7.2.1 Study site

The study was conducted near the northern access track to Lake Wabby, about 41 km from the southern tip on the eastern side of Fraser Island. The site is classified as Fraser Island dune system 1, which generally has no developed soil profile and no clearly defined A or B horizon (Sinclair 1997). The natural vegetation is mainly pioneer species such as Casuarinas [Billai], Coastal Banksias [Wallum], Pandanus [Winnam] and Cypress Pines [Kululu] (Sinclair 1997). Up until the 1950's it was possible to drive vehicles from the beach over the sand dunes to Lake Wabby and the route used was adjacent to transect 9 of this study (John Sinclair, pers. comm. 2008). There are no obvious signs of the track and no known history of human dwellings in the area, but there are small pockets of the class 3 declared weed, *Lantana camara* in the study site. The *L. camara* has probably been spread by birds without assistance from human disturbance (John Sinclair, pers. comm. 2008).

7.2.2 Field sampling

The *P. megacephala* infestation was noticed in 2004 and it is found in the native vegetation about 350 m from the beach towards Lake Wabby (a further 1.8 km away). Several attempts

to map the side boundaries of the infestation have been unsuccessful because of the impenetrable nature of the vegetation. The infestation is known to extend for at least 6 km at the beach front and at least 200 m laterally near the access track (Figure 7.1).

The 'front' edge of invasion was located in October and November 2007 using peanut butter baits to determine presence. Nine transects about 15 m apart and 47.5 m in length were then laid out with the invasion front in the middle of each transect. Ten pitfall traps, (vials 42 mm in diameter and partially filled with a mixture containing 70% ethanol and 3% glycol), were placed 2.5 m apart along each transect on each side of the assumed front (Figure 7.2). Transect 9 straddles a walking track and had a gap of 10 metres between the assumed infested zone and uninfested zones. Pitfall traps were left in position unopened for seven days and then opened for five days on the 12th November 2007.



Figure 7.1. Approximate location of the *Pheidole megacephala* infestation near the Northern Access Track to Lake Wabby, Fraser Island, in October 2007. Dots are where *P. megacephala* were recorded (orange) or not recorded (green) prior to experimental zones being applied in October 2007. Shorter straight lines represent the nine transects intensively surveyed during this project. Longer straight lines represent the additional transects surveyed in April of 2009.

Amdro® which contains the metabolic inhibitor (MI), hydramethylnon, was used to reduce native ant biotic resistance. In order for this treatment to work it was required that only native ants were exposed to the MI. Hence, during 16th–19th December 2007, a 3.5 × 7 m isolation plot was positioned on the 11th, 12th and 13th traps (thought to be the first three non- *P. megacephala* traps) in four randomly selected transects. At the same time, 90% shade cloth was positioned at approximately 45cm above ground level over traps 10–12 in two isolation and two non-isolation plots (Figure 7.2). The isolation plots were isolated

without disturbance by positioning a drift fence 5 cm below the soil surface and 25 cm in height with an 8 cm strip of Tanglefoot® applied to the fence. To ensure no ants could enter or leave the plot, all trees within the plot also had Tanglefoot® applied to a sleeve placed on their trunks. To reduce biotic resistance by ants nesting in the isolation plots, six bait stations containing Amdro® were placed within each plot. To exclude large beetles and vertebrates the bait was placed within sealed urine vials with several 1 cm holes in the lid. The Amdro® was intended to reduce biotic resistance from native ants and not to eliminate all native ants. The MI in the Amdro® breaks down within 72 hours but the isolation plots remained in place until 23 December 2007, when all pitfall traps were again opened for 4 nights and 5 days. All pitfall traps were opened for 5 days again on 13 April 2008 and 5 October 2008. The island was hit by cyclones during the December and April pitfall trapping periods and many of the traps were filled with water (but still contained ants). There were about 5 % of traps with no data on those two dates; these traps were omitted from statistical analyses. The data from these pitfall traps are referred to as ‘close to the invasion front’ throughout this chapter.

The pitfall traps from the initial four sampling dates only extended about 22.5 m each side of the invasion front. To complement the results, and to encompass ants further from the invasion front, the site was revisited in late April 2009 and three of the transects were extended with 10 traps positioned 20 m apart each side of the original invasion front. Pitfall traps were opened for 5 days and 4 nights. This component is referred to as the traps ‘at the larger spatial scale’ throughout this chapter.

7.2.3 Ant Identification

All ants in all samples were identified following the Ants of Northern Australia (Andersen 2000) and voucher specimens were lodged at the Tropical Ecosystem Research Centre at CSIRO in Darwin.

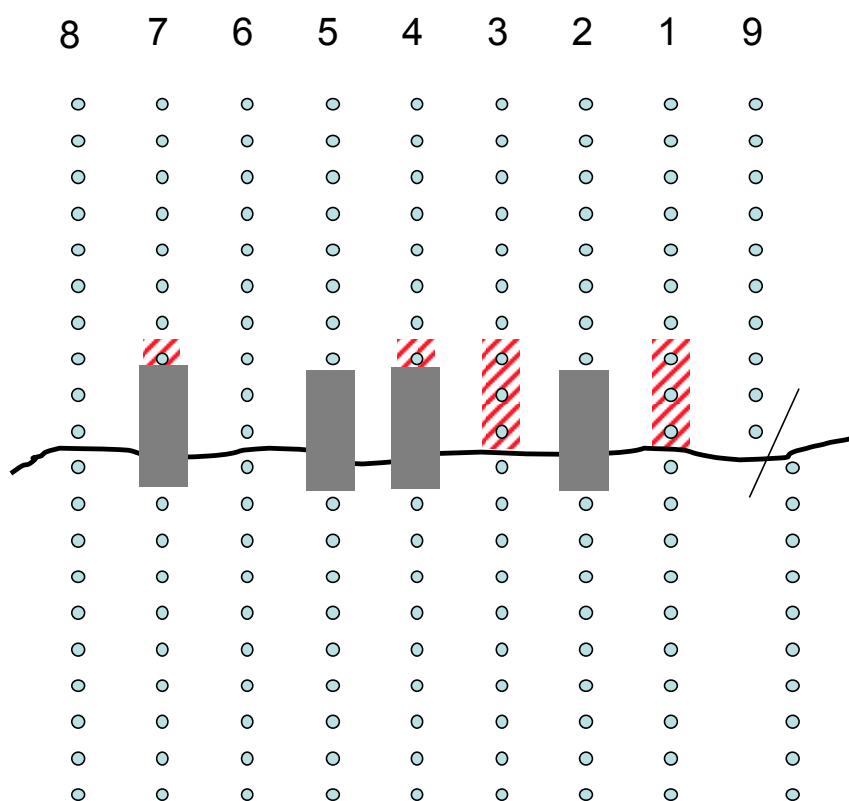


Figure 7.2. Treatments applied in December 2007 to transects traversing *Pheidole megacephala* infestation boundaries near the Northern Access track to Lake Wabby. Shade cloths extend from traps 10 to 12 and AMDRO® (hatched area) covers traps 11 to 13. The wandering black line represents the invasion 'front'. The break in transect nine represents a gap of 10 m between traps 10 and 11 as the transect straddled a walking track.

7.2.4 Data analysis

Infestation boundaries

Changes in the extent of the infestation are presented in a schematic diagram and *P. megacephala* infestation boundary movements interpreted relative to the shading and poisoning treatments. The transects were designed to have 10 traps each side of the *Pheidole megacephala* invaded area and this was the case in all treatments except one of the shade-only transects, where the invaders were actually in trap 11 at the start. Two of the three control plots also had *P. megacephala* in more than 10 traps in the first set of samples, but neither of these observations were of consequence to the design or analyses.

Efficacy of treatments

To test the effect of the poisoning treatment on the native ants, ANOVA was used to compare native ant abundance and species richness in traps 11 to 13 of all transects in a BACI (Before-After-Control-Impact) analysis. Treatment (poisoned or not) and date were treated as fixed factors with transects nested within treatments and traps the subjects in a repeated measures analysis. A mixed model analysis was used and the repeated measure fitted with an unstructured covariance structure using the mixed procedure in SAS® version 9.2 (SAS 2009). In a BACI type analysis of this design, one can treat dates as replicates nested within Before–After, however this option was not used because there was a chance of a gradual effect of the poisoning across the three after-treatment dates. It desirable but not essential that the treatments and controls have the same starting values, as it is the test of the interaction effect of treatment (poisoning) and date that indicates the treatment effect after

application. Native ant abundance and species richness were both tested after square-root transformations were applied and normality and homogeneity of residuals confirmed.

Native ants response to changes in Pheidole megacephala presence

It was possible to investigate changes in native ant species richness associated with changes in the presence of *P. megacephala* compared to changes in native only traps because the exact same points were sampled each visit. The changes in native ant species richness between successive samples for each pitfall trap were calculated and the presence of *P. megacephala* in both samples, neither sample, the first but not the second samples or vice versa was determined. A mixed model ANOVA was then performed on the changes in richness between sample dates and the status of *P. megacephala*. Each pitfall trap was fit as a repeated measure and an autoregressive covariance term was used in the model to allow for correlation between sample dates at the same trap location. The residuals were inspected for normality and homogeneity before presenting the results. The least squares means were compared using Tukey's multiple comparisons and are presented graphically.

Overall relationship of Pheidole megacephala presence with native ant abundance and species richness

Trap average species richness and abundance of native ants were compared between the traps with and traps without *P. megacephala* areas using a linear mixed model and species accumulation curves (as described in Chapter 2). The mixed model fitted dates and *P. megacephala* presence/absence as fixed effects and pitfall traps were identified as the subjects in a repeated measure analysis. The abundance data were log₁₀ transformed and the assumptions of normality and homogeneity of variances confirmed for both analyses using

residual plots. The same accumulation curve approach was also applied to the data collected at the larger spatial scale in April 2009. The analysis from the November 2007 to October 2008 is referred to as ‘close to the invasion front’ and the later analysis is labelled as ‘at the larger spatial scale’. In both analyses all traps are treated as independent samples within the infested or not infested zones and the zones are defined by whether or not *P. megacephala* were collected within the trap.

7.3 Results

Infestation boundaries

The *P. megacephala* infestation advanced in six of the nine transects during the study, including two of the three control transects (Figure 7.3). The other four transects where the advance was observed were all treated with poison, whilst the two shade-only treatments showed no advance at all (Figure 7.3). This suggests that shade-only treatments may prevent advance and that the poisoned transects may have helped the advance of *P. megacephala*. However, closer investigation of the native ant data pre-and post-treatment provided some light on the efficacy of the treatments.

Efficacy of the treatments

Traps 11, 12 and 13 in the unpoisoned transects averaged about 1.4 native species less than the same traps in the treated transects for the whole study including *before* the poison treatment was applied (Figure 7.4). The difference was not statistically significant and further, there was a significant difference between sampling dates ($F = 5.0$, $df = 3, 26$, $p <$

0.01). There was no interaction of date and poison treatment on average species richness ($F = 2.15$, $df = 3, 26$, $p = 0.12$). Importantly, there were significant differences in species richness between the transects nested within treatments ($F = 7.47$, $df = 16, 26$, $p < 0.0001$) and this effect was dependant on date of sampling ($F = 2.82$, $df = 26, 26$, $p < 0.005$). Overall, this means the poison treatment had negligible effect on native ant species richness. Average native ant abundance in the pitfall traps was significantly different between dates ($F = 24.33$, $df = 3, 18$, $p < 0.0001$) and between poisoned and unpoisoned traps ($F = 26.2$, $df = 1, 18$, $p < 0.0001$), but there was no significant interaction between the two ($F = 0.98$, $df = 3, 18$, $p = 0.42$). The poison application, therefore, did not reduce the abundance of native ants, although again the results are difficult to interpret because there was a significant difference in native ant abundance between transects nested within treatments depending on the date ($F = 2.58$, $df = 21, 18$, $p < 0.05$).

