Ecological restoration following the local eradication of an invasive ant in northern Australia.

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Abstract

There have been many management programs for invasive ants, yet few have achieved eradication. Of those that were successful, none have documented the subsequent recovery of the affected ecological system. Here I document the ecological impact and eradication of a five ha infestation of the African big headed ant *Pheidole* megacephala from an intact habitat in northern Australia, as well as the subsequent recovery of the native ant fauna. Pre-treatment, the impact of P. megacephala on the native ant fauna was clear. Native ant abundance and species richness were almost always significantly lower in infested compared to uninfested samples. Multivariate analysis statistically separated sample grids from infested and uninfested areas. Following treatment, no P. megacephala individuals were detected for two years and it was therefore declared eradicated. Ecological recovery post treatment was also clear. Twenty one months post-treatment, native ant abundance and species richness within the treated (infested) area were always almost always significantly greater than in the pre-treatment sample, corresponding with no change in the control area (uninfested area). Total species richness from plots in the treated area was identical to that from plots in the control area. Multivariate analysis showed no statistical separation of the treated or control plots. Species richness within lure plots displayed no trend within the treated area relative to the treatment boundary or locations away from the treated area. This project demonstrates the feasibility of eradicating this ant, and that ecological systems are capable of recovering following removal of an exotic invader.

Introduction

Eradication is the ultimate goal of invasive species management.

Many ants are extremely successful invaders (Passera 1994; Baskin 2002), with serious agricultural, social and environmental impacts throughout the world (Williams 1994; Holway et al. 2002). As such, many pest ant incursions have undergone management over the past century. Efficacy trials of ant control products have demonstrated that eradication is possible from small scale plots (Majer and Flugge 1984; Reimer and Beardsley 1990), and there have been some documented eradications of very small (<1 ha), young infestations (Haines and Haines 1978; Pascoe 2003; Lester & Keall 2005). However, all attempts to date of regional-scale eradications have failed, either due to the loss of control of the spread of a species (Haines et al. 1994; Buhs 2004), or because treatment was stopped due to environmental concerns of the toxicants being used (van Schagen et al. 1994).

Recently, however, some modest-scale eradications have been successfully completed. In 1990, a two ha infestation of the Little fire ant *Wasmannia auropunctata* appeared to have been exterminated on Santa Fe Island in the Galapagos (Abedrabbo 1994). The success of this project then led to another eradication attempt of the same species on Marchena Island, covering 22 ha, which also appears to have been successfully completed (Causton et al. 2005). Numerous isolated populations of the Argentine ant *Linepithema humile* covering approximately 12 ha were successfully eradicated from parts of Bunbury, Western Australia (Davis et al. 1998). In 2004, eradications of African big headed ant *Pheidole megacephala* and Tropical fire ant *Solenopsis geminata* covering 30 ha and 3 ha respectively within Kakadu National Park, Australia, were declared completed (Hoffmann & O'Connor 2004). Most recently, a four ha *P. megacephala* infestation has been reported eradicated from Mokuauia islet, Hawaii, (Plentovich 2009).

One of the most significant pest ant species that has a long history of management is *P. megacephala* (Jarvis 1931; Broekhuysen 1948; Reimer & Beardsley 1990; Hoffmann & O'Connor 2004). It is unclear when this species first arrived in northern Australia, but it was considered naturalized throughout Australia's urban east coast by the early 1900s (Tryon 1912). The ecological, agricultural and social impacts of *P. megacephala* in northern Australia are serious and well known (Hoffmann 1998; Hoffmann et al. 1999; Vanderwoude et al. 2000; Hoffmann & Parr 2008). However, despite the threat it poses, formal management on a regional or national scale is unrealistic. Nonetheless, management that prevents their spread to, or eradicates them from, remote locations is a real option and has already been demonstrated to be feasible (Hoffmann & O'Connor 2004).

