

¹Urbanisation factors impacting on ant (Hymenoptera: Formicidae) biodiversity in the Perth metropolitan area, Western Australia: two case studies

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Abstract

Two synchronous projects undertaken in 2011 examined the likely impact of increasing urban densification on invertebrate populations within urban settlement in Perth, Western Australia. One project analysed the ant fauna found in 20 gardens and lawns in small to very small properties (these having a bungalow or duplex (semi-detached) as the main residential building, and a lawn or garden area of 43 m² – 332 m²) east, south, north and west of the Central Business District (CBD). The other project examined the ant fauna at 14 sites, principally in native regrowth along the Kwinana Freeway, a major artery that runs north to south through Perth's suburbs. The gardens and lawns produced a very depauperate fauna of 26 ant species, of which a maximum of 20 were native and at least six species were exotic. The ant fauna from regrowth adjacent to the Kwinana Freeway and at two additional sites (one a bush control) was more than twice as rich, the 56 species collected including only two exotics. In the garden project, ant richness, evenness and abundance were not significantly correlated with size of the garden area. The same applied even when the exotic *Pheidole megacephala*-dominated gardens were removed from the analysis. Ordination analysis combining the two sets of data revealed a distinct clustering of most of the regrowth sites, whereas the bush control stood alone and garden or lawn sites exhibited a much looser pattern of association. We suggest that increasing the density of Perth suburbs is resulting in drastic loss of native invertebrate fauna, of which ants are a useful bioindicator. However, native vegetation regrowth along major arterial roads could act as a reservoir for invertebrate species that might otherwise disappear entirely from the Perth metropolitan area.

Keywords: urbanisation, urban infill, densification, ant species richness, *Pheidole megacephala*

Introduction

The world's human population is rapidly moving from a low-density, rural existence to a high-density, urban one (Menke et al. 2011). Cities and towns and their associated sprawl now cover 3% of the world's total land area (Faeth et al. 2011). This imprint of human activities on previously pristine environments has profound implications. Viewed from an ecological perspective, urbanisation is the alteration of existing natural ecosystems due to the increase in human habitation, and the consequent changes to the landscape. In terms of the ground surface, the original plant communities are displaced and the ground is covered with a patchwork of paved or otherwise hard and impervious surfaces (e.g., roads, carparks and buildings), remnant tracts of native vegetation, patches of exotic vegetation (e.g., lawns, gardens and parks) and areas of highly disturbed, bare ground (Catterall 2009; Menke et al. 2011). Additional pressures are present in the urban environment, including pollution, frequent disturbance and the changes to ecosystem function wrought by the altered landscape (Garden et al. 2006; Catterall 2009).

Urban infill and urban sprawl

Two elements that are crucial to understanding changes in the urban landscape are (1) urban sprawl, and (2) urban infill. Urban sprawl is not necessarily easy to define (see Johnson 2001) but in the broadest sense is the spread of an urban area outwards into the surrounding environment and the joining together of individual urban units to form conurbations. However, suburban environments, with their backyards and gardens, can contribute positively to an already urbanised environment by retaining vegetation that can act as a reservoir for fauna, providing them with resources and habitats (Smith et al. 2006). Urban infill, on the other hand, is traditionally understood to be the development or redevelopment of parcels of land in an area that is already urbanised (Wegman and Nemirow 2011). The process of urban infill reduces the land area available for plant growth.

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What is left is usually highly disturbed, or contains mainly exotic plant species or monocultured lawns, with little room for trees or shrubs. In these environments, nature strips along roadways can preserve a significant proportion of the vegetation able to grow in such conditions (Pećarević et al. 2010). Vacant lots can also perform the same function (Uno et al. 2010). In terms of landscape ecology, urban infill removes a previously existing environmental resource (namely, the backyard), reduces vegetation corridors to strips of disturbed vegetation and further fragments remnant patches of native vegetation (Samways 1994).

Resilience in urban ecosystems

With this global shift towards anthropogenic ecosystems, comes the question: how resilient are the biological components of these ecosystems to pressures imposed by human activities? Unquestionably, there is a simplification and a homogenization of the flora and fauna as certain species drop out and species that are ubiquitous in altered ecosystems arrive (Blair, 2001). Biophysical systems (e.g., hydrology, microclimate and soil profile), upon which organisms depend, very often will also alter. If such changes are considered to be dynamic, how might this be expressed in such a way as to yield predictions of outcomes in the urbanisation process? Alberti and Marzluff (2004) and Marzluff (2005) have suggested a dynamic linkage between human socio-economic and natural biophysical processes. In essence, their hypothesis states that unrestrained human activities resulting over time in urban sprawl are accompanied by the replacement of a natural steady state of abundant, well-connected land cover with disconnected and highly fragmented land cover. This process also results in a shift from a stable equilibrium to an unstable one. The equilibrium is unstable because the newly formed urban ecosystem depends for its continuance on the products of other ecosystems. If this situation is not addressed, the viability of the urban development is eventually reduced to the point of collapse; at which time the system commences reverting to the original ecology. In their papers, Alberti and Marzluff illustrate this view with figures emphasising a feed-back mechanism between factors ('Natural Vegetation Attractor' and 'Sprawl Attractor', respectively) that cause oscillation between the continued degradation of the urban ecosystem and its recovery towards a more natural system. This latter process may take centuries or millennia. Alberti and Marzluff (2004) suggest that a thoughtful approach to urban planning can ameliorate the more dire consequences of short-sighted decision-making that leads towards unstable, low-resilience urban sprawl. This requires the balancing of human and ecosystem processes in such a manner as to maximise resilience, and a proper understanding of the relationship between these processes and the physical, biological and human influences that operate in the urban environment. The latter are termed 'heterogeneity' by Alberti and Marzluff, and can be temporal and physical in character.

As a test case, Alberti and Marzluff (2004), applied their hypothesis to the avifauna and macroinvertebrates of Puget Sound, Washington State, USA (because of the focus of the present paper, only the bird study is commented on here). The authors found that avian diversity was higher in mixed settled and forested land (i.e., if there was $\geq 30\%$ forest per 100 ha unit) than in either purely natural forest or in areas of extensive urban sprawl. They concluded that even though the equilibrium created by planned development was inherently unstable, it could be maintained by judicious attention to urbanisation patterns. A similar study by Marzluff (2005) on the avifauna of Seattle, Washington State, USA, resulted in findings that were concordant with the earlier study.

The Puget Sound and Seattle reviews provide encouraging case studies for town planners in what is often a fraught process of satisfying developers and industry on the one hand and paying attention to the findings of scientists and the desires of conservation-minded homeowners and green groups on the other. However, the two authors also sound a note of warning: when the ecosystem shifts from the natural state to the sprawl state, it is often highly resistant to switching back. Marzluff (2005) also warns against a simplistic approach – a 'one size fits all' – to balancing urban development with conservation practices. In restricting the urban ecosystem to only large natural reserves interspersed with areas of high urbanisation, diversity peaks (found in moderate settlement with a rich mix of niches) will be missed.

This model is a Holarctic one, based on northern hemisphere conditions, and the authors concede that, in the case of the birds they studied, synanthropic species do not appear to have had a huge impact on the native species. The model may not be so easy to fit to a different continental setting with a different suite of organisms. For instance, Australia differs from other continents in terms of aged, highly weathered soils (Anand 2005), and its flora and fauna have had to develop specialised mechanisms to survive the infertile soils and often harsh

climatic conditions (Hopper 1996). The fact that it is an island which has been colonised relatively recently also means that the introduction of exotic species is a relatively recent phenomenon. Moreover, ants, the subject of this paper, are an organism with quite different biological and environmental requirements to birds, and, as soil-dwellers primarily, these small invertebrates may be expected to respond to a different set of ecophysical processes. The possible application of the Alberti and Marzluff model to Australian ants in an urban setting is commented on in the Discussion.