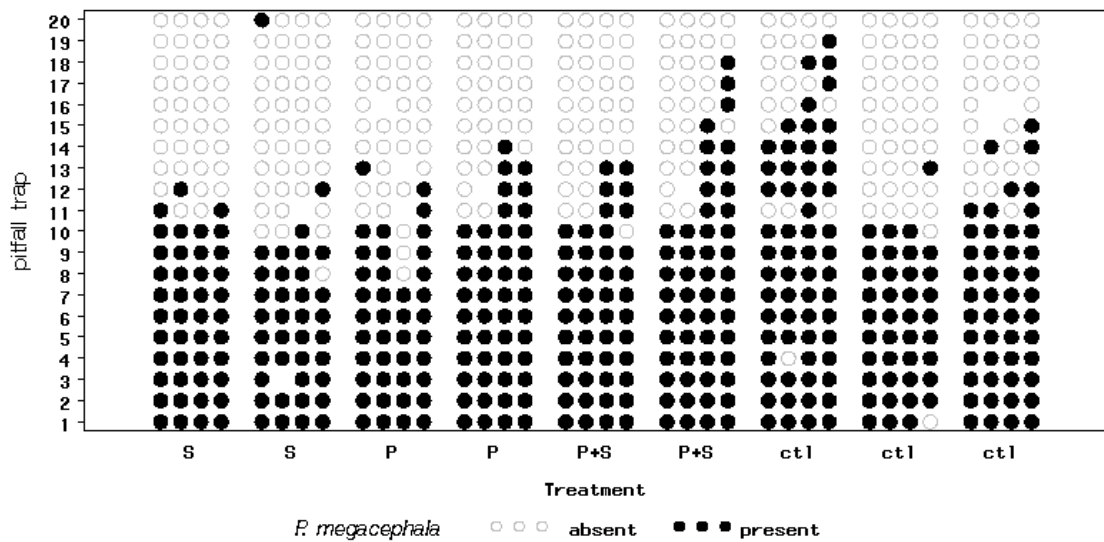


Figure 7.3. *Pheidole megacephala* occurrence in pitfall traps in nine transects near Lake Wabby. S = shaded, P = Poisoned, ctl = no treatment. The four columns for each treatment are for the dates 12 November 2007, 23 December 2007, 13 April 2008 and 5 October 2008 respectively. Occasional blank points represent pitfall traps lost during the cyclones in the middle two sampling periods.

The interaction appears to be because some of the transects within either poison treatment tended to have more ants and/or species at the end of the study and others fewer regardless of treatment type (Figure 7.5). Interestingly, traps in the three control transects close to the invasion front almost all had the same or fewer ants and fewer species as the study went on (Figure 7.5). The relationship of native ants in these traps with *P. megacephala* is considered more in the next section.

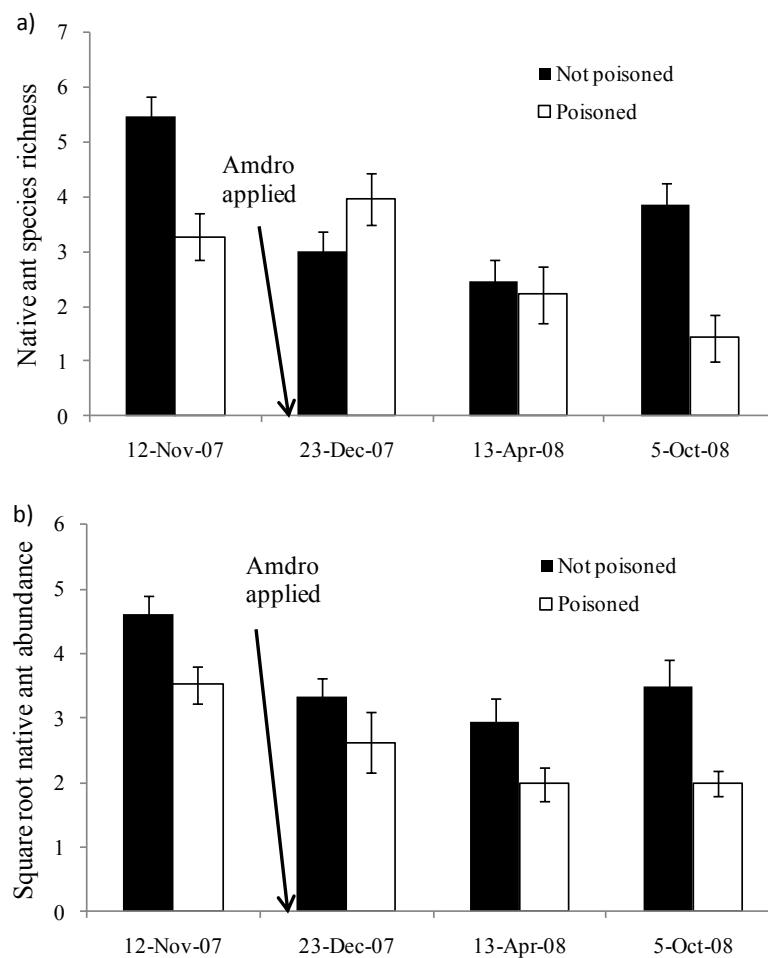


Figure 7.4. Average native ant (a) species richness and (b) abundance in the first three pitfall traps thought to be in front of the *P. megacephala* infestation at the commencement of the study. Only traps 11, 12 and 13 from each transect are included in this analysis. There were four transects with and five transects without AMDRO® applied.

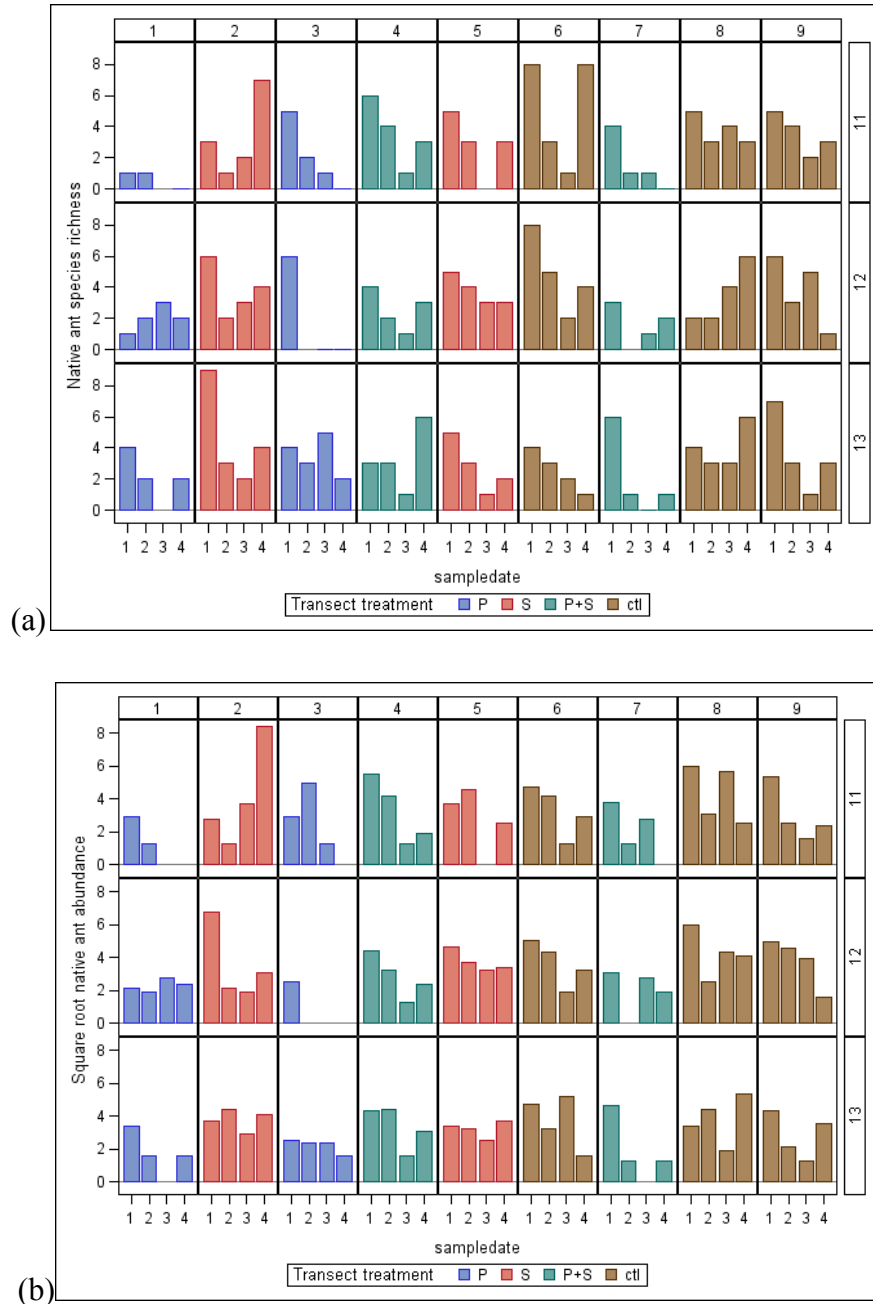


Figure 7.5. Native ant (a) species richness and (b) abundance in traps 11, 12 and 13 for each transect for four dates. 1 = November 2007, prior to treatment, 2 = December 2007, immediately after treatment, 3 = April 2008 and 4 = October 2008. S = shaded, P = Poisoned, ctl = no treatment. Poison traps were treated with AMDRO® between dates 1 and 2. Transect numbers (columns) and trap numbers (rows) correspond to Figure 7.2. For example, transects 2 and 5 are shaded no poison transects.

Relationship of Pheidole megacephala with native ants near the invasion front

There were 72 native ant species collected and identified overall, with many native species occurring in both the infested and uninfested zones (Table 7.1). *Aphaenogaster longiceps*, *Crematogaster* sp. C (*laeviceps* gp.), *Rhytidoponera chalybea*, and *Rhytidoponera metallica* tended to occur regularly, but less frequently in the infested zone (Table 7.1). On the other hand, several common species including *Mayriella abstinens*, *Nylanderia* sp. A (*vaga* gp.) and *Stigmacros aciculate* appeared to occur more frequently in the infested zone (Table 7.1).

Pheidole megacephala made up 63% of ants in the traps in which they occurred in the initial and final surveys and 72% of ants in traps they occurred in for the two surveys affected by cyclones (Table 7.2). There were always more species of native ants collected within the *P. megacephala* infested zone than the non-infested zone, but there was also more traps in the infested zone (Table 7.2). Hence native ant species richness is better compared using trap averages and species accumulations.

There were significantly more native ants on average in traps that didn't contain *P. megacephala* than traps that did ($F = 4.69$, $df = 1, 45$, $p < 0.05$). The average was only 0.9 more native ants per trap in non-*P. megacephala* traps. The difference was consistent between dates but there was a difference in the number of native ants collected on the different dates ($F = 32.5$, $df = 3, 494$, $p < 0.0001$). After correction for type 1 error, it was found that there were significantly more native ants collected on the first and final dates than either of the two cyclone affected dates (Figure 7.6).

Table 7.1. Ants collected in pitfall traps in and adjacent to a large *Pheidole megacephala* infestation near Lake Wabby, Fraser Island. Values are percentage of traps in which the species occurred. Arrows indicate the potential direction of the relationship with *P. megacephala*. For example, *Aphaenogaster longiceps* abundances were higher when *P. megacephala* were absent.