In March 2005, an infestation of *P. megacephala* was identified at Dinggirriyet (Brown's creek) campsite on the Daly River (Figure 1). There is no known infestation of this species within an approximate 50 km radius of Dinggirriyet, so this finding prompted an eradication programme by the Malak-Malak rangers (the local Indigenous land management group) in collaboration with the Commonwealth Scientific and Industrial Research Organisation. Based on a two year post-treatment assessment process, the eradication programme appears to have been a success, with the apparent elimination of the infestation. Here I document the process undertaken to achieve eradication, and report for the first time for any ant eradication the subsequent ecological recovery of the native ant fauna.

Methods

Study site

Dinggirriyet campsite was situated within a semi-deciduous vine thicket, with low to intermediate canopy heights (3-15 m) that are mostly interlocked (>90% cover) and almost no understorey (Russel-Smith 1991). Northern Australia's rain forest vegetation types house relatively depauperate ant faunas (Reichel & Andersen 1994), and this site is almost annually inundated by flood water for at least three months during the tropical wet season. Consequently, the native ant fauna is particularly poor for Australian standards.

Eradication

The project was split into three phases: (i) a scoping phase determining the exact distribution of the infestation and feasibility of eradication; (ii) treatment using toxic baits; and (iii) post treatment monitoring. Integrated into the second and third phases respectively were ecological surveys that aimed to quantify: (a) the ecological impacts of the infestation on the native ant fauna, and; (b) the subsequent ecological recovery of the native ant fauna.

(i) Scoping phase

The mapping strategy to determine the extent of the infestation was based on this ant's unicoloniality (Hölldobler & Wilson 1990). Reproductive queens of *P. megacephala* rarely disperse by flying, and thus in the absence of human intervention, new queens

do not travel further than a few metres from the parent colony. In addition, the distinction between individual colonies is vague resulting in continuous multi-queen infestations, which over time can cover tens to hundreds of hectares, yet with distributional limits that can be accurately determined to within a few metres (Vanderwoude et al. 2000; Hoffmann & O'Connor 2004; Dejean et al. 2008; Hoffmann & Parr 2008).

The extent of the infestation was determined using methods from related work throughout northern Australia (Hoffmann et al. 1999; Vanderwoude et al. 2000; Hoffmann & O'Connor 2004). An approximate limit of the infestation was first determined by visually inspecting the presence of *P. megacephala* moving away from the campground until the ant could no longer be found. This process was repeated along informal transects spaced approximately 20 m apart, which crossed the perceived boundary radiating out from the campground. The exact limit of the infestation was confirmed by attracting the ants to spoonfuls of tuna placed every two metres for a further 20 m from where the ants were last observed. The tuna lures were inspected after approximately half an hour for the presence/absence of *P. megacephala*.

Due to the almost 100% canopy cover provided by the vegetation over most of the site, work was able to be conducted at all hours throughout the day. In the few areas where canopy cover was low, work was conducted between 7-10 am and 4-6 pm when temperatures did not restrict the activity of this ant.

The systematic mapping of the infestation was conducted within half a day in March 2005. Following the field examination we believed that eradication was a feasible option and an action plan to treat and monitor eradication success was developed and costed. Funding for the project was subsequently approved by the federal Department of Environment and Heritage through the Northern Territory's Natural Resource Management Board.

(ii) Treatment phase

A single treatment was conducted over 1-4 August 2006 using the commercially available formicide Amdro[®]. Amdro was chosen for use because: 1, it is a well known and effective treatment product for *P. megacephala* (Reimer & Beardsley 1990; Zerhusen & Rashid 1992; Hoffmann & O'Connor 2004); 2, its effects are very rapid (approximately 24 hours) therefore minimizing the likelihood of further spread as well as the project timeframe; 3, the active constituent, hydramethylnon, has an extremely low toxicity to terrestrial vertebrates, and rapidly breaks down into harmless metabolites after exposure to light (Meer *et al.* 1982); and 4, the bait matrix (corn granules with soybean oil) is only attractive to seed harvesting ants which make up a minority of the north Australian mesic ant fauna (Reichel and Andersen 1996; Andersen et al. 2007), comprising only three native *Pheidole* species in the study area. Such a specific and short-lived product is ideal for use within intact systems.