Urbanisation and ants

Among the fauna that remains in highly urbanised environments, ants (family Formicidae) are a particularly suitable group to be used as a proxy for other invertebrate populations in determining the environmental impact of urban sprawl and urban infill (Majer et al. 2007). In general, they are ubiquitous, abundant, have high species richness, are easily sampled and are sensitive to changing conditions (Majer 1983; Menke et al. 2011). Moreover, some ant taxa are favoured by urbanisation and others are adversely affected (Garden et al. 2006). Urbanisation favours those ants that have pioneering or tramp characteristics, such as omnivory and flexible nesting habits (Silverman 2005), and is disadvantageous to those species that are highly specialised, require a substantial food or nesting resource or are sensitive to the presence of other, aggressive ant species (Uno et al. 2010).

The structure of Australian ant communities has been analysed, and suites of Australian species with different physiological, behavioural and habitat characteristics have been identified (Andersen 1990; 1995): these are placed in guilds called functional groups. Ant functional group data have often been used by Australian ecologists, in particular, in recent years (e.g., Greenslade 1978; Andersen 1990; 1995; Majer and Nichols 1998), and can be represented meaningfully with descriptive statistics combined with graphical tools such as bar charts.

Urbanisation and ants in the Perth Metropolitan area

Over the four years to June 2009, Perth was adjudged the fastest-growing Australian capital city. During that time, approvals of clustered dwellings (i.e., semi-detached, row or townhouses) as a proportion of all dwelling approvals was greater than 20% for most local government bodies surrounding the Perth Central Business District (CBD), and was less than 17% for only three inner suburban municipalities. Overall, three-dwelling clusters had increased over two-dwelling clusters since 2001, and in addition, the proportion of approvals for flats, units and apartments had also increased since 2001 (Australian Bureau of Statistics 2010). Not only is the population of Perth increasing rapidly, but a significant proportion of those involved with planning support a continued high population growth rate for Perth, albeit with a reduced emphasis on vehicular transport. An American model of urban planning espoused by some influential local planners, the so-called 'New Urbanism' model, emphasises connected streets with paths, higher density of residential development and local centres. Traditional urban sprawl and car dependence is discouraged (Falconer et al. 2010). This enthusiasm for an enhanced densification process in the Perth metropolitan area has profound implications for the remaining native invertebrate fauna, as the alienation of residual native ground cover and even the loss of habitable exotic vegetation continue apace. Ants continue to provide a proxy by which this change can be measured.

Urban development *per se* is not always incompatible with healthy native ant assemblages (Menke et al. 2011): thus, highly disturbed median strips in New York City were found to support more than 13 ant species with no correlation between ant species composition and the size of the vegetated area (Pećarević et al. 2010). Small bush remnants in Sydney have also been found to contain higher ant species richness than larger remnants (Gibb and Hochuli 2002). Since the mid 1970's, consistent efforts have been made to examine and interpret the changing status of ant populations in suburban Perth. Curtin University staff and students, led by Professor J. Majer, have been at the forefront of this work, with other research being undertaken by staff connected with State bodies such as the Department of Agriculture and Food. One finding has been that the relative proportions of generalist and opportunistic species have increased with urbanisation, while climate specialists and large, solitary foragers (*sensu* Andersen 1990; 1995) have declined (Majer and Brown 1986). However, when they conducted their study, the latter two authors only encountered two synanthropic ant species, with one of these (*Tetramorium simillimum* F. Smith) misidentified as a native species. More recent research (Heterick et al.

2000; May and Heterick 2000) has presented evidence that additional exotic species such as the Argentine ant (*Linepithema humile* (Jerdon)) and the African big-headed ant (*Pheidole megacephala* (Fabricius)) have made inroads into residential areas that formerly supported populations of native species.

This paper reports on two subprojects, one involving the sampling of small garden and lawn areas in suburban properties situated around the CBD, and the other involving the sampling of ants along a regrowth corridor adjoining a major arterial road. Based on the existing literature and previous work done in the Perth metropolitan area, the expectation at the outset of the two studies was that ant diversity would be shown to have declined even further in the smaller urban spaces now available for colonisation. Additionally, we hypothesised that exotic, invasive species would be even more entrenched in the most built-up sites, i.e., those where urban infill was most pronounced. We also anticipated that bush regrowth zones would provide habitat akin to refugia in which native ant species might have a greater likelihood of successful colonisation in the face of competition with alien ant species. In discussion of our findings we also comment on the applicability of the Alberti and Marzluff (2004) conceptual model to urban ants in Australia.

Materials and Methods

The first study involving 20 Perth properties was undertaken in autumn between 26 March and 12 April 2011 (Figure 1). The properties selected had a lawn or garden area of 43 m² – 332 m² and a bungalow or duplex as the main dwelling. Nine plastic pitfall traps, arranged in a square grid formation, were inserted into the ground to their rims in an area of grassed lawn on each property. The traps were 3.5 cm in diameter and 10 cm deep, and were filled with approximately 30 ml of ethylene glycol. These traps were left open for 7 days and then collected. Hand collections of ants, standardised for time, were also made at each of the properties, but no additional species were collected. Apart for a brief rain period towards the end of the sampling event, the weather was fine for the duration of the sampling period. Each property was scored for watering regime (watered or unwatered) and the approximate number of plant species within the sampling grid was noted. Ants were sorted and identified at the Curtin University Entomology Laboratory.

The second study involved embankments adjacent to the Kwinana Freeway, which had been rehabilitated by the planting or seeding of a range of native plant species (see Table 1), and was conducted in autumn between 2 and 10 March 2011. Pitfall traps of the same dimensions and also containing approximately 30 ml of ethylene glycol were used in this study. The traps were collected after being open 7 days. However, the methodology differed from that of the above study in that the traps were sunk to rim level at 5 m intervals along each of two 50 m transects ('Transect-S' and 'Transect-F') at 14 sites. Thirteen of these transects were set within triangular-shaped quadrants formed by a ramp road entering or exiting the Kwinana Freeway, and rising to meet an overhead bridge (Figure 2). The location of the quadrants in relation to the bridge is indicated by the four ordinal points, i.e., northwest, northeast, southwest and southeast. The sites represented different ages of rehabilitated vegetation regrowth (considered as chronosequences), these being zero years (one site), 1 year (one site), 1-10 years (one site), 3 years (one site), 4-29 years (one site), 5-6 years (one site), 5-33 years (one site), 9-10 years (five sites) and 29 years (one site). A single control site (0.79 ha) consisting of remnant Jarrah (*Eucalyptus marginata*)-Banksia (*Banksia* spp.) woodland was also included in the sampling. In terms of landforms and soils, it belongs to the Bassendean complex, and the vegetation is representative of the original open forest woodland of the area. Larger nearby sites reserved under the 'Bush Forever' program are characterised in detail in Government of Western Australia (2000) pp. 240-250. While the use of a single control is not regarded as ideal, it was the only site available in close proximity that contained the original vegetation found in the other Freeway sites. However, the ant fauna of native vegetation on this soil type has already been characterised by Rossbach and Majer (1983). Thirteen of these sites, including the control site, were located in ground adjoining the Kwinana Freeway, and one site was located next to the arterial Leach Hwy. The preparation for the work, information on health and safety and location of sites was assisted by staff from Main Roads Department. Ants were sorted and identified as in the first study.

Data analysis

The data analysis was conducted in the same manner for both studies. The statistical software package PAST (Hammer et al. 2001) was used to determine the Shannon diversity index (H') and Pielou's (1969) evenness index (J') for each site or property.

The Fisher alpha index was also used for the sake of comparison. This measure of diversity is recommended by Magurran (1988) on the basis of low sensitivity to sample size, good discriminant ability, robustness (i.e., it is relatively insensitive to extreme values such as may occur at the tails of actual distributions of very abundant or very sparsely occurring species), and applicability to a variety of ecological situations.