Species	native zone				<i>P. megacephala</i> zone				
	12-Nov-07	23-Dec-07	13-Apr-08	5-Oct-08	12-Nov-07	23-Dec-07	13-Apr-08	5-Oct-08	
<i>Aenictus turneri</i>				2		1			
<i>Anochetus</i> sp. B (<i>graeffei</i> gp.)	2			2					
<i>Anonychomyrma</i> sp. A (<i>nitidiceps</i> gp.)						1			
<i>Anonychomyrma</i> sp. B (<i>niticeps</i> gp.)	5								
<i>Aphaenogaster longiceps</i> Smith	54	53	43	55	↓	11	10	6	10
<i>Bothroponera</i> sp. A	6	9	7	5		14	10	9	4
<i>Camponotus</i> sp. A (<i>novaehollandiae</i> gp.)	6	4	3	3		9	9	3	1
<i>Cardiocondyla atalanta</i>									1
<i>Cardiocondyla</i> sp. A (<i>nuda</i> gp.)		1	1						1
<i>Carebara</i> sp. B	1	1		6		1	2		8
<i>Cerapachys</i> sp. A (<i>singularis</i> gp.)	2			5		2			
<i>Colobostruma biconvexa</i> Shattuck	1	1				3	3		2
<i>Colobostruma</i> sp. B (<i>frogatti</i> gp.)						1	1		
<i>Colobostruma</i> sp. C							1		
<i>Crematogaster</i> sp. A (<i>laeviceps</i> gp.)	1								
<i>Crematogaster</i> sp. B (<i>cornigera</i> gp.)	7			17			1		4
<i>Crematogaster</i> sp. C (<i>laeviceps</i> gp.)	14	14	7		↓	1	3	2	
<i>Crematogaster</i> sp. D (<i>queenslandica</i> gp.)			10						
<i>Eurhopalothrix</i> sp. A				2				1	1
<i>Heteroponera imbellis</i>	1								
<i>Hypoponera</i> sp. A						1			1
<i>Hypoponera</i> sp. B	1	3		5			4	1	3
<i>Hypoponera</i> sp. C	2	3						1	
<i>Hypoponera</i> sp. G			1	3				3	1
<i>Iridomyrmex bicknelli</i> Emery	1		1						1
<i>Leptogenys bidentata</i>	1		3	3		1	1	1	
<i>Leptomyrmex cnemidatus</i> Wheeler			1	8		11	7	9	11
<i>Leptomyrmex rufithorax</i> Forel	6	4	3	6		2	1	4	4
<i>Mayriella abstinens</i> Forel	6	6	4	6	↑	19	22	25	20
<i>Mayriella ebbei</i>				2			1		1
<i>Mayriella overbecki</i> Viehmeyer						1	2		
<i>Melophorus</i> sp. A (<i>mjobergi</i> gp.)				2					
<i>Mesoponera australis</i> Forel		5				1	3		
<i>Monomorium</i> sp. A (<i>laeve</i> gp.)						3			
<i>Monomorium</i> sp. C (<i>kilianii</i> gp.)	4			2		10		1	6
<i>Monomorium</i> sp. D (<i>carinatum</i> gp.)	1			2		10	4	3	9
<i>Monomorium</i> sp. E (<i>nigrium</i> gp.)	2			2		1			4
<i>Monomorium</i> sp. F (<i>nigrium</i> gp.)		1				1	2		
<i>Monomorium</i> sp. I (<i>laeve</i> gp.)	4			6		5	1		4
<i>Myrmecia brevinoda</i> Forel	2		1	2				2	2
<i>Myrmecia nigrocincta</i> Smith		1							1
<i>Myrmecia</i> sp. A (<i>urens</i> gp.)	1						1		1

Table 7.1 (cont.).

Species	native zone				<i>P. megacephala</i> zone				
	12-Nov-07	23-Dec-07	13-Apr-08	5-Oct-08	12-Nov-07	23-Dec-07	13-Apr-08	5-Oct-08	
<i>Notoncus</i> sp. A (<i>enormis</i> gp.)	1				1			1	
<i>Notoncus</i> sp. B (<i>enormis</i> gp.)				2		1		1	
<i>Notoncus</i> sp. C (<i>enormis</i> gp.)		1	3	3					
<i>Nylanderia</i> sp. A (<i>vaga</i> gp.)	38	18	14	32	↑	74	62	50	67
<i>Nylanderia</i> sp. C (<i>vaga</i> gp.)						1			
<i>Nylanderia</i> sp. E (<i>minitula</i> gp.)				2		4	2		4
<i>Ochetellus</i> sp. A (<i>glaber</i> gp.)						2			1
<i>Odontomachus</i> sp. A (<i>turneri</i> gp.)		4	3	2		1	1		
<i>Pheidole megacephala</i> Fabricius						100	100	100	100
<i>Pheidole</i> sp. A (<i>variabilis</i> gp.)	24	8	1	8		8	3	1	1
<i>Pheidole</i> sp. B (group A)	27	26	19	42		35	38	22	28
<i>Pheidole</i> sp. C (group E)	24	8	33	35		18	10	8	13
<i>Pheidole</i> sp. D (group A)	5	14	9	17		1	1	1	
<i>Pheidole</i> sp. E (<i>ampla</i> gp.)	13	5	6	11		4	4	2	4
<i>Pheidole</i> sp. F (group C)	6					1			
<i>Pheidole</i> sp. J (group G)	2					1			
<i>Pheidole</i> sp. L (group C)	1			14		1	1		3
<i>Podomyrma gratio</i>		1							
<i>Polyrhachis ammon</i> gp.	1	1		3				1	4
<i>Polyrhachis atropos</i> gp.	1								
<i>Polyrhachis chaiomyrma</i> gp.						1			
<i>Polyrhachis hedomyrma</i> gp.				2		1			1
<i>Polyrhachis hookeri</i> Lowne		1	1						
<i>Polyrhachis pilosa</i> Donisthorpe								1	
<i>Rhytidoponera chalybaea</i>	30	31	36	35	↓	9	12	12	6
<i>Rhytidoponera metallica</i>	83	56	33	33	↓	19	13	7	7
<i>Rhytidoponera</i> sp. (<i>convexa</i> gp.)		5	3	5			5	2	3
<i>Rhytidoponera</i> sp. 2 nr. <i>victoriae</i>		6					1		
<i>Rhytidoponera</i> sp. nr. <i>crinata</i>	1								
<i>Solenopsis</i> sp. A	26	13	12	27		13	17	13	31
<i>Stigmacros aciculata</i> McAreavey	11	3		6	↑	34	13	1	23
<i>Stigmacros epinotalis</i>	5		1			7	1	1	2
<i>Stigmacros</i> sp. C (<i>pusilla</i> gp.)						2			
<i>Stigmacros</i> sp. D (<i>pusilla</i> gp.)	1					5	3		1
<i>Stigmacros</i> sp. E (<i>impressa</i> gp.)						1			
<i>Stigmacros</i> sp. F (<i>pusilla</i> gp.)						1			1
<i>Strumigenys emmae</i>	1								1
<i>Tapinoma</i> sp. A (<i>minutum</i> gp.)	4								3
<i>Technomyrmex antonii</i>							1		
<i>Technomyrmex sophiae</i>	1		1	5				1	
<i>Tetramorium turneri</i> Forel	1	4		2					

Table 7.2. Percentage of *Pheidole megacephala* in traps and native ant species richness in infested and uninfested zones near Lake Wabby.

	native zone				<i>P. megacephala</i> zone			
	12-Nov-07	23-Dec-07	13-Apr-08	5-Oct-08	12-Nov-07	23-Dec-07	13-Apr-08	5-Oct-08
Number of traps	84	80	69	66	96	94	107	114
% <i>P. megacephala</i> in traps					63	72	72	64
Native ant species richness	48	33	29	43	49	41	31	47

In the study close to the invasion front, there was a significant difference in the average number of native species between dates ($F = 39.3$, $df = 3$, 523, $p < 0.0001$) and between traps with and without *P. megacephala* ($F = 39.1$, $df = 1$, 41, $p < 0.0001$). The traps with only native ants contained an average of 0.75 more native ant species than the traps containing *P. megacephala*. The interaction of date and *P. megacephala* presence was almost significant ($F = 2.32$, $df = 3$, 523, $p = 0.07$) but there were always more native species in native ant only traps, the difference varying between 0.3 more in December 2007 and 1.2 more in October 2008 (Figure 7.7).

The same trend was observed in the larger spatial scale study (Figure 7.7) although with the reduced power from fewer samples, the average of 3.6 native ant species per trap without *P. megacephala* was not significantly different to the 3.02 native species per trap in the infested zone ($F = 1.11$, $df = 1$, 56, $p = 0.29$).

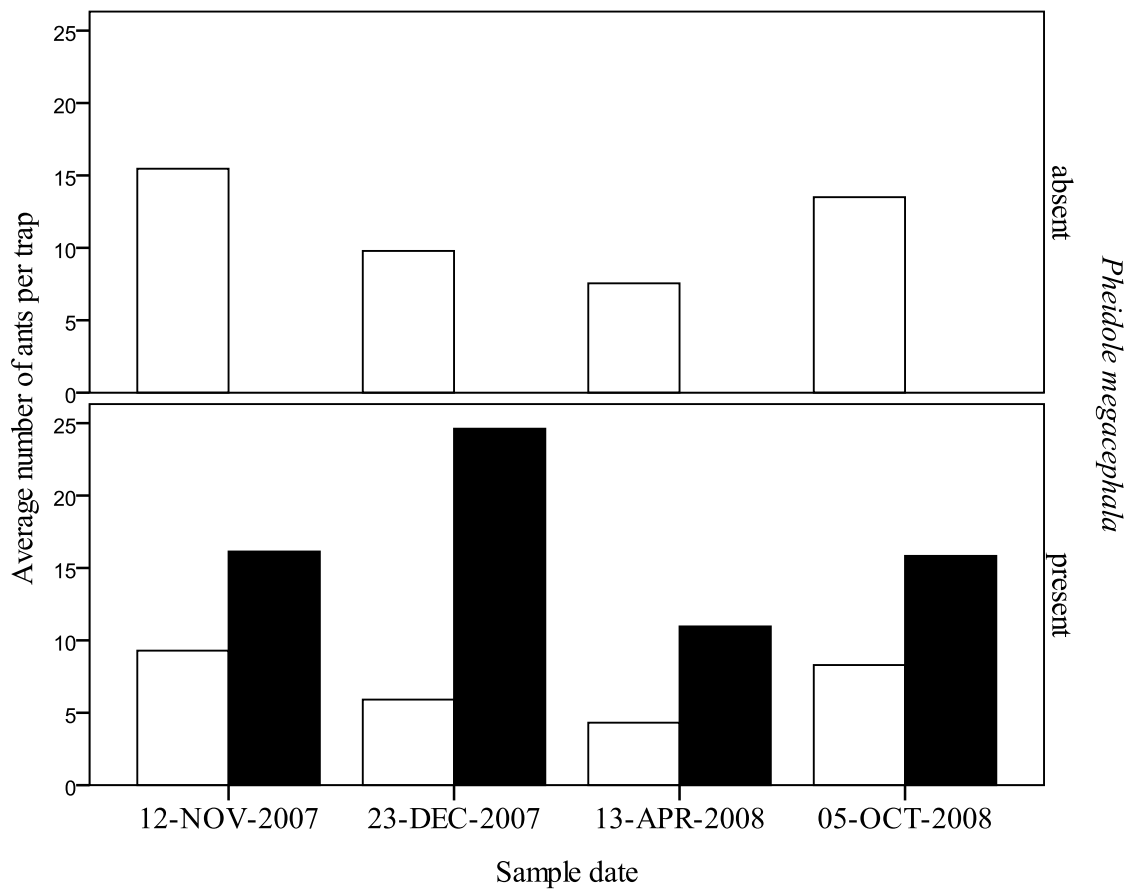


Figure 7.6. Average ant abundances in pitfall traps near Lake Wabby, Fraser Island. The solid bars are *Pheidole megacephala* abundances and the hollow bars are native ant abundances.

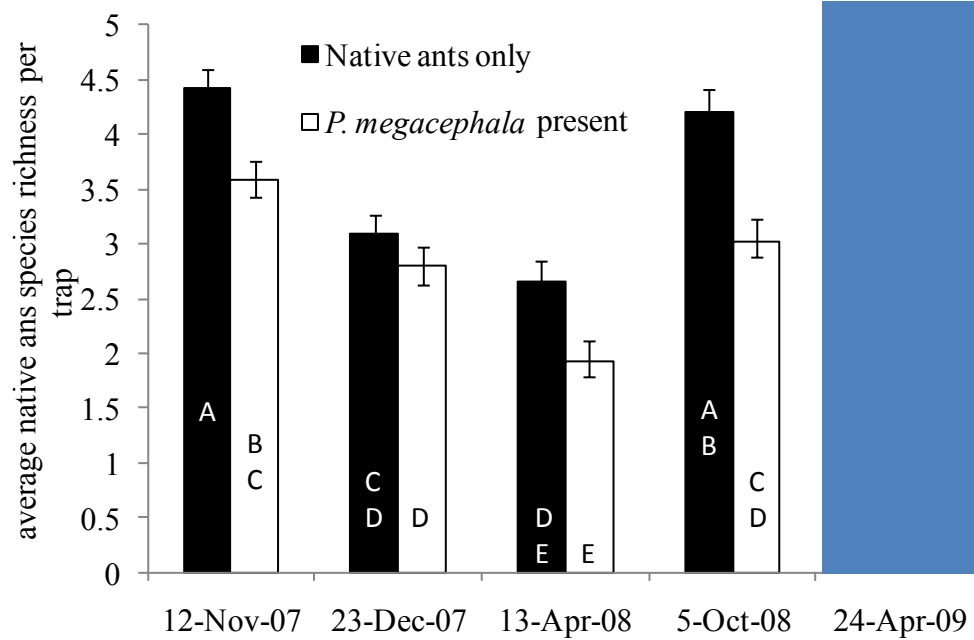


Figure 7.7. Average native ant species richness in pitfall traps near Lake Wabby, Fraser Island. Letters identify Tukey's Honestly Significantly different groups. The samples of 24 April 2009 are taken at a larger spatial scale than the others and are not included in the ANOVA.