Due to the large size (five ha) of the infestation, and the difficultly of traversing through the dense vegetation, the site was systematically sub-divided into parallel treatment paths using long string lines. The bait was spread by hand using a team of people aligned in a row walking along the treatment paths. A five metre buffer zone

7

was also treated to ensure complete coverage. As far as reasonably possible, the bait was dispersed evenly through the site at the recommended rate of 2.5 kg / ha.

(iii) Post-treatment assessment phase

In the absence of standard protocols for determining eradication success (FAO 1998), I consider here that eradication is indicated by an absence of the target species for two years after treatment, as has been the minimum standard within most publications of ant eradications (Hoffmann et al. in press). Post-treatment surveys were conducted after nine (May 2007) and 21 months (May 2008). The first detailed inspection involved intensive surveys using attractant spoonfuls of tuna (lures) throughout the entire treatment area. Assessments were conducted systematically to cover the entire area, but lures were placed randomly. We aimed to have a lure density greater than the nest density of *P. megacephala* within similar environments in northern Australia (1 per 8 m²; Hoffmann unpublished data). This was based on the biological assumption that foraging distance is related to nest density, and nests are unlikely to remain undetected if the sampling intensity (density of lures) is greater than the average nest density. Tuna lures were visually inspected after 30 minutes for the presence or absence of *P. megacephala*. The location of each lure was recorded in GPS and later uploaded into a GIS. The team of 14 people conducting the survey mostly had little if any prior experience with ant identification, so much effort was placed on adequate training and supervision to ensure accurate identification of P. megacephala. To aid identification, all people were provided with cards that clearly displayed workers of P. *megacephala* and other similar native species. Above all, I believe that there was adequate supervision by those capable of identifying P. megacephala to avoid misidentifications.

The second detailed assessment comprised all surveys measuring ecological recovery detailed below. Had *P. megacephala* been found persisting by any detection method at any time post-treatment, only the specific area remaining infested as well as a five metre buffer would have been re-treated using the same methodologies in the initial treatment.

Ecological impacts

Prior to treatment, two surveys were conducted using pitfall traps to investigate the ecological impacts of *P. megacephala*, as well as to provide baseline data to assess ecological recovery post-treatment. Pitfall traps were plastic containers (internal diameter of 42 mm), filled three quarters with 70% ethyl glycol as a preservative. Traps were operated for 48 hours.

The first assessment used six grids of pitfall traps, three grids (I1-3) within the infested area and three (U1-3) within the surrounding uninfested area (Figure 1). Grids II - I3 follow a presumed age gradient of oldest to youngest infested respectively along the widest area of intact environment and were located 90, 40 and 10 m from the invasion front. Twelve traps were used in each grid, arranged in a three by four array with 10 m spacing between traps.

The second assessment used three transects (T1-3), centrally located over, and positioned perpendicular to, the perceived edge of the invasion front (Figure 1). A single pitfall trap was placed every five metres along each transect, extending 20m into and away from the limit of *P. megacephala*'s distribution. Both assessments

using pitfall trap were conducted 1 day prior to treatment, and 26 months post treatment.

A third method was used post-treatment to assess ecological recovery of the ant fauna, due to the low numbers of ants collected in the pitfall traps, as well as to enhance confidence of eradication. Forty one plots (hereafter referred to as lure plots), 22 from within the treated area and 19 from the surrounding untreated area were positioned randomly throughout the intact vine-thicket within treated and untreated areas (i.e. not the campsite, dry drainage lines or river banks). The distance from each lure plot's centroid to the closest edge of the prior invasion front were measured in GIS to provide a measure of time since invasion (i.e. plots farther from the invasion front had been infested with *P. megacephala* longer than plots closer to the invasion front) and hence a potential gradient of prior ecological impact. Tuna lures (spoonful size of tuna) were used in a three by four array with 5 m spacing between lures. After 30 minutes, all ants within three centimeters of each lure were identified and a species list was pooled for each lure plot.