For the Garden study, ant species richness, Shannon diversity and species evenness for each property were regressed against garden area, property size or number of plant species, using linear regression analysis performed with IBM SPSS Statistics version 19. A Fisher alpha analysis was also undertaken as an additional measure of diversity for the purpose of comparison. SPSS was used to perform a one-way ANOVA to determine the difference between sites in terms of watering regime and location. A non-metric multidimensional scaling (NMDS) ordination plot was produced by the PAST program (Hammer et al. 2001) and a cluster analysis dendrogram was produced by the PRIMER version 6 program, each program utilising Bray-Curtis similarity. For the ordination plot, the abundance data were fourth-root transformed to lessen the influence of highly abundant species. The cluster analysis dendrogram was produced utilizing species presence/absence. The properties were compared with the sites from the second project (see details below). Following cluster analysis, a Mann-Whitney U test was performed to examine the difference between the two major branches of the dendrogram in terms of species richness, diversity and evenness. A subset of the properties identified via cluster analysis was further examined for correlations between garden area and species, richness, diversity and evenness.

For the Freeway study, land area was not a factor and neither were watering regime nor number of plant species. A SIMPER analysis was also performed to find those ant taxa contributing most to the dissimilarity between the garden sites and the Freeway sites.

Ant functional group (see Introduction), another means of predicting the response of ant communities to disturbance, were also considered in these two studies.

Results

(1) *Garden study*

A total of 19918 ants from 16 genera and 26 species were collected from the pitfall traps (Table 2). Six of these species, namely, *Cardiocondyla nuda* (Mayr), *Linepithema humile*, *Pheidole megacephala*, *Pheidole* sp. JDM 874, *Tetramorium bicarinatum* (Nylander) and *Tetramorium simillimum*, were exotic and have been naturalised in Australia; the remaining 20 species were native. Of the total ants, 14283 (71.7%) were exotics. At least one exotic ant species was recorded from all twenty properties, and two or more exotic species were often present. The most abundant ant species across all properties was *P. megacephala*, with 11776 individuals (59.1% of the total). *Tetramorium simillimum* (1,582; 7.9%) was the next most abundant of the exotic ants, followed by *T. bicarinatum* (746; 3.7%). Of the native species, *Iridomyrmex chasei* Forel (3925 individuals, or 19.7% of the total) was the most abundant, followed by *Cardiocondyla atalanta* Forel (661; 3.3%). The mean number of ants collected at each property was 996. The greatest abundance of ants (4671, all but one of which was *P. megacephala*), was recorded from site SE5, and the lowest abundance of ants was 84 (two native and two exotic species) from site NE2.

Species richness, diversity and evenness

Species richness varied from 11 species at site NW1 to just one species (the exotic *P. megacephala*) found at site SW5. The mean species richness across all properties was 5.8. The tally for properties containing the exotic *P. megacephala* was conspicuously low, with only one such site (SE3; 10 species) having more than four ant species. The Shannon diversity index was highest at site NW3 (0.77) and lowest at site SW5 (0.00). Again, properties where *P. megacephala* was present had markedly lower species diversity (0.00-0.53 (the garden with the highest value having only one *P. megacephala* worker)) compared with non-infested properties (0.08-0.77). The corresponding evenness values were 0.00-0.66, compared with 0.11- 0.77 without *P. megacephala*. Fisher alpha indices ranged from 0.10 (SW5), where 1641 *P. megacephala* workers only were trapped, to 5.82 in 6E, in

which evenly low numbers of 20 mainly native species were recorded (see Table 2 for the full range of indices). Across all properties, no statistically significant correlation was found between species richness and property size or plant richness. The size of the garden or lawn also did not appear to have a major impact on ant diversity; for when these properties, and two others where *P. megacephala* was recorded in moderate numbers, were removed from the analysis, and the remaining ant data tested for dependency between Shannon diversity and garden area, there was found to be a moderate but statistically insignificant R value ($R = 0.52$, $P = 0.08$; Figure 3(a)). The Fisher alpha index R value was even lower ($R = 0.09$, $P = 0.77$; Figure 3(b)). However, the Shannon and Fisher alpha diversity indices, despite their different assumptions, reflect an essentially similar trend in ant diversity with a linear correlation coefficient $R = 0.81$ when the one was regressed against the other. The Shannon value for ant species evenness and garden area was similar to the Shannon diversity value ($R = 0.50$, $P = 0.09$; Figure 3(c)).

Community composition

Cluster analysis revealed a strong pattern, indicated by a bifurcation just below the 20% similarity tick on the Y-axis, between the ant assemblages of sites SW1, SW2, SW3, SW5, SE4, SE5 and the remainder of the sites (Figure 4). *Pheidole megacephala* was in high abundance at these six properties. Mann-Whitney U-tests showed that species richness, species diversity and species evenness were all significantly lower in *P. megacephala* gardens ($P \ll 0.01$ in all cases). A similar pattern emerged for the three sites (NW5, NE2 and SE1) in which *L. humile* was present. The remaining gardens, including SE3 and SW4 (where *P. megacephala* was present in low numbers) and NE3 (dominated by *Tetramorium bicarinatum*), all had a similar species composition and did not separate out before the 40% similarity tick on the Y-axis.

Functional groups

Seven functional groups and subgroups were represented among the Garden material, these being tramp species (the largest group), Subordinate Camponotini, Opportunists, Hot climate specialists, Generalised myrmicines, Dominant Dolichoderinae and Cryptic species. No Cold climate specialists or Solitary predators were recovered. The functional group categories represented by the garden ant material are displayed in Figure 7(1).

(2) *Freeway study*

A total of 6,558 ants consisting of 56 species were sampled at the 14 sites (Table 3). The only exotic species sampled were *P. megacephala* (2 individuals) and *T. simillimum* (127 individuals). These two species constituted 2.0% of the total catch. The most abundant ant was *I. chasei* (1370 individuals, or 20.9% of the total), followed by *Crematogaster laeviceps chasei* Forel (1143; 17.4%) and *Iridomyrmex bicknelli* Emery (823; 12.5%). The mean number of ants collected at each site was 468. The greatest number of ants was recorded from site 3 (1872, of which 1136 specimens were *C. laeviceps chasei*) and the least number was recorded at site 0 (18 individuals).

Species richness, diversity and evenness

Unfortunately, due to limitations in the design (i.e., replicates were available only for 6A, 6C, 6D, 6E and 6F), species richness, diversity and evenness figures and statistics are not equivalent for the respective chronosequences and any attempt to represent them graphically would be misleading. However, no pair of transects within each site yielded fewer than six species, the lowest number being 6 in site 0 and the greatest number 26 in site 3.

(3) *Community composition*

Cluster analysis revealed only one strong bifurcation below the 20% similarity tick on the Y-axis. This was the bush control block (Figure 5). At a higher level of similarity, the bare sand site 0 (0 years of rehabilitation) and site 6F (nine to ten years of rehabilitation) were more similar to each other than they were to the other sites.

Between them, these two sites had only one myrmicine species and *Melophorus* were also rare or absent. Overall, the dendrogram for this study has a more even topology than that for the Garden study, indicating greater evenness of ant abundance across the sites.

Functional groups

Nine functional groups and subgroups were represented among the Freeway material. In addition to those collected in gardens, Cold climate specialists and Solitary predators were also recovered. Opportunists, Hot climate specialists, Generalised myrmicines and Dominant Dolichoderinae were represented in approximately equal proportions. The functional group categories represented by the Freeway ant material are displayed in Figure 7(2).

Overall Community composition (both studies)

The NMDS ordination of Freeway sites was done using the Bray-Curtis similarity index with the ant abundance fourth-root transformed so that it could be incorporated with the garden ant abundance data to produce an ordination figure that was a composite of both sets of data. The result was an ordination figure with 53.65% (i.e., 0.5365) of the variability explained by Axis 1 (= Coordinate 1) and 18.54% (i.e., 0.1854) of the variability explained by Axis 2 (= Coordinate 2). Using a suitable ellipse level to enclose clusters of most similar plots (this was 70% ellipse concentration) there was found to be a clear demarcation in multidimensional space between the bush control ant assemblage from the Freeway study and the other assemblages (Figure 6). The ant data points from the remaining Freeway transects clustered together, inside of or on the boundary of one ellipse. The data points from the garden sites were more loosely spread across multidimensional space. However, three linked assemblages of ants could still be detected among the latter. The three sites in which Argentine ants had been collected (i.e., NE2, NW5 and SE1) were only loosely associated with the main cluster of sites, NE2 and NW5 falling outside of the ellipse at the 70% setting. Sites NW5 and NE3 were unique in that large numbers of the introduced *Tetramorium bicarinatum* were collected: this ant was absent from all other sites in both studies. The six properties (i.e., SE4, SE5, SW1, SW2, SW3 and SW5) in which African big-headed ants (*P. megacephala*) were most abundant formed another cluster, and the remaining properties that were mainly dominated by the native *I. chasei* (i.e., SE2, NE1, NE4, NE5, NW2, NW3 and NW4) formed a third cluster. All of these sites, with the exception of SW5, were within the ellipse at the 70% level, but nonetheless well-separated. Sites SE3 and SW4, with small numbers of the African big-headed ant, occupied an intermediate position between the *I. chasei* and the *P. megacephala* clusters.