Species accumulation curves were generally similar in the number of native ant species in the infested and uninfested zones (Figure 7.8). The curves were almost identical in both zones in the pre-treatment survey and the uninfested zone in the final survey for the study close to the invasion front (Figure 7.8). The two dates where samples were affected by cyclones returned fewer native ant species per pitfall trap in both zones (Figure 7.8). Although there were only 15 and 36 traps used for each zone, the accumulation of species at the larger spatial scale in April 2009 were similar in shape to the other curves.

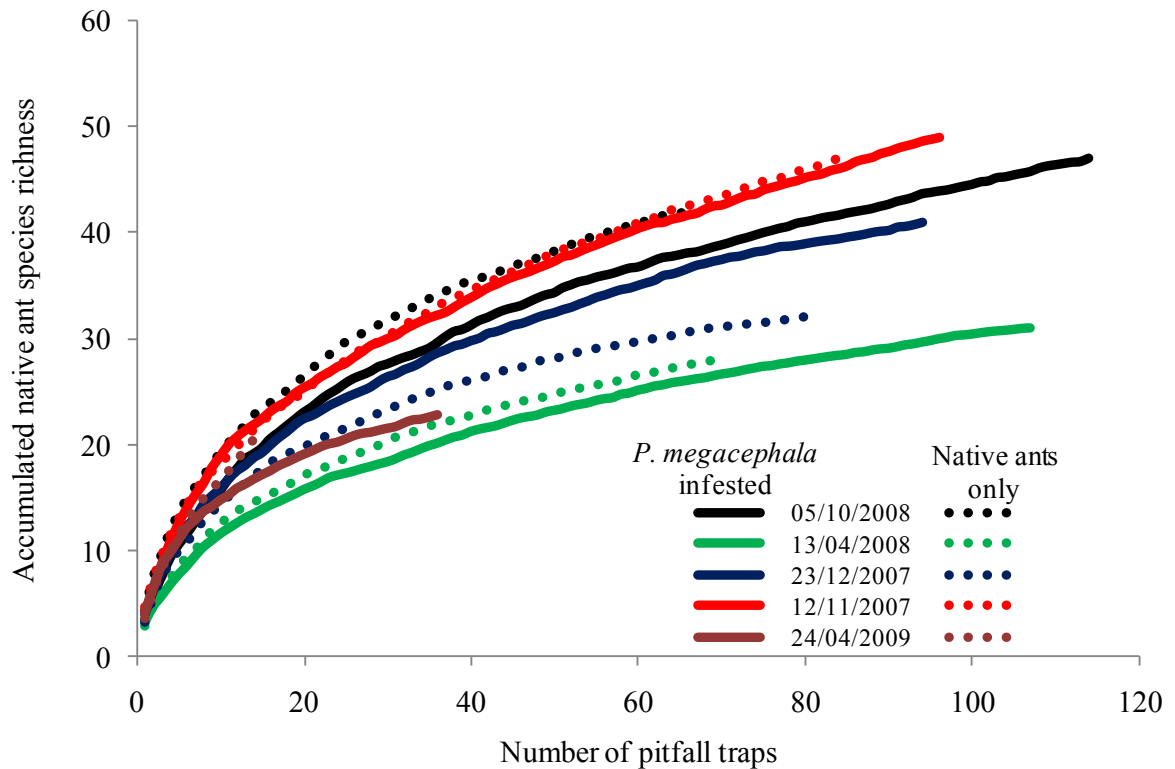


Figure 7.8. Species accumulation curves for native ant species richness in *Pheidole megacephala* infested (solid lines) and uninfested (dotted lines) zones near Lake Wabby.

When the curves were taken to asymptote, there were more native ant species predicted to occur in the *P. megacephala* zone on each sampling date for the study close to the invasion front study (Figure 7.9). The confidence intervals overlap on all dates except the final date where the curves suggest significantly more taxa in the infested zone than the native zone (Figure 7.9). The larger spatial scale study predicted similar numbers of native ant species in traps with *P. megacephala* or traps with only or native ants (Figure 7.9).

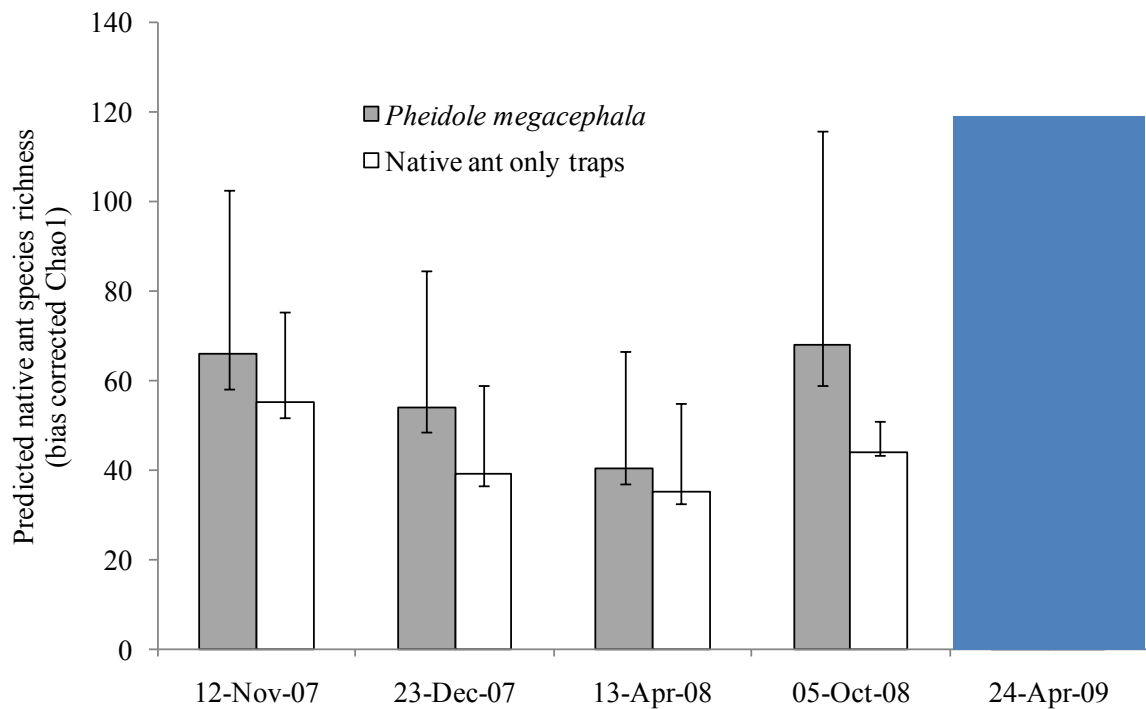


Figure 7.9. Bias-corrected Chao1 predicted (+/- confidence intervals) native ant species richness in *Pheidole megacephala* infested (shaded) and uninfested zones near Lake Wabby. The samples on 24 April 2009 are taken at a larger spatial scale and lower sampling intensity.

Native ant response to arriving or departing P. megacephala at the invasion front

There was no significant difference in the average change in species richness between successive samples regardless of whether *P. megacephala* presence changed or remained the same ($F = 2.06$, $df = 3, 31$, $p = 0.13$). Species richness changes were however significant between sample dates ($F = 24.92$, $df = 2, 31$, $p < 0.0001$), and subsequent analysis showed that the average increase of 1.3 in native species per trap between the 3rd and 4th dates was significantly higher than the decreases of 1.2 and 0.7 between the 1st and 2nd and 2nd and 3rd dates, respectively. There was no interaction effect as all changes in native ant species

richness were consistent within each date for the four combinations of *P. megacephala* treatment (Figure 7.10).

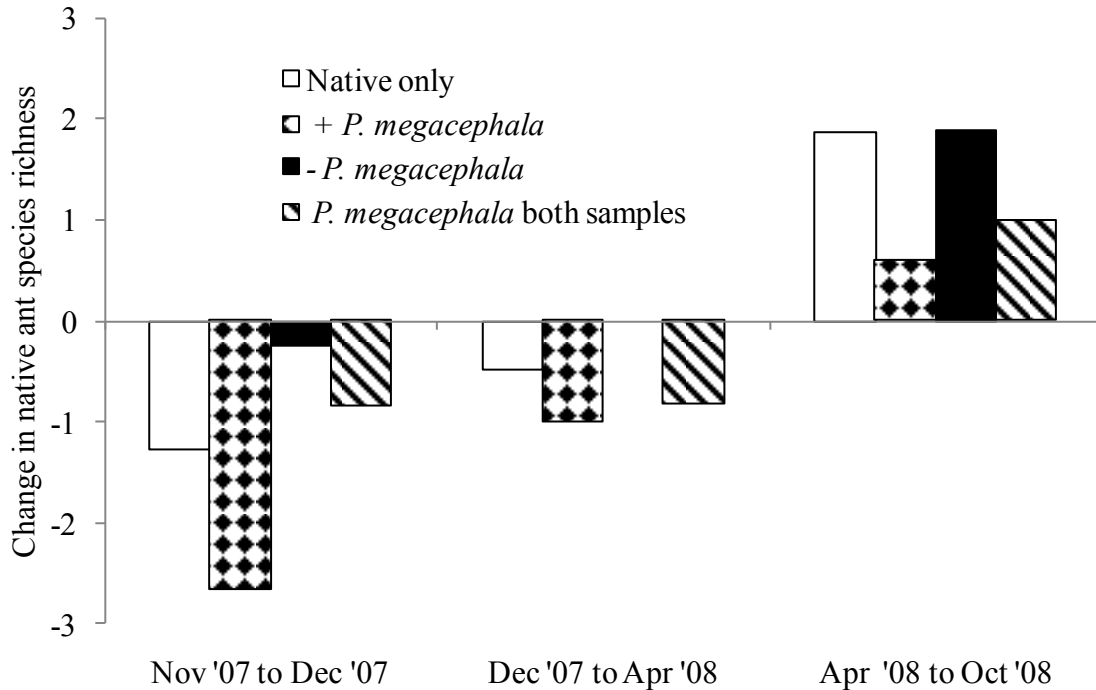


Figure 7.10. Average changes in pitfall trap native ant species richness between successive sample dates and the relationship with the appearance (+), disappearance (-), or presence/absence in successive samples of *Pheidole megacephala*, near Lake Wabby, Fraser Island. Positive values indicate an increase in species richness between samples.

7.4 Discussion

Both treatments had minimal effect. The hydromethylnon was not taken in large quantities and there was no discernible effect of the native ants that were exposed to it (Figures 7.3–7.5). Another misjudgement was made when inspecting the traps after the first sampling and prior to the treatments being applied, as on transect six, *P. megacephala* was noticed in trap 10 and absent in trap 11. This meant the treatment was applied at trap 11, however the invaders were also in traps 12–14 in that transect. Fortunately, this transect was left as a

control and no serious confounding of a treatment occurred. The shading treatment may have had a different effect than intended. Whilst the temperatures under the shade cloths were lower than the adjacent area, the humidity was actually slightly lower as well. This was probably because the shade cloths tended to catch leaf litter, and the ground remained drier as the new artificial 'roof' tended to disperse rain water to the outside of the plot. Hence soil moisture was also affected by the cloth treatment. If the experiment was to be re-attempted, I would trial several methods of native ant control before starting, and I would require the shading treatment to have several more levels, include soil moisture controls (Menke and Holway 2006).