Ants were identified to species, and a full collection of voucher specimens is held at the CSIRO Tropical Ecosystems Research Centre in Darwin. For simplicity, the only other exotic ant species found, *Paratrechina longicornis*, is considered together with the native species as only two individuals were collected.

Analyses

Univariate analyses in studies of invasions such as this often suffer from inherent pseudoreplication in that the invasion is not replicated, so statistical samples are not from independent treatments (Hurlbert 1984). Consequently, analyses of such studies also typically suffer from low statistical power due to the small number of statistical samples utilised in order to minimise pseudoreplication (Krushelnycky & Gillespie 2008). However, within comparative mensurative experiments such as this, (as opposed to manipulative experiments) the issue of pseudoreplication is less about the replication of treatments, and more about the spatial restriction of the samples within the treatment areas, as well as the level of isolation of the samples to each other (Hurlbert 1984). In other words, pseudoreplication is more relevantly defined as where all samples within a single 'treatment' are collected within a restricted range of the possible area, as opposed to throughout the greatest range of space. As such, pitfall traps rather than grids or transects were considered as statistical samples within infested or uninfested zones in order to improve the statistical power of tests. This is justified because the use of either plots or traps as statistical samples does not resolve the fundamental issue of having only a single infestation (treatment), sampling was conducted throughout the greatest possible extent of intact environment within the infested area, as well as along the boundaries and surrounding uninfested areas, and because both sampling distances between traps (5 m for transects and 10 m for plots) allow traps to be considered independent samples from the scale of an ant as most ant species forage only within a few metres of the nest (Hölldobler & Wilson 1990).

Unpaired t-tests were conducted when comparing ant metrics between infested and uninfested areas within a sample time, and paired t-test were conducted for analyses between the two sample times of 2006 and 2008. Transect data were shifted in all

11

cases prior to analysis so that the most distal occurrence of *P. megacephala* occurred at the 0 m mark.

Ant abundance data were combined in a multivariate ordination to explore differences in composition and structure of the ant communities between infested and uninfested grids pre- and post baiting using Primer (Clarke and Gorley 2001). A similarity matrix of grids was constructed from the abundance data of all ant species (excluding P. megacephala) using a Bray-Curtis Association Matrix. Plots were then ordinated using non-metric multidimensional scaling. ANOSIM (Analysis of Similarity) was used to test for clustering of grids according to infested and uninfested and sample time. ANOSIM uses non-parametric permutation procedures applied to (Bray-Curtis) similarity matrices based on rank similarities between samples. ANOSIM returns an R-statistic which gives a measure of how spatially distinct groups are, with values ranging from -1 to 1, most commonly 0 to 1. The closer the R-value is to 1 the more separated the groups are in ordination space, while a value close to zero indicates no separation of groups (Clarke and Warwick 2001). To improve statistical power, the uninfested plots of both sample times were utilised in all analyses. SIMPER analysis was used to determine which species provided the greatest contributions to the ordination. This analysis was conducted for the whole ordination rather than for discriminating contributions to differing clusters of plots because there was no statistical differentiation in the 2008 sample as determined by ANOSIM.

Results

The fauna

Excluding *P. megacephala*, seventeen species of ant were collected in pitfall traps, or observed at tuna lures throughout the course of the project. Two undescribed *Pheidole* species comprised the majority of the native fauna, contributing 61% and 21% of the total catch (excluding *P. megacephala*) in grids and 72% and 13% in transects. In 2006, *P. megacephala* abundance in infested samples was not statistically different from native ant abundance in uninfested samples in both the grids (Unpaired t-test, t = 3.05 p = 0.761; Figure 2a) and the transects (Unpaired t-test, t = 1.01 p = 0.32; Figure 3a).

Ecological impacts

In the 2006 samples, native ant abundance was significantly lower in infested compared to uninfested samples in both the grids (Unpaired t-test, t = 4.7, p < 0.0001; Figure 2a) and transects (Unpaired t-test, t = 5.07, p < 0.0001; Figure 3a). Species richness too was lower in all infested samples compared to uninfested samples, significantly so within the grids (Unpaired t-test, t = 4.11, p = 0.0001 for grids and t = 1.47 p = 0.15 for transects) (Figure 2b). Total species richness within the infested grids was just over half of that in the uninfested grids (seven versus 11).