The SIMPER analysis revealed that the African big-headed ant (26.49%) contributed most to the dissimilarity between the Garden study and the Freeway study. The second most important species was *Iridomyrmex chasei* (16.66%). These two species were collected in very large numbers from a number of the gardens, but were in much lower numbers at the Freeway sites, *P. megacephala* being represented by only two workers. *Tetramorium simillimum* (7.48%), *Iridomyrmex bicknelli* (4.85%, mainly in Freeway sites) and *Tetramorium bicarinatum* (4.58%, abundant in just two gardens but absent elsewhere) were other major contributors. Altogether, these five species contributed 64.3% of the cumulative dissimilarity between garden sites and Freeway sites.

The ant functional group results indicate an extremely depauperated fauna in the gardens but a much more diverse fauna in the Freeway sites (Figure 7). Of the groups proposed by Andersen (2000), specialist predators and the sub-group cold-climate specialists were completely absent from the Garden study in which tramp species, Opportunists, Dominant Dolichoderinae and Cryptic species made up most of the catch. In the Freeway study, all of the seven major groups and two of the three sub-groups were represented, with numbers evenly distributed between most of the groups and sub-groups. Only two tramp species were represented in the Freeway material.

Discussion

As predicted in the Introduction, the two studies revealed two quite different ant profiles. Somewhat unfortunately, however, the structural limitations of the methodology followed in the Freeway study limit closer and more detailed analysis of differences in species richness and evenness for the two studies. The raw data

from the first study, on a first inspection, are consistent with data from similar studies conducted in the Perth metropolitan area (e.g., Heterick et al. 2000; May and Heterick 2000; Callan and Majer 2009) and reveal a highly impacted ant fauna, with a relatively large proportion of introduced and opportunistic species (38% of the total ant richness – this figure can be derived from Table 2 and Figure 7) and a dearth of more specialised forms. Properties where the African big-headed ant was present are particularly depauperate, as indicated by the Mann-Whitney U tests. In all, only six of the functional groups and sub-groups discussed by Andersen (1990, 1995, 2000) were present, with Cold climate and Tropical climate specialists and Solitary predators being completely absent. However, the design of the previous studies done in urban properties (i.e., Heterick et al. 2000; May and Heterick 2000) was different insofar as the choice of the 12 gardens used for each of those studies was determined by their ant composition. In the first study, four gardens infested by *P. megacephala* were compared with eight control gardens containing only native species, and in the second study four gardens infested by *L. humile* and three infested by *P. megacephala* were compared with five native control gardens. The total number of nominal ant species identified in the three studies is very similar (i.e., 26 in the current study, 27 in Heterick et al. 2000 and 26 in May and Heterick 2000), but due to taxonomic advances and reduction in taxonomic ‘lumping’, the totals in the two earlier investigations should probably be expanded slightly. More significantly, however, one or both of the two previous studies revealed genera typically connected with native woodland (e.g., *Anisopheidole*, *Anonychomyrma*, *Hypoponera*, *Papyrius* and *Tapinoma*) that were not identified in the current study. The only indisputably novel taxa that were included in the 2011 Garden study were *Carebara* sp1 and *Tetramorium impressum* (a common opportunist in both urban and rural habitats). Currently, there are no comparable data from other major Australian cities (the nearest approach is Nattrass and Vanderwoude (2001) in relation to fire ants (*Solenopsis invicta* Buren) in the Brisbane area), and these would be desirable in order to investigate whether Perth urban ant fauna is subject to particular climatic, biotic or other environmental influences.

In the Garden study, although no significant correlation was identified when ant species richness was compared with three specific variables, i.e., property size, garden area or plant richness, in properties infested by the African big-headed ant, there were weak and non-significant positive correlations between garden area and ant species diversity and ant species evenness, respectively. The addition of a suite of gardens with a size greater than 350 m² may result in the detection of significant positive correlation between garden size and ant species diversity at the $\alpha = 0.05$ level. Nonetheless, the fact remains that, in terms of sheer abundance, there was an overwhelming preponderance (almost 72%) of ants of exotic origin, consisting principally of the African big-headed ant. Garden size was not itemized in detail by Majer and Brown (1986) (although it is mentioned), but suburb age was recorded. Those authors found a significant (i.e., $P < 0.05\%$) positive correlation between ant species diversity and ant species richness and area of garden and age of garden, respectively. The findings are incorporated in a single figure (Figure 1 in the Majer and Brown (1986) paper), and do not reveal data points on the continuum. Significantly, however, and allowing for the much more rudimentary taxonomy (most of the ants in Majer and Brown’s study being referred to by voucher numbers), the number of introduced and opportunistic species in the 1986 study is approximately 26% (eight functional groups and sub-groups present), and the number of introduced and opportunistic species reduces again to approximately 19.5% (eight functional groups and sub-groups present) in the Kwinana Freeway study (from Table 3). The three studies may in fact be even further apart on a continuum: although included by inference in ‘Dominant Dolichoderinae’ in Andersen’s 1990 and 1995 papers, the species *Iridomyrmex chasei*, *I. suchieri* and *I. suchieroides* are typical of highly disturbed sites where they reach their greatest numbers (Brian Heterick, this paper, pers. comm.), and thus have more in common with the Opportunists functional group than with many of their own congeners. This makes the ecological dimensions of the Garden study even more skewed when it is compared with the Freeway study and that recorded by Majer and Brown (1986). All of this suggests that areas of regrowth and possibly larger lawn and garden sizes are conducive to both increased ant richness, an increased number of functional groups (particularly Solitary predators and Cold climate specialists) and a proportionately smaller number of species adapted to disturbed habitats. An examination of the mean ant species richness (9.8 species per garden) recorded by Majer and Brown (1986) and that recorded for the current study (5.8 species per garden, reducing to 4.1 species if the introduced taxa are taken out of the equation) is also instructive: the gardens examined by the two earlier authors were part of generally much larger properties (mainly the old ‘quarter-acre-block’) than those used in the present garden study. Properties of these dimensions have disappeared rapidly since the 1990’s due

to urban infill. Equally predictably, considering the much greater surface area involved and the different vegetation features, the Freeway study recorded higher mean ant species richness (17.1 species per quadrant) than either of the garden studies. The SIMPER analysis confirms the important role of exotic and opportunistic ant species in driving changes in ant communities when habitat loss is factored in.

The fact that there is unlikely to be any overlap between the gardens used by Majer and Brown and the Garden study in this paper means no definitive conclusions can be drawn about when changes in the ant fauna of Perth gardens since 1986 may have occurred. Nevertheless, the studies by May and Heterick (2000) and Heterick et al. (2000), combined with the data from the Garden study, make it very likely that exotic species have permeated much of the Perth metropolitan area since the cessation of heptachlor spraying for Argentine ants in the late 1980's (see Figures 2 and 3 in Heterick et al. (2000) and the Discussion in that paper). This process appears to be ongoing. As suggested in the first paragraph of the Discussion, local extinction events may have taken place in urban gardens near to the CBD as recently as the last 10 years.

The high ant species richness, ant diversity and ant evenness values of the Freeway study compared with the same values for the Garden study are also consistent with the findings of Graham et al. (2009) who found that, in disturbed landscapes, ant species richness was greatest with moderate relative disturbance (i.e., 43%) and evenness (=‘equitability’) greatest with no disturbance. The very low, even negligible diversity and evenness values but high ant abundance in the Garden study also reflect the findings of Graham et al. (2009) on ant species richness and abundance in highly disturbed sites. In the latter study, ant species richness was reduced (with a unimodal regression curve) but ant abundance was greatest in the presence of relatively high disturbance (i.e., 85%).