The study results were further limited by the arrival of unexpected (not forecast) cyclones during two of the sampling periods. This may have been a major reason for the lack of significant trends in the analyses for the traps where *P. megacephala* were seen arriving or departing between samples. This is evidenced by the general decrease in the first two periods and increase in the last period for all indicators (Figure 7.10). Another potential limitation is the nature of the sites themselves. One possibility is that the area is heavily naturally disturbed as supported by the high presence of opportunistic species like *Nylanderia 'vaga'*. The site is close to the ocean and heavily buffeted by winds. The canopy is probably occasionally opened up as evidenced by the *Lantana* in some spots. I assumed *Lantana* was evidence of previous human settlement, but there are no records of any dwellings and John Sinclair (Pers. Comm. 2008) suggests *Lantana* was probably just dispersed there by birds.

The number of native ants recorded in the pitfall traps in the invaded zone were surprising, because in the previous 4 years of regular visits using thousands of baits at this site there had

never been a single native ant observed. The native species richness in the infested zone (Table 7.3) is considerably higher than any previously reported in areas invaded by *P. megacephala* in Australia (Table 1.2). This probably highlights a major concern from all the published research being confounded by disturbance. The study site at Lake Wabby is different from the other studies as there is no history of human dwellings or disturbance in the vicinity. The results generally agree with the similar study in the undisturbed habitats near Dill Village (Chapter 5). That is, the abundance and richness of native ants in undisturbed habitats was very similar in traps or areas where *Pheidole megacephala* occur to where it didn't.

The results overwhelmingly support the notion that biotic resistance through diversity of native ants is largely unaffected by the presence of *P. megacephala*. The potential for disruptions to native ant ecosystem functioning roles hasn't been addressed in these sites and warrants further investigation. There is a general perception that the presence of *P. megacephala* results in a suppression of many native ants and subsequently a suppression of the ecosystem services provided by the native ants such as seed dispersal (Hoffmann 1998). But with so many studies occurring in already disturbed habitats, the lack of different guilds of ants is probably of little consequence to those ecosystems. The sites at Lake Wabby and Dilli Village show that, in undisturbed habitats, the native ant biodiversity as represented by abundance and species richness, is largely the same whether *P. megacephala* are present or not. It is the capacity of *P. megacephala* to monopolise resources (see Chapter 6) that could be a problem.

After the data from the study close to the invasion front were collated there was disbelief at the number of native ant species recorded. The additional survey in April 2009 was carried

out because there was a perception that the initial samples may have been so close to the invasion front that they were sampling native ants that were foraging in the invaded zone when *P. megacephala* were inactive. However, the consistency of the results from the larger spatial scale support the initial findings of very high native ant abundance and species richness in the infested zone. The size of this infestation is very large (at least several hectares) and it can be presumed that the area sampled in this larger scale study has had *P. megacephala* for several decades.

Aphaenogaster longiceps and *Pheidole megacephala* appear to be mutually exclusive. *A. longiceps* is the most widespread and abundant native ant species on Fraser Island (Chapter 2) but it is rarely seen in traps with *P. megacephala* (Chapter 3, Chapter 5, Table 7.3). Even when it occurs in the area adjacent to the infestation *A. longiceps* are extremely abundant. *A. longiceps* are unlikely to be competitive in interactions with *P. megacephala* (Alan Andersen, pers. comm.) but it may be a general indicator of some other factor such as lack of disturbance. If the two species did co-occur there would be interest in competitive interactions between the two because both are voracious seed harvesters (W Robinson unpub.data).

Future research may follow up on whether of the ecosystem services provided by ants are different between the native ant and *P. megacephala* infested areas. Because they are known to monopolise resources, *P. megacephala* may be able to disrupt seed dispersal by native ants. *P. megacephala* have also been associated with large outbreaks of scale insects and these outbreaks can be associated with vegetation damage from sooty mould outbreaks (Dejean and Matile Ferrero 1996). However, most scale insect studies are in agricultural landscapes and there is also no statistical evidence to determine whether *P. megacephala* are

the cause or the effect in scale outbreaks anyway. So, sound experiments that look at ecosystem services such as scale tendering and seed dispersal really are required before statements about the impact of *P. megacephala* in native vegetation on Fraser Island can be made.

7.5 Conclusions

- *The influence of biotic resistance and temperature and humidity on the boundaries of a P. megacephala infestation were investigated.*
- *The occurrence of the cyclones and the lack of efficacy of the treatments disrupted the experiment and the results are yet another post-invasion survey, but has more value than most studies because of repeat visits.*
- *The P. megacephala infestation near Lake Wabby is large and advanced considerably during this study.*
- *There was very high native ant abundance and species richness even though P. megacephala were numerically dominant.*
- *At this stage there was no evidence to support the suggestion that P. megacephala are a threat to native ant ecosystem services in undisturbed native vegetation on Fraser Island.*
- *Further experiments that look at how Pheidole megacephala invasions affect ecosystem services such as tendering scale and viability and dispersing of seeds are required.*

8 Conclusions

8.1 Thesis summary of key findings

This thesis identified a need for knowledge on the terrestrial invertebrate biodiversity on Fraser Island and potential threats to that biodiversity. The importance and suitability of ants for advancing biodiversity knowledge for Fraser Island was documented in a literature review which also highlighted the potential threats to biodiversity provided by tramp ant species.

The thesis provides the first known comprehensive ant species list for Fraser Island, with special emphasis on epigaeic species. The taxa were compared to other relevant regional faunas including the Noosa–Cooloola region (Greenslade and Thompson 1981) and North Stradbroke Island (Majer 1985a). The average of 3 species per genera across the whole island was much higher than any neighbouring regional faunas, but within individual vegetation types, there were fewer species collected per genera than Majer's (1985a) study on North Stradbroke Island. Fraser Island has a rich in ant fauna with the diversity predicted to approach 300 species, as recorded in the nearby Cooloola-Noosa region by Greenslade and Thompson (1981). In contrast with the Cooloola-Noosa fauna, which has more areas of drier habitats (Greenslade and Thompson 1981), the Fraser Island fauna was characterised by low relative species richness, frequency of occurrence and abundance of Eyrean biogeographic and Dominant Dolichoderinae functional groups. The low relative abundance of these dominant taxa identified that the Fraser Island ant biodiversity values could be vulnerable to invasions from introduced ant species.

The relationship between native ant biodiversity and two introduced ant species, *Pheidole megacephala* and *Paratrechina longicornis* were examined around Kingfisher Bay Resort and Village (KBRV). The results documented that raw species richness is not a good indicator to use when assessing impacts of ant invasions, with species turnover identified as a sounder technique because it is unbiased and was used throughout the remainder of the thesis. In zones where *P. longicornis* were numerically abundant and locally dominant, native ant species richness was high but species turnover was lower than in a nearby native ant zone. The dominance of *P. longicornis* supported previous published research showing their dominance in other areas with naturally low numbers of aggressive native taxa (Farnsworth 1993, Meier 1994, Wetterer et al. 1999). *P. megacephala* was also associated with very low native ant abundances, richness and species turnover at KBRV. However, given that many previous studies had identified disturbance as a key factor in *P. megacephala* infestations (e.g. Majer 1985; Heterick 1997; Hoffmann 1998; Heterick et al. 2000), and in reducing native species richness (e.g. Burbidge et al. 1992, Andersen and Morrison 1998, Hoffmann and Andersen 2003), a clear need to understand the role of disturbance in *P. megacephala* infestations and their impacts was identified.

The role of disturbance in boundary changes of a *P. megacephala* infestation was investigated at Dilli Village, where annual surveys were carried out for periods of up to 5 years. The 5-year data set allowed for interpretations of the influence of several disturbances on the extent of the infestation boundaries and confirmed the added value of longitudinal studies compared to snap shot studies (e.g. Sanders et al. 2001, Hoffmann and Parr 2008). The effects of mechanical clearing of vegetation had varying effects on the infestation, with a significant boundary expansion then contraction along a cleared walking

path that was allowed to regrow. Yet there was a significant expansion then stabilization of the infestation along a cleared and regularly managed linear fire break, but another managed firebreak saw no change in the infestation boundary. It was confirmed that *P. megacephala* nest close to the surface (Broekhuysen 1948), and that ants were vulnerable to desiccation (Greenslade 1971, Majer 1985b, Hoffmann et al. 1999) as evidenced by range contractions after fires that reduced vegetation cover. However, there was preliminary evidence of rapid invasion by *P. megacephala* from edge populations following fires, a similar finding to (Reimer and Beardsley Jr 1990). This was predicted to be because the fires also reduced native ant biotic resistance, as fires in Australian ecosystems usually favour Dominant Dolichoderinae (Andersen 1991, Collett 1998, York 2000), which are uncommon of Fraser Island.

A complementary longitudinal study that surveyed epigeic ants over 5 years at Dilli Village found considerably higher native ant abundances and species richness within a *P. megacephala* infested area than any previously published research (Majer 1985a, Heterick 1997, Hoffmann 1998, Hoffmann and Hohenhaus 1998, Hoffmann et al. 1999, Heterick et al. 2000, May and Heterick 2000, Vanderwoude et al. 2000, Hoffmann and Parr 2008, Callan and Majer 2009, Hoffmann 2009). Strikingly, there was a very rich native ant turnover in the infested area at Dilli Village, with 65 native ants species being caught in the area infested with *P. megacephala*. Only one other study, also longitudinal, in Madeira, has found no difference in native ant biodiversity indicators between *P. megacephala* infested and uninfested areas (Wetterer et al. 2006). The results from this medium-term longitudinal approach confirmed that results from snapshot studies need to be treated cautiously (Sanders et al. 2001, Holway et al. 2002b) and that biotic resistance defined simply as high native

species richness did not discourage *P. megacephala* invasions. Put simple, when there was no reduced native ant species list pre-invasion, then there was no reduced native ant species list post-invasion. The role of local climatic conditions were identified as a potential limiting factor in the infestation.

A simple experiment at Dilli Village then confirmed that *P. megacephala* foraged around the clock (Broekhuysen 1948, Carnegie 1960, Greenslade 1971) when conditions were suitable. I determined that *P. megacephala* rarely foraged above 40°C or below 20% relative humidity in open areas, but exceeded these limits in native vegetation areas. *Iridomyrmex bicknelli*, *Monomorium sydneyense* and *Nylanderia vaga* were regularly observed at the bait stations but partitioned foraging to avoid *P. megacephala*.

The cumulative knowledge from the above results equated to the need to investigate the combined role of biotic resistance, environmental conditions and the impacts of native ants on *P. megacephala* invasions and vice versa. The invasive ant literature suffers heavily from lack of experiments with most research being performed post invasion (Holway et al. 2002b) and true cause and effect difficult to identify. In particular, all of the published research on *P. megacephala* invasions are confounded by disturbance. Hence, and a field experiment in an undisturbed areas was set up in an attempt to elucidate the relative importance of the above factors affecting *P. megacephala* infestation effects.

The occurrence of cyclones and a lack of efficacy of the treatments disrupted the experiment, however the findings strongly supported the earlier key findings in this thesis from Dilli Village, viz; very high native ant abundance and species richness and turnover even though *P. megacephala* were numerically dominant. Native ant assemblages in

undisturbed areas that are invaded by *P. megacephala* are on Fraser Island are species rich and similar in composition to uninvaded areas. The thesis identified that whilst native ant compositions varied little in undisturbed areas whether invaded by *P. megacephala* or not, the ability of the invader to monopolise resources could have serious consequences. That is, the ecosystem services provided by native ants may be compromised by *P. megacephala* invasions (Hoffmann 1998, Hoffmann and Hohenhaus 1998, Hoffmann et al. 1999) and further investigations into ecosystems services on Fraser Island should be considered.

8.2 Knowledge advanced by this thesis

This thesis presents the first comprehensive species list of ants occurring in Fraser Island and documents the Torresian biogeographic of the majority of the islands ant fauna.