The relationship of *P. megacephala* abundance with native ant abundance and species richness was always negative, but only the regression of ant abundance from transect samples proved significant ($R^2 = 0.223$, p = 0.012). All other regression analyses were confounded by consistently low native species abundance or species richness.

Multivariate analysis showed clear separation of the infested grids in 2006 and uninfested grids of both sample times, which was also statistically significant (ANOSIM: Global R = 0.92, p = 0.012; Figure 5).

The eradication

The first post-treatment assessment utilized 16,407 lures over 48,243 m² giving an average lure density of one per 2.9 m². Some areas could not be adequately assessed due to safety issues (e.g. along cliff edges beside the waterways, some impenetrable vegetation clumps) so the lure density of the actual area sampled would have been slightly greater. Indeed direct counts of flags within three random 10 x 10 m grids conducted during work to assess work quality gave a lure density of one per 0.9 m². No *P. megacephala* were detected in this survey, nor were any detected at any time for two years post-treatment using any detection method. Consequently, I declared *P. megacephala* eradicated.

Ecosystem recovery

Both average native ant abundance and species richness in the treated (previously infested) area were always greater in the 2008 samples compared to the 2006 samples from both grids and transects, but only species richness in transects did not increase significantly (Figures 2,3; Table 1). Total species richness from the grids in the treated area was identical to that from grids in the uninfested area (both eight species) in the 2008 sample. Simultaneously, there was no visible or statistical change in these ant metrics within the uninfested area between 2006 and 2008 (Table 1) other than species richness in transects which was lower in 2008. The great abundance of two of the three *Pheidole* species post-treatment (70% of total abundance within the three treated

plots), which were the species most likely to be affected by the treatment, indicates that there was either little or no adverse non-target impacts, and that effects of *P*. *megacephala* were greater and longer lasting than any adverse treatment effects.

Multivariate analysis of the ant fauna shows the 2008 treated grids positioned much closer to the uninfested plots than the 2006 samples, with the infested grid within the longest-infested zone (I1) maintaining greatest compositional dissimilarity. Most importantly there was no statistical separation of the treated or uninfested grids in 2008, (ANOSIM: Global R = 0.29, p = 0.11; Figure 4), indicating that their respective faunas are similar. These results indicate that changes in the treated area between 2006 and 2008 represent substantial ecological recovery, and were due to removal of *P. megacephala*, not to differing environmental conditions during the two sample times. SIMPER analysis indicated that the patterns of the ordination were predominantly (98%) attributed to the four most abundant species, being two *Pheidole* species (77% and 6% contribution), the arboreal Green tree ant *Oecophylla smaragdina* (8%) and a *Paratrechina* species (7%).

Species richness within lure plots further suggest recovery of the affected system, as there was no trend within the treated area relative to the treatment boundary or to locations away from the treated area (Figure 5). The lack of trend outside of the treated area also confirms that there was no unforeseen environmental gradient influencing ant diversity.

Discussion

15

No eradication effort can ever be fully certain that not even one viable population persists. I do, however, claim to have found no *P. megacephala* within two years post-treatment using multiple methods that should have been more than sufficient in detecting any remaining populations. Therefore, I believe that *P. megacephala* has been eradicated.

Although the area involved was quite small (five ha), this successful outcome is significant for two reasons. First, most eradication attempts on invasive ants have failed (Hoffman et al. in press), so this is one of only a handful of projects that demonstrate that this task is achievable. Factors influencing eradication success and failure have already been reviewed multiple times (Myers et al. 2000; Hoffmann & O'Connor 2004; Mack & Lonsdale 2002; Simberloff 2009; Hoffmann et al. in press), so I limit discussion of this first point to what I believe are the two most important key factors relating to this project.