Trends in the ordination (Figure 6) indicate that Perth garden ant fauna is substantially different from that found in adjoining native woodland habitat. There is also no suggestion that the fauna may be co-extensive with that found in regrowth corridors. The conclusion to be drawn is that small gardens and lawns in the Perth metropolitan area simply lack the habitat requirements of the vast majority of native ant species once found in the region (Rossbach and Majer 1983). These requirements would undoubtedly include adequate food supplies (seeds, nectar, honeydew and invertebrate carrion and prey), nest sites, soil that is sufficiently stable for ground nesters and protection from aggressive invasive ant species such as Argentine and African big-headed ants. Conversely, spatially larger areas seeded with native plants, such as the sites used for the Freeway study, have the capacity to support a relatively healthy population of native ants representing a good spread of functional groups. The carrying capacity may be increased even further if larger stones and logs, and leaf and twig litter are introduced to multiply the number of niches available for ant nests. The main caveat is that, if such sites are surrounded by housing estates with a high level of infill, these secondary bush corridors may eventually be infiltrated by exotic ants from the housing areas. Early stages of invasion may be detectable in sites 3 and 4 of the Freeway study, where a solitary African big-headed ant was collected in each case. The weedy but apparently benign exotic, *Tetramorium simillimum*, is already present at five regrowth sites of different ages. Majer (1985) found that ant species richness declined markedly in rehabilitated sand-mined sites on Stradbroke Island older than six years, due to the explosion in numbers of African big-headed ants. The rehabilitated regrowth sites in the Freeway study may be at similar risk, particularly with escalating clearing for new suburbs to the south of Perth.

Comparison with studies done in central and northern Europe (e.g., Vepsäläinen et al. 2008; Ślipiński et al. 2012) highlights several important differences to the situation in Australia, the most striking of which is the potential size of the ant population examined and the impact of urbanisation upon it. Whereas the two works mentioned discuss around 30 species of urban ants, the potential number of species in and around the Perth metropolitan area is far greater. Heterick (2009) identifies 218 ant taxa in the Swan Coastal Plain, which is now dominated by the sprawling Perth Metropolitan area. Possibly 200 or more species may once have inhabited the area now occupied by the greater Perth region (which also includes the Jarrah Forest Botanical District). The other major difference is the impact of invasive species in South-western Australian. Not only does the Garden study reveal a depauperated ant population, but also the presence of no less than six invasive species whose origin mostly lies overseas. This is not the case with the above two European studies, where all taxa appear to be Palaearctic in origin. Also unlike the study of Ślipiński et al., the Garden ant fauna contains unique elements, native as well as non-native (see Tables 2 and 3), that suggest that it is not merely a simplified or nested subset of the Kwinana Freeway ant fauna.

Despite the generally depressing picture presented by this survey of the state of Perth's native ant fauna in urban gardens, there was at least one surprise: this was the appearance in the catch of a minute, dimorphic myrmicine, a species of *Carebara* (formerly, *Oligomyrmex*). *Carebara* species are facultative predators on brood and/or eggs of other ants and termites (Shattuck 1999). In the Garden study, only a solitary minor worker was found on each of sites SE3 and NE3, respectively. This species appears to be quite distinct to an undescribed *Carebara* present in the Darling Range, just to the east and south-east of Perth, and there is a high likelihood that it is not a species native to the area. Site SE3 also recorded moderate numbers of the African big-headed ant, while the introduced *Tetramorium bicarinatum* was by far the most abundant ant on site NE3. Termite-infested wood and plentiful litter were present on at least site NE3, and termites may form part of the diet of the *Carebara* colony from which the solitary worker was drawn. The fact that four cryptic species (15% of the total catch) were found in the Garden study also suggests that native ants with a cryptic lifestyle are generally able to withstand to some degree the impact of invasive species and garden and lawn maintenance practices that are anathema to most epigaeic ant taxa. This conclusion is not novel: Heterick et al. 2000 also observed that Opportunists and Cryptic species are the ants most resilient to high levels of disturbance and the incursion of introduced species.

The conclusions that can be drawn from these two studies illustrate the importance of cultivating suitable habitat for those native organisms that otherwise cannot survive in a highly urbanised environment. Although the process of densification is currently seen as an imperative by various government and civil authorities because of Perth's rapidly growing population, proper environmental planning should incorporate green areas of native regrowth and/or relictual bushland so as to retain at least some semblance of the original flora and fauna. Ants, as a proxy for other invertebrate taxa, are an important indicator of the success of this process. The Kwinana Freeway, with its accompanying strips of rehabilitated native vegetation, cuts a swathe through both northern and southern suburbs, and thus represents both a possible reservoir and a refugium for native ant species through much of the central Perth metropolitan area. The issue is not a purely aesthetic one: this paper confirms the findings of similar studies in the Perth region, namely, that a few ants, notably peridomestic pests such as the Argentine and African big-headed ants, flourish in areas of pure infill, and these will become an increasing nuisance to householders where no provision is made for the natives.

Due to the design limitations mentioned above; i.e., (i) the fact that the vegetation seen in both surveys was either regrowth or purely exotic and (ii) the small scale of the two studies that were not designed to test the model proposed by Alberti and Marzluff (2004), we restrict comment on that model purely to tentative observations. Thus, the results from the Garden ant study appear to represent an extreme situation of a fauna decimated by urban sprawl, with (in this case) no natural land cover whatever remaining. The hardiest natives have survived in some gardens, but in others the original ant profile has been completely destroyed, and no native species occur. These latter gardens are dominated by exotic ants that are well adapted to outcompete native species due to their tramp characteristics (e.g., multiple queens, adaptation to ephemeral nests, unicoloniality, etc.). Based on the abovementioned conceptual model, the provision of some native ground cover by householders may reduce resilience in favour of a different equilibrium and encourage the colonisation of native ant species, while the cessation of artificial reticulation may simultaneously discourage humidity-loving exotics. However, the trend towards greater consolidation of urban infill with mooted high-rise, and replacement of lawns by concrete aprons is likely to further depress the number of ant species capable of living in an even more extreme environment. The Freeway study illustrates a quite different situation that more closely approximates the planned development scenario. Here, the ants in the respective chronosequences represent seral stages towards a climax community. There is a qualification, however: the presence of a weedy exotic (*Tetramorium simillimum*) in even the oldest of the chronosequences suggests that an ant community truly representative of the original ecosystem may be many years further down the track, if it ever eventuates. In a study of sand-mined areas near Eneabba, Western Australia, (Bisevac and Majer 1999) some ant species present in native heathland had not returned in even the oldest rehabilitated plots. Subtle changes in soil profile, loss of mycorrhizal associations and absence of certain native plant species that cannot be cultured artificially may be irreversible and permanent. Because Australian plants and animals are highly specialised and often environmentally sensitive, the switch back to the *status quo* prior to urbanisation may be much more difficult than is the case in the northern hemisphere

Acknowledgments

We would like to thank all householders involved in the study for their cooperation, Professor Jonathan Majer and two anonymous referees, for comments on an earlier draft, Dr Nihara Gunawardene for providing statistical advice, Mr Shane Collins of the Mains Road Department for logistical support and approval to work within the road reserve (the Freeway study) and Curtin University for providing materials, equipment and facilities for the research. Special thanks go to Ms Tracey Ovington of the Main Roads Department for providing the information displayed in Table 1.