The thesis documents that the scale of sampling and method used for delineating invasive ant species boundaries affect the measures used to describe the impact, and that native ant species turnover is the best unbiased indicator for comparing invaded and uninvaded zones.

The thesis confirmed that *Pheidole megacephala* infestations are associated with low native species turnover in disturbed habitats on Fraser Island. It showed that responses in *P. megacephala* infestation boundaries to various disturbances are variable, and probably related to one or more of; micro climate, native ant biotic resistance, proximity to other infestations and long-term climate change.

The thesis provides tolerances to temperature and humidity for *P. megacephala* foragers and reports on active foraging 24 hours a day when micro climatic conditions are favourable. It

documents temporal partitioning of foraging on a food resource by native ants, demonstrating avoidance of competitive interactions of several native species with *P. megacephala*.

The thesis documented that in undisturbed habitats on Fraser Island, there was little discernible difference in native ant species richness, species turnover, or abundance between *P. megacephala* infested or uninfested areas. This results is contrary to all previously published studies on this species and demonstrates two fundamental aspects that can improve future research. 1) well-designed experiments and/or long-term studies have considerable advantage over post-hoc or snapshot type studies, and 2) The role of disturbance must be taken into account when investigating the impacts of invasive ant infestations.

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This project spanned several years and involved hundreds of people at various stages and I could fill pages listing all those involved in one way or another. It would be unfair of not to single out a couple of people without whom the thesis simply would not exist. Peter Collier and Melinda McNaught made outstanding contributions, racking up hundreds of hours in the field, often working without my presence. They both also spent hundreds of hours sorting ants from pitfalls samples as did Tanja Windegger, Rhys Smith and Emily Rigby. The data collected in March 2004 was used by Peter Collier in his Honour's thesis (Collier 2004) on which I was the primary supervisor.

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In the interest of brevity I will attempt to list other people and organisations to make significant contributions in no particular order and apologise to those I may have overlooked.

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References

- Andersen, A. N. 1986. Diversity, seasonality and community organisation of ants at adjacent heath and woodland sites in southeastern Australia. *Australian Journal of Zoology* **34**:53 - 64.
- Andersen, A. N. 1990. The use of ant communities to evaluate change in Australian terrestrial ecosystems: a review and a recipe. *Proceedings of the Ecological Society of Australia* **16**:347 - 357.
- Andersen, A. N. 1991. Responses of ground-foraging ant communities to three experimental fire regimes in a savanna forest of tropical Australia. *Biotropica* **23**:575 - 585.
- Andersen, A. N. 1993. Ants as indicators of restoration success at a uranium mine in tropical Australia. *Restor. Ecol.* **1**:156 - 167.
- Andersen, A. N. 1995. A classification of Australian ant communities, based on functional groups which parallel plant life-forms in relation to stress and disturbance. *Journal of Biogeography* **22**:15 - 29.
- Andersen, A. N. 1997. Functional groups and patterns of organization in North American ant communities: a comparison with Australia. *Journal of Biogeography* **24**:433 - 460.
- Andersen, A. N. 2000. *The ants of northern Australia: a guide to the monsoonal fauna.* CSIRO, Collingwood.
- Andersen, A. N. and A. Brault. 2010. Exploring a new biodiversity frontier: subterranean ants in northern Australia. *Biodiversity and Conservation* **19**:2741 - 2750.
- Andersen, A. N., A. Fisher, B. D. Hoffmann, J. L. Read, and R. Richards. 2004. Use of terrestrial invertebrates for biodiversity monitoring in Australian rangelands, with particular reference to ants. *Austral Ecology* **29**:87 - 92.
- Andersen, A. N., B. D. Hoffmann, W. J. Muller, and A. D. Griffiths. 2002. Using ants as bioindicators in land management: simplifying assessment of ant community responses. *Journal of Applied Ecology* **39**:8 - 17.
- Andersen, A. N. and S. C. Morrison. 1998. Myrmecochory in Australia's seasonal tropics - effects of disturbance on distance dispersal. *Aust. J. Ecol.* **23**:483 - 491.
- Andersen, A. N. and A. D. Patel. 1994. Meat ants as dominant members of Australian ant communities: an experimental test of their influence on the foraging success and forager abundance of other species. *Oecologia* **98**:15 - 24.

- Andersen, A. N., T. D. Penman, N. Debas, and M. Houadria. 2009. Ant community responses to experimental fire and logging in a eucalupt forest of south-eastern Australia. *Forest Ecology and Management* **258**:188 - 197.
- Andersen, A. N., L. T. van Ingen, and R. I. Campos. 2007. Contrasting rainforest and savanna ant faunas in monsoonal northern Australia: a rainforest patch in a tropical savanna landscape. *Australian Journal of Zoology* **55**:363 - 369.
- Arnan, X., C. Gaucherel, and A. N. Andersen. 2011. Dominance and species co-occurrence in highly diverse ant communities: a test of the interstitial hypothesis and discovery of a three-tiered competition cascade. *Oecologia* **166**:783 - 794.
- Auld, T. D. 1999. The role of ants and mammals in dispersal and post-dispersal seed predation of the shrubs *Grevillea* (Proteaceae). *Plant Ecology* **144**:201 - 213.
- Banks, W. A. and D. F. Williams. 1989. Competitive displacement of *Paratrechina longicornis* (Latreille) (Hymenoptera Formicidae) from baits by fire ants in Mato Grosso Brazil. *Journal of Entomological Science* **24**:381 - 391.
- Baskin, Y. 2002. A plague of rats and rubber vines. Island Press, Washington.
- Belbin, L. 1989. PATN Technical Reference. CSIRO Division of Wildlife and Ecology, P.O. Box 84, Lyneham, ACT, 2602. 167p.
- Bestelmeyer, B. T., Agosti, D., Alonso, L. E., et al. 2000. Field techniques for the study of Ground-Dwelling Ants: An Overview, Description, and Evaluation. Pages 122-144 in D. Agosti, Majer, J. D., Alonso, L. E., Schultz, T. R., editor. *Ants: Standard methods for measuring and monitoring biodiversity*. Smithsonian Institution Press, Washington DC.
- Brandao, R. F. and R. V. S. Paiva. 1994. The Galapagos ant fauna and the attributes of colonizing ant species. Pages 1 - 10 in D. F. W. Williams, editor. *Exotic Ants: Biology, Impact, and Control of Introduced species*. Westview Press, San Francisco.
- Broekhuysen, G. J. 1948. The Brown house ant (*Pheidole megacephala*, Fabr.) in South Africa. Union of South Africa, Department of Agriculture Bulletin **266**:1 - 40.
- Burbidge, A. H., K. Leicester, S. McDavitt, and J. D. Majer. 1992. Ants as indicators of disturbance at Yanchep National Park, Western Australia. *Journal of the Royal Society of Western Australia* **75**:89 - 95.
- Byers, J. E., S. Reichard, J. M. Randall, I. M. Parker, C. S. Smith, W. M. Lonsdale, I. A. E. Atkinson, T. R. Seastedt, M. Williamson, E. Chornesky, and D. Hayes. 2002. Directing research to reduce the impacts of nonindigenous species. *Conservation Biology* **16**:630 - 640.

- Callan, S. and J. Majer. 2009. Impacts of an invasion of African big-headed ants, *Pheidole megacephala* (Fabricus), in urban bushland in Perth, Western Australia. *Pacific Conservation Biology* **15**:102-115.
- Carnegie, A. J. M. 1960. Effects of temperature variations on the activities of the Brown house Ant, *Pheidole megacephala* F. race *punctulata* Mayr. (Hymenopt.: Formicidae). *The Journal of the Entomological Society of Southern Africa* **23**:304 - 311.
- Chao, A. 1984. Non-parametric estimation of the number of classes in a population. *Scandinavian Journal of Statistics* **11**:265 - 270.
- Chao, A. 1987. Estimating the population size for capture-recapture data with unequal catchability. *Biometrics* **43**:783 - 791.
- Churchill, T. 2007. Exploring Brisbane's invertebrates. Page 12. Brisbane City Council, Brisbane.
- Coddington, J. A., I. Agnarsson, J. A. Miller, M. z. Kuntner, and G. Hormiga. 2009. Undersampling bias: the null hypothesis for singleton species in tropical arthropod surveys. *Journal of Animal Ecology* **78**:573 - 584.
- Collett, N., G. 1998. Effects of two short rotation prescribed fires in autumn on surface-active arthropods in dry sclerophyll eucalypt forests of west-central Victoria. *Forest Ecology & Management* **107**:253 - 273.
- Collier, P. 2004. Myrmecofauna of Fraser Island. honours. Honours thesis, University of the Sunshine Coast.
- Collingwood, C. A., B. J. Tigar, and D. Agosti. 1997. Introduced ants in the United Arab Emirates. *Journal of Arid Environments* **37**:505 - 512.
- Colwell, R. K. 2009. EstimateS: Statistical estimation of species richness and shared species from samples. Version 8.2. User's Guide and application. Persistent URL <purl.oclc.org/estimates>.
- Colwell, R. K., C. X. Mao, and J. Chang. 2004. Interpolating, extrapolating, and comparing incidence-based species accumulation curves. *ecology* **85**:2717 - 2727.
- Cook, J. L. 2003. Conservation of biodiversity in an area impacted by the red imported fire ant, *Solenopsis invicta* (Hymenoptera: Formicidae). *Biodiversity and Conservation* **12**:187 - 195.
- Craig, J. P. 1985. Forestry Fraser Island [3 sheets].in Queensland Department of Forestry, editor. Department of Forestry, Brisbane.

- Dejean, A. and D. Matile Ferrero. 1996. How a ground-dwelling forest ant species favors the proliferation of an endemic scale insect (Hymenoptera: Formicidae; Homoptera: Stictococcidae). *Sociobiology* **28**:183-195.
- Delabie, J. H. C., I. C. Do Nascimento, P. Pacheco, and A. B. Casimiro. 1995. Community structure of house-infesting ants (Hymenoptera: Formicidae) in Southern Bahia, Brazil. *Florida Entomologist* **78**:264-270.
- Delabie, J. H. C., B. L. Fisher, J. D. Majer, and I. W. Wright. 2000. Sampling effort and choice of methods. *in* D. Agosti, J. D. Majer, L. E. Alonso, and T. R. Schultz, editors. *Ants: Standard methods for measuring biodiversity*. Smithsonian Institution, Washington.
- DiGirolamo, L. A. and L. R. Fox. 2006. The influence of abiotic factors and temporal variation on local invasion patterns of the Argentine ant (*Linepithema humile*). *Biol. Invasions* **8**:125 - 135.
- Dorazio, R. M., A. J. Royle, B. Soderstrom, and A. Glimskar. 2006. Estimating species richness and accumulation by modelling species occurrence and detectability. *ecology* **4**:842 - 854.
- Eldridge, D. J. and C. A. Myers. 1998. Enhancement of soil nutrients around nest entrances of the funnel ant *Aphaenogaster barbigula* (Myrmicinae) in semi-arid eastern Australia. *Australian Journal of Soil Research* **36**:1009 -1017.
- Elton, C. S. 1958. *The Ecology of Invasions*. Wiley, New York.
- EPA. 2005. Great Sandy Region: Management plan 1994-2010. Page 124 *in* QPWS, editor. *The State of Queensland*.
- Farnsworth, E. 1993. Interactions between *Cecropia peltata* L. (Moraceae) and *Paratrechina longicornis* (Latrielle) (Formicidae) at a Sinkhole in the Guanica Dry Forest, Puerto Rico. *Caribbean Journal of Science* **29**:124-125.
- Fernández-Escudero, I. and A. Tinaut. 1999. Factors determining nest distribution in the high-mountain ant *Proformica longiseta* (Hymenoptera: Formicidae). *Ethology Ecology & Evolution* **11**:325 - 338.
- Fisher, B. L. 1999. Improving inventory efficiency: A case study of leaf-litter ant diversity in Madagascar. *Ecological Applications* **9**:714 - 731.
- Folgarait, P. J. 1998. Ant biodiversity and its relationship to ecosystem functioning: a review. *Biodiversity and Conservation* **7**:1221 - 1244.
- Fowler, H. G., M. N. Schlindwein, and M. A. de Medeiros. 1994. Exotic ants and community simplification in Brazil: a review of the impact of exotic ants on native ant assemblages. Pages 151-162 *in* D. F. W. Williams, editor. *Exotic Ants: Biology, Impacts, and Control of Introduced Species*. Westview Press, San Francisco.