First, of all of the tramp ant species (Passera 1994), I personally regard *P*. *megacephala* as the easiest to eradicate. This relative ease is due to numerous factors. While many invasive ant species require expert identification in the laboratory, this species can be readily identified in the field from the hundreds of other *Pheidole* species outside of the *megacephala* complex by its distinct soil workings and general morphology, particularly its laterally enlarged post-petiole. Its strong unicoloniality and high nest densities produce sharp distribution boundaries, making infestation delimitation very easy and accurate. This unicoloniality coupled with the lack of a nuptial flight severely limits its localized rate spread, and makes its distribution from an initial point of introduction highly predictable. Most importantly, this ant is highly susceptible to readily available products, and as demonstrated here, even by a single treatment.

Second is the lack of non-target issues. Probably the greatest hindrance to the success of invasive ant management is the concerns over non-target impacts. Eradication methods or attempts have been deemed inappropriate elsewhere due to the delicate nature of the infested habitat and the likely impacts on non-target species. Examples include the use of fire and organo-chlorides in the Galapagos Islands (Abedrabbo 1994) and the landscape scale baiting in areas of low population density of *A. gracilipes* on Christmas island (Marr et al. 2003). In other cases, projects achieving effective control or widespread eradication have been stopped due to deregistration of the active treatment compound, because of wider environmental implications, prior to the development of an acceptable and effective alternative treatment product (van Schagen et al. 1994; Buhs 2004). This project benefited from no concerns of non-target impacts despite being conducted within a largely intact environment. The bait used was quite target specific, the active toxicant used was relatively environmentally friendly, and there were no native species of particular concern.

The second significance of this project is that no prior completed ant eradication has ever demonstrated rehabilitation of the native fauna. At most, prior work has noted the persistence or rapid increases in the abundance of certain native ant species posttreatment (Abedrabbo 1994; Hoffmann & O'Connor 2004) or persisting differences of taxonomic group metrics between treated and untreated areas (Marr et al. 2003). Regardless, these studies all notably demonstrate that blanket coverage of a toxicant over a large area does not necessarily eradicate all ant species, probably most likely because highly invasive ant species are largely superior at dominating and usurping resources, including toxic baits (Human & Gordon 1996; Holway 1999; Marr et al. 2003), thereby largely preventing native species gaining access to the toxic baits.

Rehabilitation is important, not only in the sense of ecological integrity, but also to prevent succession of another exotic species into the ecological gap left by the eradicated species (Myers et al. 2000). Indeed *P. megacephala* eradications have resulted in subsequent invasion by *S. geminata* in both Hawaii and northern Australia (Plentovich et al. 2009; Hoffmann unpublished data). While not formally quantified, I did note an increase in the occurrence of the tramp Black crazy ant *Paratrechina longicornis* through some of the treated area, however, this species is not known to have environmental consequences of concern.

Two biological aspects of this invasion are noteworthy. First, *P. megacephala* abundance levels pre-treatment were equivalent to those of the native ants, not significantly greater as is often the case with this ant (Hoffmann et al. 1999; Hoffmann & Parr 2008) and other invasive ant species (Porter & Savignano 1990; Le Breton et al. 2003; Abbott 2005; DiGirolamo & Fox 2006), at least in the early stages of invasion. Unfortunately, nothing can be said from this study of why invasive ants often attain much greater population densities than native ants, and why it didn't occur here. Second, *P. megacephala* clearly has superior competitive abilities compared to native *Pheidole* species. This is clear because *P. megacephala* was associated with a markedly reduced native ant fauna which was comprised predominantly (82%) of two native *Pheidole* species.

Conclusions

This project contributes to a growing body of work demonstrating the feasibility of ant eradications. Moreover, it has also demonstrated that ecological systems are capable of recovering following removal of an exotic invader. While there is no doubt that this system was relatively simple thereby enabling rapid recovery, complex systems are regularly documented to regenerate following all types of disturbance (Rosenberg et al. 1986; Spellerberg 1993; Andersen et al. 2003; Luque et al. 2007), and the same should be possible following removal of exotic ants. Given the demonstrated simplicity of eradicating this ant coupled with clear environmental benefits, management of this species, particularly in conservation areas, should be regarded as a realistic option.