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Figure and Tables

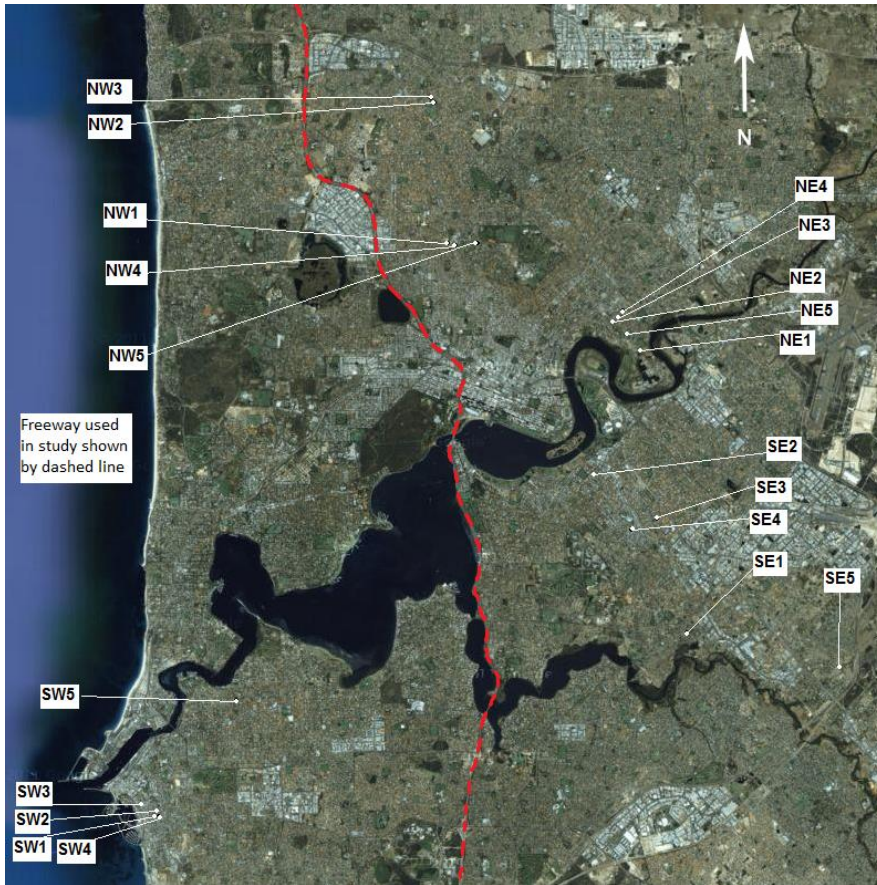
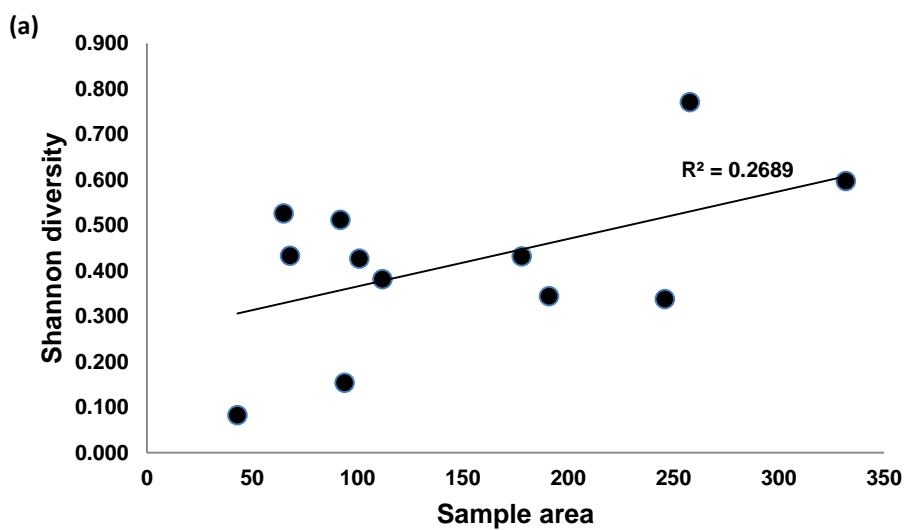


Figure 1. Location of properties used for the Garden study within the Perth Metropolitan Area [<http://maps.google.com.au/>]. The red dashed line represents the Kwinana Freeway.



Figure 2. Location of regrowth sites used for the Freeway study within the Perth metropolitan area. The red dashed line represents the Kwinana Freeway extension and the southern Perth metropolitan corridor surrounds it (textured areas) [<http://maps.google.com.au/>].



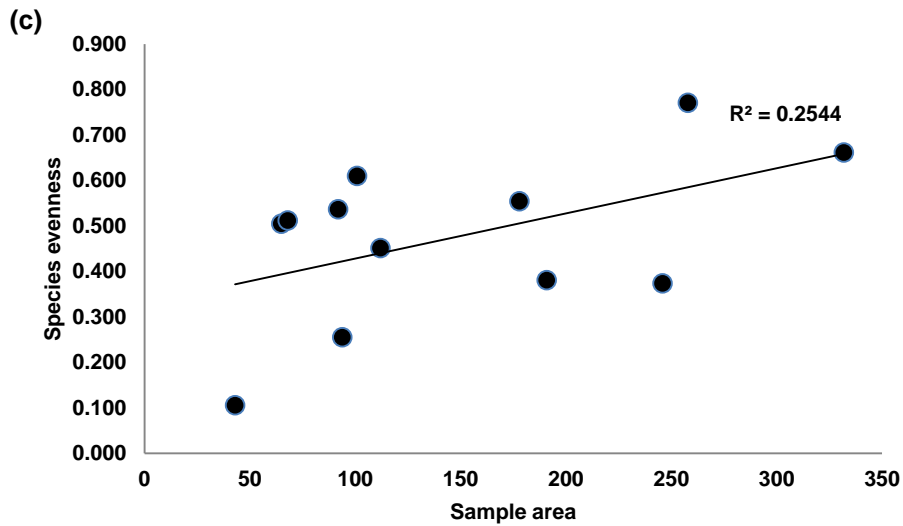
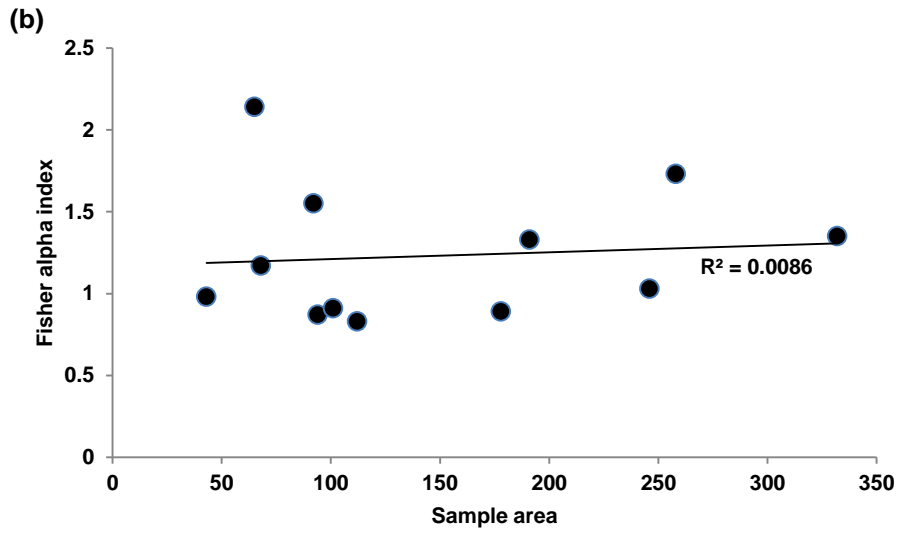


Figure 3. Shannon diversity index (a) Fisher alpha index of diversity (b) and Shannon species evenness (c) of non-*Pheidole megacephala* infested properties plotted against garden area, with line of best fit.