- Gibb, H. and D. F. Hochuli. 2003. Colonisation by a dominant ant facilitated by anthropogenic disturbance: effects on ant assemblage composition, biomass and resource use. *Oikos* **103**:469 - 478.
- Gillespie, R. G. and N. J. Reimer. 1993. The effect of alien predatory ants (Hymenoptera: Formicidae) on Hawaiian endemic spiders (Araneae: Tetragnathidae). *Pacific Science* **47**:21 - 33.
- Gotelli, N. J. 1996. Ant community structure: effects of predatory ant lions. *ecology* **77**:630 - 638.
- Greenslade, P. J. M. 1971. Interspecific competition and frequency changes among ants in Solomon Islands coconut plantations. *Journal of Applied Ecology* **8**:232 - 352.
- Greenslade, P. J. M. 1972. Comparative ecology of four tropical ant species. *Insectes Sociaux* **19**:195 - 212.
- Greenslade, P. J. M. 1973. Sampling ants with pitfall traps: Digging-in effects. *Insectes Sociaux* **20**:343 - 353.
- Greenslade, P. J. M. and C. H. Thompson. 1981. Ant distribution, vegetation, and soil relationships in the Cooloola-Noosa River area, Queensland. Pages 192 - 207 in A. N. Gillison, Anderson, D. J, editor. *Vegetation Classification in Australia*. CSIRO and ANU Press, Canberra.
- Groden, E., F. A. Drummond, J. Garnas, and A. Franceour. 2005. Distribution of an Invasive Ant, *Myrmica rubra* (Hymenoptera: Formicidae), in Maine. *Journal of Economic Entomology* **98**:1774 - 1784.
- Haines, I. H., J. B. Haines, and J. M. Cherrett. 1994. The impact and control of the Crazy ant, *Anoplepis longipes* (Jerd.), in the Seychelles. Pages 206 - 218 in D. F. W. Williams, editor. *Exotic Ants: Biology, Impacts, and Control of Introduced Species*. Westview Press, San Francisco.
- Haskins, C. P. and E. F. Haskins. 1965. *Pheidole megacephala* and *Iridomyrmex humilis* in Bermuda: equilibrium or slow replacement? *ecology* **46**:736 - 740.
- Heterick, B. E. 1997. The interaction between the Coastal brown ant, *Pheidole megacephala* (Fabricus), and other invertebrate fauna of Mt Coot-tha (Brisbane, Australia). *Aust. J. Ecol.* **22**:218 - 221.
- Heterick, B. E., J. Casella, and J. D. Majer. 2000. Influence of Argentine and Coastal brown ant (Hymenoptera: Formicidae) invasions on ant communities in Perth gardens, Western Australia. *Urban Ecosystems* **4**:277 - 292.
- Hinkley, S. and T. R. New. 1997. Pitfall trapping for surveying ant assemblages: lessons from a study at Mount Piper, Victoria. *Memoirs of the Museum of Victoria* **56**:369 - 376.

- Hoffmann, B. D. 1998. The Big headed ant *Pheidole megacephala*: a new threat to monsoonal northwestern Australia. *Pacific Conservation Biology* **4**:250 - 255.
- Hoffmann, B. D. 2004. Exotic ants threaten indigenous lands. Pages 26 - 28 *Australasian Science*.
- Hoffmann, B. D. 2009. Ecological restoration following the local eradication of an invasive ant in northern Australia. *Biol. Invasions on line*: .
- Hoffmann, B. D. and A. N. Andersen. 2003. Responses of ants to disturbance in Australia, with particular reference to functional groups. *Austral Ecology* **28**:444 - 464.
- Hoffmann, B. D., A. N. Andersen, and G. J. E. Hill. 1999. Impact of an introduced ant on native rain forest invertebrates: *Pheidole megacephala* in monsoonal Australia. *Oecologia* **120**:595 - 604.
- Hoffmann, B. D., A. D. Griffiths, and A. N. Andersen. 2000. Responses of ant communities to dry sulfur deposition from mining emissions in semi-arid tropical Australia, with implications for the use of functional groups. *Austral Ecology* **25**:653 - 663.
- Hoffmann, B. D. and R. N. Hohenhaus. 1998. Big-headed ants: tiny marauder threatens northern ecosystems. *Wildlife Australia Winter*:13 - 16.
- Hoffmann, B. D. and S. O'Connor. 2004. Eradication of two exotic ants from Kakadu National Park. *Ecological Management and Restoration* **5**:98 - 105.
- Hoffmann, B. D. and C. L. Parr. 2008. An invasion revisited: the African big-headed ant in northern Australia. *Biol. Invasions* **10**:1171 - 1181.
- Hölldobler, B. and E. O. Wilson. 1990. *The Ants*. Bellknapp Press, Cambridge, Massachusetts.
- Hölldobler, B. and E. O. Wilson. 1994. *Journey to the ants: a story of scientific exploration*. Harvard University Press, Cambridge, Massachusetts.
- Holway, D. A. 1998a. Effect of Argentine ant invasions on ground-dwelling arthropods in Northern California riparian woodlands. *Oecologia* **116**:252 - 258.
- Holway, D. A. 1998b. Factors governing rate of invasion: a natural experiment using Argentine ants. *Oecologia* **115**:206 - 212.
- Holway, D. A. 2005. Edge effects of an invasive species across a natural boundary. *Biological Conservation* **121**:561 - 567.
- Holway, D. A. and T. J. Case. 2001. Effects of colony-level variation on competitive ability in the invasive Argentine ant. *Animal Behaviour* **61**:1181 - 1192.

- Holway, D. A., L. Lach, A. V. Suarez, N. D. Tsutsui, and T. J. Case. 2002a. The causes and consequences of ant invasions. *Annual Review Of Ecology and Systematics* **33**:181 - 233.
- Holway, D. A., A. V. Suarez, and T. J. Case. 1998. Loss of intraspecific aggression in the success of a widespread invasive social insect. *Science* **282**:949 - 952.
- Holway, D. A., A. V. Suarez, and T. J. Case. 2002b. Role of abiotic factors in governing susceptibility to invasion: a test with Argentine ants. *ecology* **83**:1610 - 1619.
- Human, K. G., S. Weiss, A. Weiss, B. Sandler, and D. M. Gordon. 1998. Effects of abiotic factors on the distribution and activity of the invasive Argentine ant (Hymenoptera: Formicidae). *Environmental Entomology* **27**:822 - 833.
- Illingworth, J. F. 1935. *Pheidole megacephala* (Fabr.). *Proceedings of the Hawaiian Entomological Society* **9**:3.
- Jaffe, K. and J. Lattke. 1994. Ant fauna of the French and Venezuelan islands in the Caribbean. Pages 181 - 190 *in* D. F. W. Williams, editor. *Exotic Ants: Biology, Impacts, and Control of Introduced Species*. Westview Press, San Francisco.
- Jahn, G. C. and J. W. Beardsley. 1994. Big-headed ants, *Pheidole megacephala*: interference with the biological control of gray pineapple mealybugs. *in* D. F. W. Williams, editor. *Exotic ants: biology, impacts, and control of introduced species*. Westview Press, San Francisco.
- Johnson, R. A. 2001. Biogeography and community structure of North American Seed-harvester ants. *Annual Review of Entomology* **46**:1 - 29.
- Jones, C. G., J. H. Lawton, and M. Shachak. 1994. Organisms as ecosystems engineers. *Oikos* **69**:373 - 386.
- Kaspari, M. 2000. Do imported fire ants impact canopy arthropods? Evidence from simple arboreal pitfall traps. *The Southwestern Naturalist* **45**:118 - 122.
- KBRV. 2009. *EnvironmentalHistory.doc*. Page Fact file: Resort Environmental History. KingfisherBay.com.
- King, J. R., A. N. Andersen, and A. D. Cutter. 1998. Ants as bioindicators of habitat disturbance: validation of the functional group model for Australia's humid tropics. *Biodiversity and Conservation* **7**:1627 - 1638.
- Krushelnycky, P. D., S. M. Joe, A. C. Medeiros, C. C. Daehler, and L. L. Loope. 2005. The role of abiotic conditions in shaping the long-term patterns of a high-elevation Argentine ant invasion. *Diversity and Distributions* **11**:319 - 331.

- Krushelnycky, P. D., L. L. Loope, and S. M. Joe. 2004. Limiting spread of a unicolonial invasive insect and characterization of seasonal patterns of range expansion. *Biol. Invasions* **6**:47 - 57.
- Lafleur, B., L. M. Hooper-Bùi, M. E. P., and J. P. Geaghan. 2005. Soil fertility and plant growth in soils from pine forests and plantations: Effect of invasive red imported fire ants *Solenopsis invicta* (Buren). *Pedobiologia* **in press**.
- Le Breton, J., J. Chazeau, and H. Jourdan. 2003. Immediate impacts of invasion by *Wasmannia auropunctata* (Hymenoptera: Formicidae) on native litter ant fauna in a New Caledonian rainforest. *Austral Ecology* **28**:204 - 209.
- Liang, K. Y. and S. L. Zeger. 1986. Longitudinal data analysis using generalized linear models. *biometrika* **73**:13 – 22.
- Lobry de Bruyn, L. A. 1999. Ants as bioindicators of soil function in rural environments. *Agriculture, Ecosystems and Environment* **74**:425 - 441.
- Lodge, D. M. 1993. Biological invasions: lessons for ecology. *Trends in Ecology & Evolution* **8**:133 - 137.
- MacMahon, J. A., J. F. Mull, and T. O. Crist. 2003. Harvester ants (*Pogonomyrmex* spp.): their community and ecosystem influences. *Annual Review of Ecology and Systematics* **31**:265 - 291.
- Majer, J. D. 1985a. Recolonization 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. 1985b. Seasonality of ants (Formicidae) in South-Western Australia. Pages 23 - 26 *in* P. Greenslade and J. D. Majer, editors. *Soil and Litter invertebrates of Australian mediterranean-type ecosystems*. Western Australian Institute of Technology, Perth.
- Majer, J. D. 1994. Spread of Argentine ants (*Linepithema humile*), with special reference to Western Australia. Pages 163 - 173 *in* D. F. W. Williams, editor. *Exotic ants: biology, impacts, and control of introduced species*. Westview Press, San Francisco.
- Majer, J. D. and A. E. de Kock. 1992. Ant recolonisation of sand mines near Richards Bay, South Africa - An evaluation of progress with rehabilitation. *South African Journal of Science* **88**:31 - 36.
- Majer, J. D., J. H. C. Delabie, and M. R. B. Smith. 1994. Arboreal ant community patterns in Brazilian cocoa farms. *Biotropica* **26**:73 - 83.
- Majer, J. D., S. O. Shattuck, A. N. Andersen, and A. J. Beattie. 2004. Australian ant research: fabulous fauna, functional groups, pharmaceuticals, and the fatherhood. *Australian Journal of Entomology* **43**:235 - 247.