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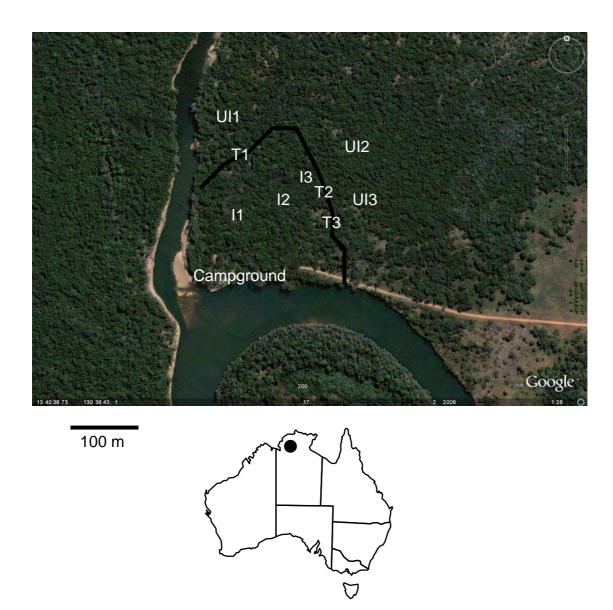


Figure 1. Location of Dinggirriyet campsite, *Pheidole megacephala* infestation (area between rivers and solid black line) and the study grids (I1-3 and UI1-3) and transects (T1-3).

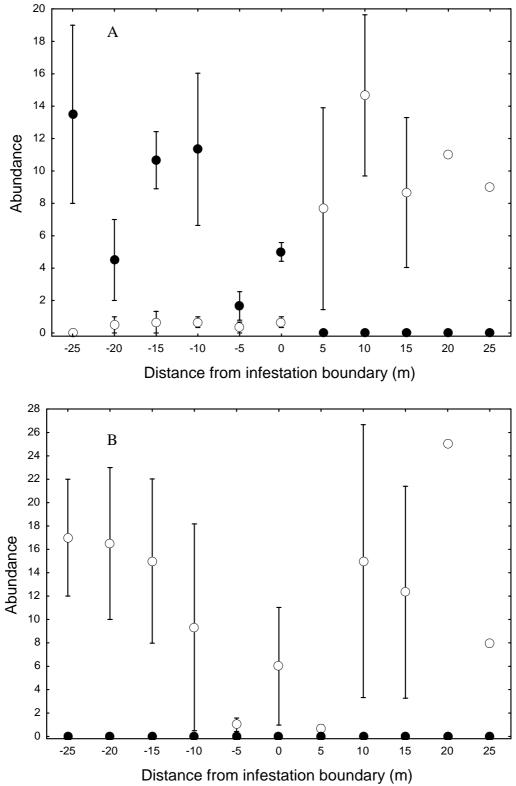


Figure 2. Abundance of *P. megacephala* (filled circles) and native ant species (open circles) along three transects crossing the infestation boundary (0 m) in 2006 (A) and 2008 (B).