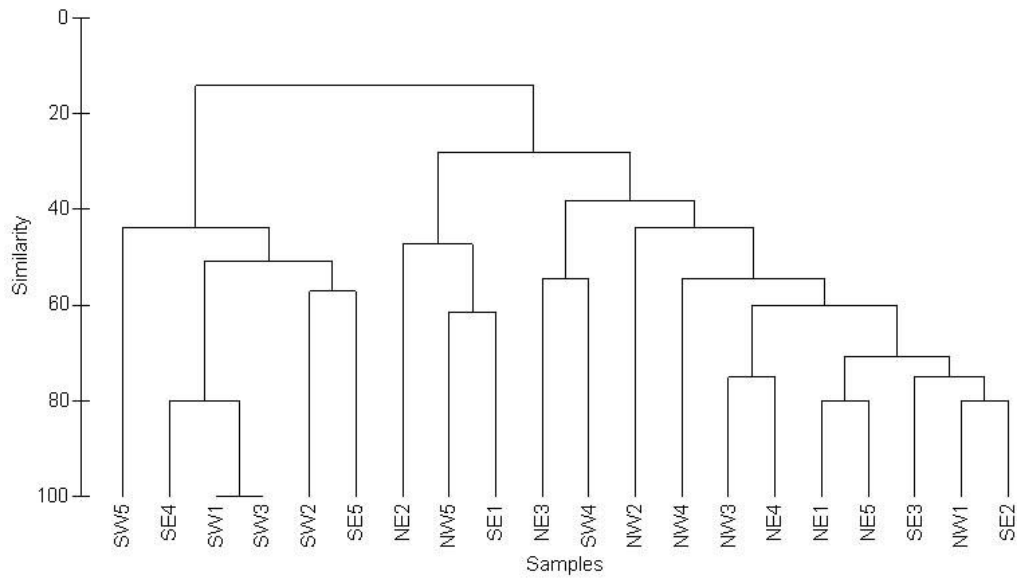


Figure 4. Cluster analysis dendrogram showing similarity between the ant assemblages of different sites in the Garden study.

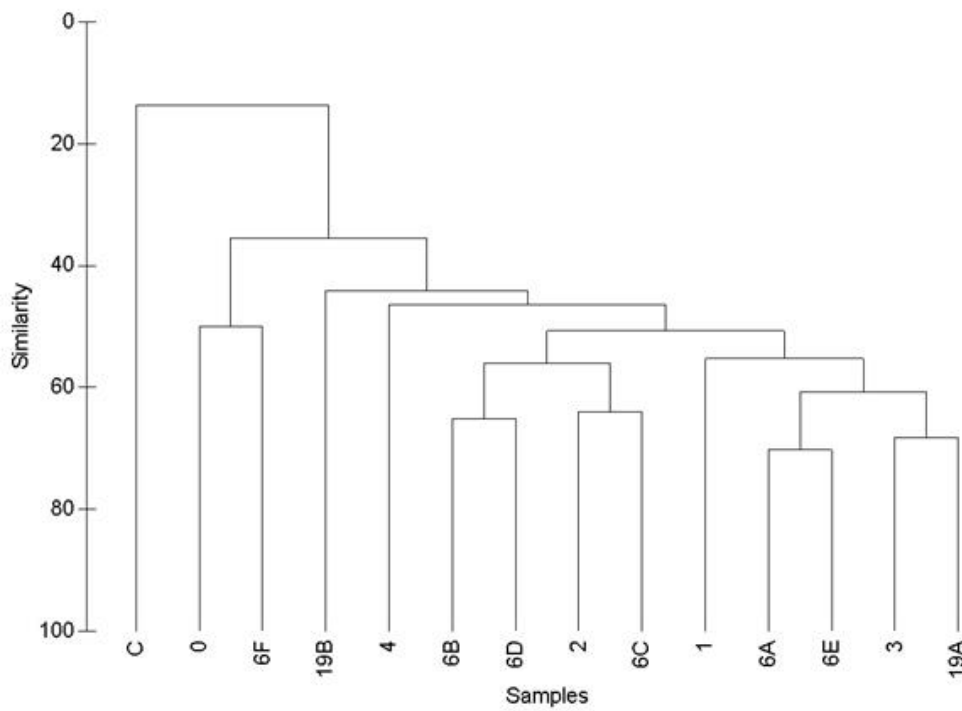


Figure 5. Cluster analysis dendrogram showing similarity between the ant assemblages of different sites in the Freeway study.

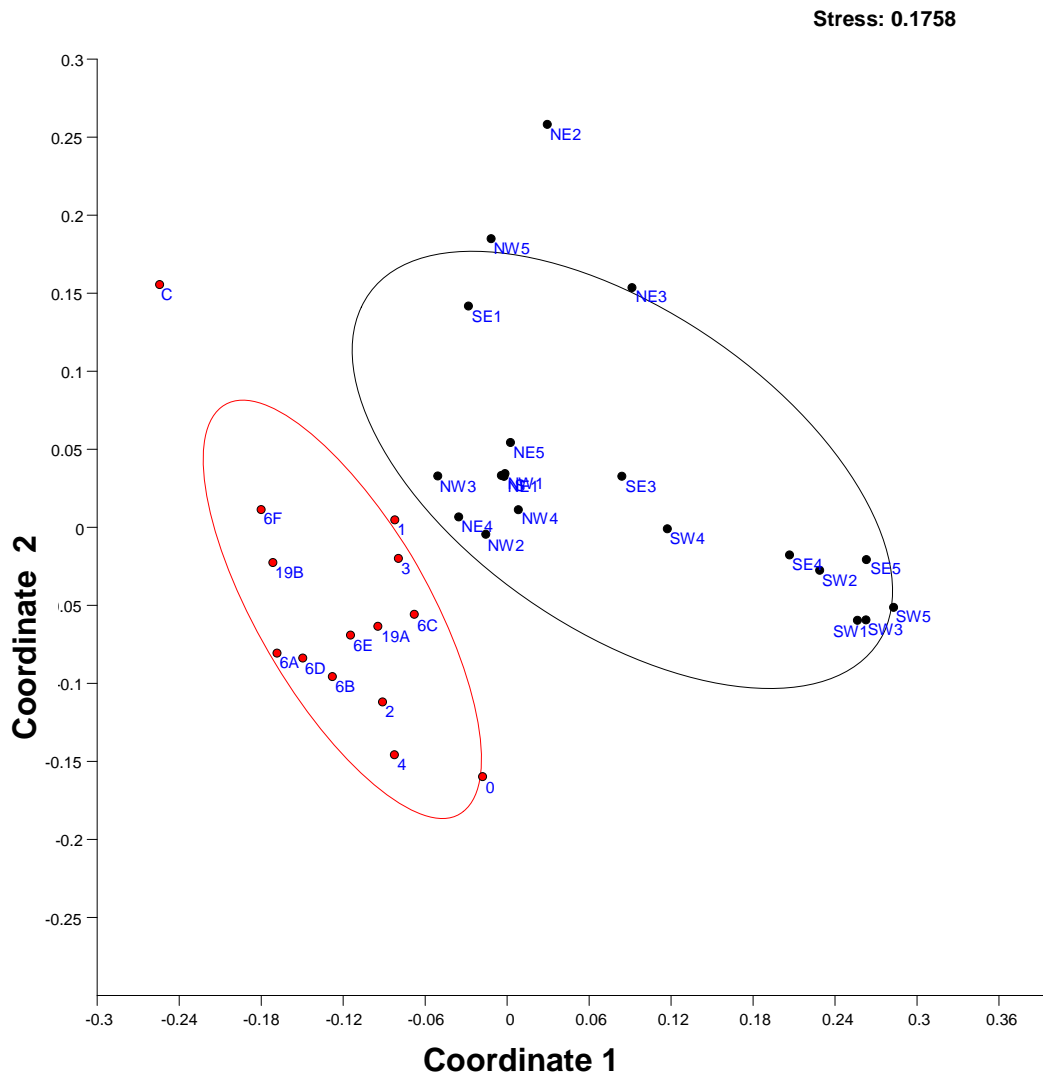


Figure 6. Ordination by non-metric multidimensional scaling of fourth-root transformed ant assemblage numbers from 20 gardens, one bush control site and 13 sites of rehabilitated bushland. Sites from the rehabilitated bushland are represented by a number and gardens by a letter as the initial character. C was a bushland remnant site used as a control. Ellipses enclose the most similar sites: ellipse concentration level set at 70%.