- May, J. E. and B. E. Heterick. 2000. Effects of the Coastal brown ant, *Pheidole megacephala* (Fabricus), on the ant fauna of the Perth metropolitan region, Western Australia. *Pacific Conservation Biology* **6**:81 - 85.
- McGlynn, T. P. 1999a. Non-native ants are smaller than related native ants. *The American Naturalist* **6**:690 - 699.
- McGlynn, T. P. 1999b. The worldwide transfer of ants: geographical distribution and ecological invasions. *Journal of Biogeography* **26**:535 - 548.
- Meier, R. E. 1994. Coexisting patterns and foraging behaviour of introduced and native ants (*Hymenoptera Formicidae*) in the Galapagos Islands (Ecuador). Pages 44 - 62 in D. F. W. Williams, editor. *Exotic ants: biology, impacts, and control of introduced species*. Westview Press, San Francisco.
- Menke, S. B. and D. A. Holway. 2006. Abiotic factors control invasion by Argentine ants at the community scale. *Journal of Animal Ecology* **75**:368 - 376.
- Morrison, L. W. 2000. Mechanisms of interspecific competition among an invasive and two native fire ants. *Oikos* **90**:238 - 252.
- Morrison, L. W. 2002. Long-term impacts of an arthropod-community invasion by the imported fire ant, *Solenopsis invicta*. *ecology* **83**:2337 - 2345.
- Morrison, L. W. and S. D. Porter. 2005. Testing for population-level impacts of introduced *Pseudacteon tricuspis* flies, phorid parasitoids of *Solenopsis invicta* fire ants. *Biological Control* **33**:9 -19.
- Natrass, R. and C. Vanderwoude. 2001. A preliminary investigation of the ecological effects of fire ants (*Solenopsis invicta*) in Brisbane. *Ecological Management and Restoration* **2**:220 - 223.
- Ness, J. H. and J. L. Bronstein. 2004. The effects of invasive ants on prospective ant mutualists. *Biol. Invasions* **6**:445 - 461.
- Nicholls, Z. 2005. The response from two native ant communities to the introduction of the non-native ant *Paratrechina longicornis*. Honours. University of the Sunshine Coast.
- Nikitin, M. I. 1979. Geographical distribution of three species of small ants common in New South Wales. *Australian Entomological Magazine* **5**:101 - 102.
- Nkem, J. N., L. A. L. de Bruyn, C. D. Grant, and N. R. Hulugalle. 2000. The impact of ant bioturbation and foraging activities on surrounding soil properties. *Pedobiologia* **44**:609 - 621.
- Osunkoya, O. O., C. Polo, and A. N. Andersen. 2011. Invasion impacts on biodiversity: responses of ant communities to infestation by cat's claw creeper vine, *Macfadyena unguis-cati* (Bignoniaceae) in subtropical Australia. *Biol. Invasions* **13**.

- Parr, C. L. and S. L. Chown. 2001. Inventory and bioindicator sampling: Testing pitfall and Winkler methods with ants in a South African savanna. *Journal of Insect Conservation* **5**:27 - 36.
- Passera, L. 1994. Characteristics of tramp species. Pages 23 - 43 *in* D. F. W. Williams, editor. *Exotic ants: biology, impacts, and control of introduced species*. Westview Press, San Francisco.
- Peng, R. K., K. Christian, and K. Gibb. 1999. The effect of colony isolation of the predacious ant, *Oecophylla smaragdina* (F.) (Hymenoptera : Formicidae), on protection of cashew plantations from insect pests. *International Journal of Pest Management* **45**:189 - 194.
- Peterson, A. T. and N. A. Slade. 1998. Extrapolating inventory results into biodiversity estimates and the importance of stopping rules. *Diversity and Distributions* **4**:95 - 105.
- Porter, S. D. and D. A. Savigno. 1990. Invasion of polygyne fire ants decimates native ants and disrupts arthropod community. *ecology* **71**:2095 - 2106.
- QPWS. 2005. GREAT SANDY REGION: Management plan 1994 – 2010. *in* EPA, editor. The State of Queensland. ISSN 1037-4698.
- Rao, N. S., G. K. Veeresh, and V. C. A. 1989. Association of Crazy Ant, *Anoplolepis longipes* (Jordan) with different fauna and flora. *Indian Journal of Ecology* **16**:205-208.
- Reichel, H. and A. N. Andersen. 1996. The rainforest ant fauna of Australia's Northern Territory. *Australian Journal of Zoology* **44**:81 - 95.
- Reimer, N., J. W. Beardsley, and J. G. 1990. Pest ants in the Hawaiian islands. *in* R. K. Vander Meer, K. Jaffe, and A. Cedeno, editors. *Applied myrmecology: a world perspective*. Westview Press, Oxford.
- Reimer, N. J. 1994. Distribution and impact of alien ants in vulnerable ecosystems. Pages 11 - 22 *in* D. F. W. Williams, editor. *Exotic ants: biology, impact, and control of introduced species*. Westview Press, San Francisco.
- Reimer, N. J. and J. W. Beardsley Jr. 1990. Effectiveness of hydramethylnon and fenoxycarb for control of Big-headed ant (Hymenoptera: Formicidae), an ant associated with mealybug wilt of pineapple in Hawaii *Journal of Economic Entomology* **83**:74 - 80.
- Samways, M. J., R. Osborn, and F. Carliel. 1997. Effect of a highway on ant (Hymenoptera: Formicidae) species composition and abundance, with a recommendation for roadside verge width. *Biodiversity and Conservation* **6**:903 - 913.

- Sanders, N. J., K. E. Barton, and D. M. Gordon. 2001. Long-term dynamics of the distribution of the invasive Argentine ant, *Linepithema humile*, and native ant taxa in northern California. *Oecologia* **127**:123 - 130.
- Sanders, N. J., N. J. Gotelli, N. E. Heller, and D. M. Gordon. 2003. Community disassembly by an invasive species. *Proceedings of the National Academy of Sciences of the United States of America* **100**:2474 - 2477.
- SAS. 2009. SAS OnlineDoc® 9.2. SAS Institute Inc, Cary, NC.
- Schnell, A. J. and J. M. Dangerfield. 2003. Ant community succession within eucalypt plantations on used pasture and implications for taxonomic sufficiency in biomonitoring. *Austral Ecology* **28**:553 - 565.
- Shattuck, S. O. and P. McMillan. 1998. Revision of the species of the *Iridomyrmex conifer* group (Hymenoptera: Formicidae), with notes on their biology. *Australian Journal of Zoology* **46**:301 - 315.
- Sinclair, J. and R. Morrison. 1990. *Fraser Island and Cooloola*. Weldon Publishing, Sydney.
- Sinclair, J. E. 1997. *Discovering Fraser Island and Cooloola*. Australian Environmental Publications, Gladesville, N.S.W.
- Soares, S. M., J. H. Schoederer, and O. De Souza. 2001. Processes involved in species saturation of ground-dwelling ant communities (Hymenoptera: Formicidae). *Austral Ecology* **26**:187-192.
- Sokal, R. R. and F. J. Rohlf. 1981. *Biometry*. 2nd edition. W. H. Freeman and Company, New York.
- Stanley, M. and W. Robinson. 2007. The relative attractiveness of baits to *Paratrechina longicornis*. *Environmental Entomology* **100**:509 - 516.
- Stiles, J. H. and R. H. Jones. 1998. Distribution of the Red imported fire ant, *Solenopsis invicta*, in road and powerline habitats. *Landscape Ecology* **13**:335 - 346.
- Stokes, M. E., C. S. Davis, and G. G. Koch. 2001. *Categorical data analysis using the SAS system*. SAS Publishing, Cary.
- Suarez, A. V., D. T. Bolger, and T. J. Case. 1998. Effects of fragmentation and invasion of native ant communities in coastal southern California. *ecology* **79**:2041 - 2056.
- Suarez, A. V., D. A. Holway, and T. J. Case. 2001. Patterns of spread in biological invasions dominated by long-distance jump dispersal: insights from Argentine ants. *Proceedings of the National Academy of Sciences of the United States of America* **98**:1095 - 1100.

- Trombulak, S. C. and C. A. Frissell. 2000. Review of ecological effects of roads on terrestrial and aquatic communities. *Conservation Biology* **14**:18 - 30.
- Tryon, H. 1912. The naturalisation of an exotic ant (*Pheidole megacephala*, Fab.). *The Queensland Naturalist* **1**:224 - 229.
- Tsutsui, N. D. and A. V. Suarez. 2003. The colony structure and population biology of invasive ants. *Conservation Biology* **17**:48 - 58.
- van Schagen, J. J., P. R. Davis, and M. A. Widmer. 1994. Ant pests of Western Australia, with particular reference to the Argentine ant (*Linepithema humile*). Pages 174 - 180 in D. F. W. Williams, editor. *Exotic ants: biology, impacts, and control of introduced species*. Westview Press, San Francisco.
- Vanderwoude, C., L. A. Lobry De Bruyn, and A. P. N. House. 2000. Response of an open-forest ant community to invasion by the introduced ant *Pheidole megacephala*. *Austral Ecology* **25**:253 - 259.
- Vasconcelos, H. L., J. M. S. Vihens, and G. J. A. Caliri. 2000. Responses of ants to selective logging of a central Amazonian forest. *Journal of Applied Ecology* **37**:508 - 514.
- Vermeij, G. J. 1996. An agenda for invasion biology. *Biological Conservation* **78**:3 - 9.
- Vitousek, P. M., C. M. D Antonio, L. L. Loope, and R. Westbrooks. 1996. Biological invasions as global environmental change. *American Scientist* **84**:468 - 478.
- Walters, A. C. and D. A. Mackay. 2003. An experimental study of the relative humidity preference and survival of the Argentine ant, *Linepithema humile* (Hymenoptera, Formicidae): comparisons with a native *Iridomyrmex* species in South Australia. *Insectes Sociaux* **50**:355 - 360.
- Walters, A. C. and D. A. Mackay. 2004. Comparisons of upper thermal tolerances between the invasive Argentine ant (Hymenoptera: Formicidae) and two native Australian ant species. *Ann. Entomol. Soc. Am.* **97**:971 - 975.
- Ward, P. S. 1987. Distribution of the introduced Argentine ant (*Iridomyrmex humilis*) in natural habitats of the Lower Sacramento Valley and its effects on the indigenous ant fauna. *Hilgardia* **55**:1 - 16.
- Wardle, D. A. 1999. Biodiversity, ecosystems and interactions that transcend the interface. *Trends in Ecology & Evolution* **14**:125 - 127.
- Way, M. J. 1963. Mutualism between ants and honeydew-producing Homoptera. *Annu. Rev. Entomol.* **8**:307-344.
- Wetterer, J. K., X. Espalder, A. L. Wetterer, D. Aguin-Pombo, and A. M. Franquinho-Aguiar. 2006. Long-term impact of exotic ants on the native ants of Madeira. *ecological entomology* **31**:358 - 368.

- Wetterer, J. K., S. E. Miller, D. E. Wheeler, C. A. Olson, D. A. Polhemus, M. Pitts, I. W. Ashton, A. G. Himler, M. M. Yospin, K. R. Helms, E. L. Harken, J. Gallaher, C. E. Dunning, M. Nelson, J. Litsinger, A. Southern, and T. L. Burgess. 1999. Ecological dominance by *Paratrechina longicornis* (Hymenoptera: Formicidae), an invasive tramp ant, in Biosphere 2. *Florida Entomologist* **82**:381 - 388.
- Wetterer, J. K. and B. C. O'Hara. 2002. Ants (Hymenoptera: Formicidae) of the Dry Tortugas, the outermost Florida Keys. *Florida Entomologist* **85**:303 - 307.
- Wetterer, J. K. and A. L. Wetterer. 2004. Ants (Hymenoptera: Formicidae) of Bermuda. *Florida Entomologist* **87**:212 - 221.
- Wheeler, W. M. 1908. The Ants of Porto Rico and the Virgin islands. *Bulletin of the American Museum of Natural History* **24**:117 - 158.
- Wilkie, K. T. R., A. L. Mertl, and J. F. A. Tranello. 2007. Biodiversity below ground: probing the subterranean ant fauna of Amazonia. *Naturwissenschaften* **94**:725 - 731.
- Wilson, E. O. 2003. *Pheidole* in the new world. Harvard University Press, Boston.
- Wilson, E. O. and R. W. Taylor. 1967. The ants of Polynesia (Hymenoptera: Formicidae). *Pacific Insects Monographs* **14**:1 - 109.
- Woinarski, J. C. Z., A. N. Andersen, T. B. Churchill, and A. J. Ash. 2002. Response of ant and terrestrial spider assemblages to pastoral and military land use, and to landscape position, in a tropical savanna woodland in northern Australia. *Austral Ecology* **27**:324 - 333.
- Wojcik, D. P. 1994. Impact of Red imported fire ants on native ant species in Florida. Pages 269 - 281 in D. F. W. Williams, editor. *Exotic ants: biology, impacts, and control of introduced species*. Westview Press, San Francisco.
- York, A. 2000. Long-term effects of frequent low-intensity burning on ant communities in coastal blackbutt forests of southeastern Australia. *Austral Ecology* **25**:83 - 98.



Plate 5. *Crematogaster* sp. and spider, Fraser Island.