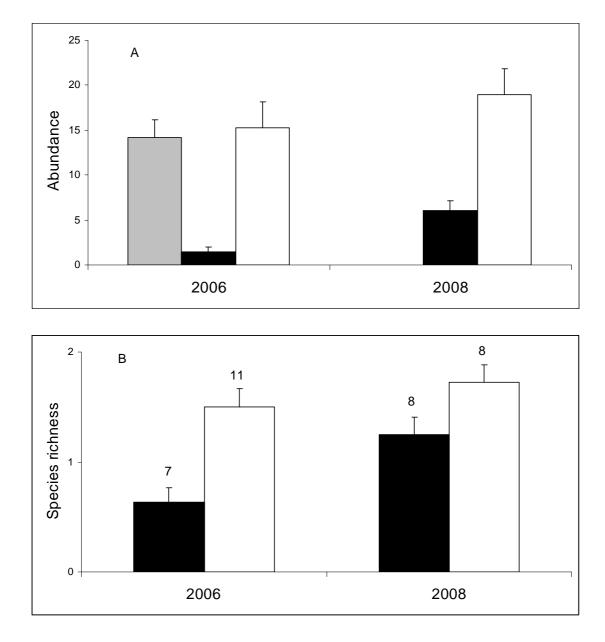


Figure 3. Average abundance (+/- SE) (graph A) and species richness (graph B) per pitfall trap of *Pheidole megacephala* (grey column) and native ants from grids within the infested (black columns) and uninfested (white columns) areas in 2006 and 2008. Numbers at the tops of columns in graph B are total species richness.

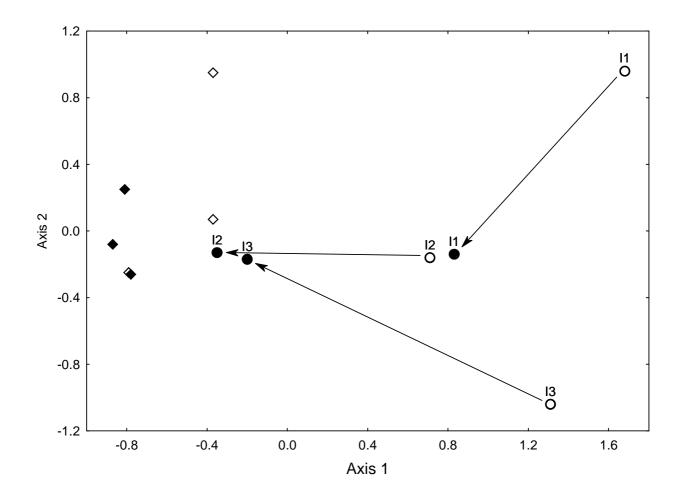


Figure 4. Two-dimensional non-metric multidimensional scaling ordination of ant species-level abundance data collected in infested (I1–I3; circles) and uninfested (diamond) grids in 2006 (open symbols) and 2008 (filled symbols). Stress = 0.04

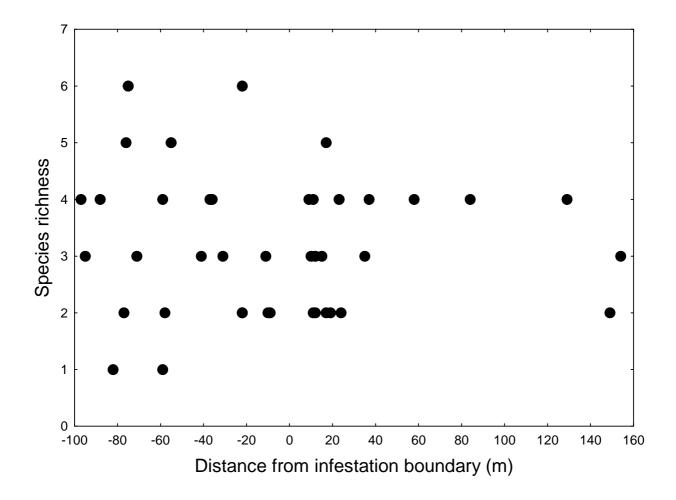


Figure 5. Ant species richness found at tuna lure arrays in 41 plots within (negative distances) and away (positive distances) from the infestation boundary in 2008.

Table 1. Paired t-tests of native ant abundance and richness per pitfall trap between the 2006 and 2008 samples in treated (n = 36 in grids and 16 in transects) and control samples (n = 36 in grids and 11 in transects).

Metric	t	Р
Treated samples		
Abundance in grids	4.03	0.0003
Abundance in transects	3.74	0.002
Species richness in grids	3.11	0.004
Species richness in transects	0.52	0.61
Control samples		
Abundance in grids	1.09	0.28
Abundance in transects	0.08	0.936
Species richness in grids	0.86	0.4
Species richness in transects	3.46	0.006