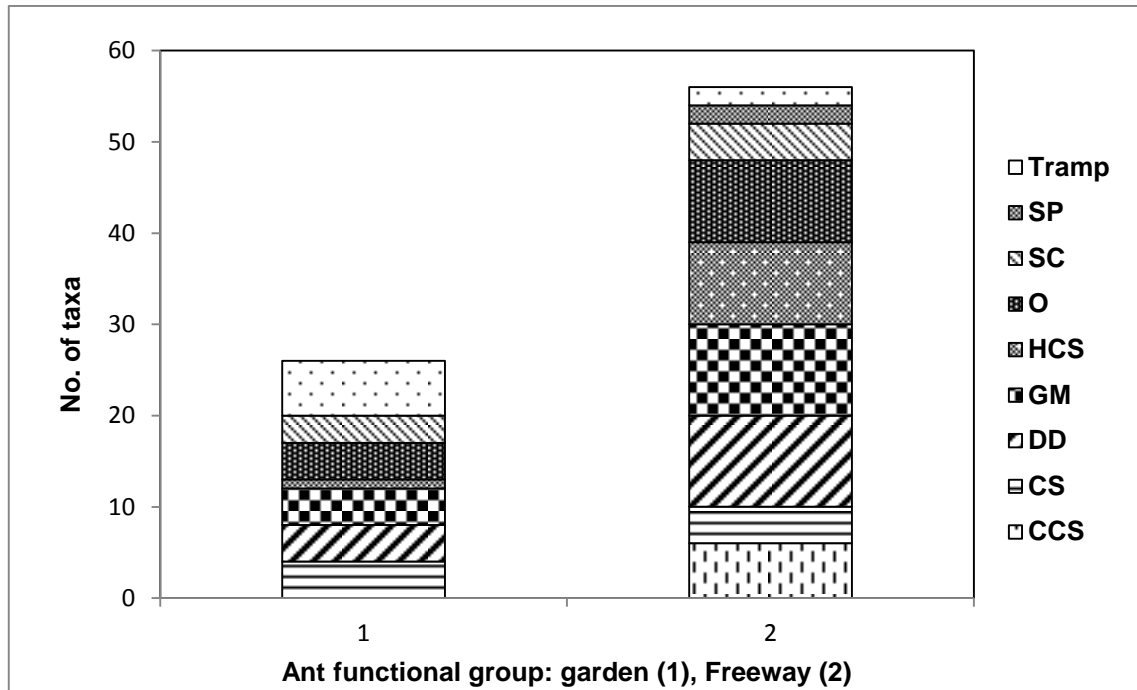


Figure 7. Ant functional groups and sub-groups represented in the Garden (1) and Freeway (2) studies. Legend: SP – Solitary predators; SC – Subordinate Camponotini; O – Opportunists; HCS – Hot climate specialists; GM – Generalised myrmicines, DD – Dominant Dolichoderinae, CS – Cryptic species, CCS – Cold climate specialists

Table 1. Floral characteristics and exact location of the sites used in the Freeway study. Apart from Site 0, which was bare sand, all sites supported some native vegetation. Site C had a cover of remnant native vegetation, and the other sites had a vegetative cover of planted or seeded native plants.

Site No.	Date of Planting/Seeding	Age of Plantings/seedlings as at 2011 (years)	Location	Plant species (nb., all WA native species, though not necessarily local)
C	-	-	South Street / Kwinana Freeway	Remnant native vegetation
0	-	-	Emerald Park development, Mortimer Road	Bare sand
1	2010	1	Leach Highway / Orrong Road	<i>Acacia</i> spp., <i>Acanthocarpus preissii</i> , <i>Agonis flexuosa</i> , <i>Allocasuarina humilis</i> , <i>Anigozanthus</i> spp., <i>Arthropodium preissii</i> , <i>Banksia</i> spp., <i>Calocephalus brownii</i> , <i>Calothamnus</i> spp., <i>Conostylis</i> spp., <i>Eremophylla glabra</i> , <i>Gompholobium</i> spp., <i>Grevillea</i> spp., <i>Hakea</i> spp., <i>Hemiandra pungens</i> , <i>Hovea pungens</i> , <i>Kunzea ericifolia</i> , <i>Melaleuca</i> spp., <i>Olearia axillaris</i> , <i>Patersonia occidentalis</i> , <i>Rhagodia baccata</i> , <i>Scaevola crassifolia</i> , <i>Templetonia retusa</i>
2	2008	3	Safety Bay Road / Kwinana Freeway	<i>Acacia lasiocarpa</i> , <i>Anigozanthus manglesii</i> , <i>Bossiaea eriocarpa</i> , <i>Carbobrotus virescens</i> , <i>Conostylis</i> spp., <i>Eucalyptus rudis</i> , <i>Hovea trisperma</i> , <i>Kennedia prostrata</i> , <i>Macrozamia riedlei</i> , <i>Melaleuca</i> spp., <i>Patersonia occidentalis</i> , <i>Rothanthe chlorocephala</i> ssp. <i>rosea</i> , <i>Scaevola crassifolia</i> , <i>Stirlingia latifolia</i> , <i>Verticordia densiflora</i> , <i>Xanthorrhoea</i> sp.
3	1982, 2006/2007	4-29	Leach Highway / Kwinana Freeway	(not available)
4	Seeded 2005, planted 2006	5-6	Roe Highway / Kwinana Freeway	<i>Allocasuarina humilis</i> , <i>Banksia</i> spp., <i>Conostylis</i> spp., <i>Corymbia calophylla</i> , <i>Eucalyptus todiana</i> , <i>Hypocalymma</i> spp., <i>Regelia</i> spp., <i>Melaleuca</i> spp., <i>Xanthorrhoea preissii</i> and others
6A	2001, 2002	9-10	Berrigan Drive / Kwinana Freeway	<i>Acacia</i> spp., <i>Banksia</i> spp., <i>Calothamnus</i> spp., <i>Eucalyptus</i> spp., <i>Hypocalymma</i> spp., <i>Kunzea</i> spp., <i>Melaleuca</i> spp., <i>Regelia</i> spp. and others
6B	2001, 2002, 2010	1-10	Armada Road / Kwinana Freeway	Open Banksia Woodland: <i>Acacia</i> spp., <i>Allocasuarina</i> spp., <i>Anigozanthus humilis</i> , <i>Banksia</i> spp., <i>Bossiaea eriocarpa</i> , <i>Calothamnus quadrifidus</i> , <i>Conostylis aculeata</i> , <i>Dasyopogon bromeliifolius</i> , <i>Hardenbergia comptoniana</i> , <i>Hibbertia hypericoides</i> , <i>Kennedia prostrata</i> , <i>Kunzea ericifolia</i> , <i>Petrophile linearis</i> , <i>Regelia inops</i>
6C	2001, 2002	9-10	Rowley Road / Kwinana Freeway	Open Eucalypt Woodland: <i>Acacia</i> spp., <i>Banksia</i> spp., <i>Calothamnus</i> spp., <i>Corymbia calophylla</i> , <i>Eucalyptus marginata</i> , <i>Eucalyptus todiana</i> , <i>Melaleuca</i> spp. and others
6D	2001, 2002	9-10	Anketell Road / Kwinana Freeway	<i>Acacia</i> spp., <i>Allocasuarina fraseriana</i> , <i>Banksia attenuata</i> , <i>Banksia menziesii</i> , <i>Calothamnus</i> spp., <i>Corymbia calophylla</i> , <i>Eucalyptus rudis</i> , <i>Eucalyptus todiana</i> , <i>Melaleuca</i> spp. and others
6E	2001, 2002	9-10	Mortimer Road / Kwinana Freeway	Open Eucalypt Woodland: <i>Acacia</i> spp., <i>Banksia</i> spp., <i>Calothamnus</i> spp., <i>Corymbia calophylla</i> , <i>Eucalyptus marginata</i> , <i>Eucalyptus todiana</i> , <i>Melaleuca</i> spp. and others
6F	2001, 2002	9-10	Mundijong Road / Kwinana Freeway	<i>Acacia</i> spp., <i>Anigozanthus</i> spp., <i>Eremaea pauciflora</i> , <i>Hakea</i> spp., <i>Hardenbergia comptoniana</i> , <i>Kunzea</i> spp., <i>Melaleuca</i> spp., <i>Pericalymma elliptica</i> , <i>Petrophile linearis</i> , <i>Phyllanthus calycinus</i> , <i>Viminaria juncea</i>
19A	1979, 1982, 1989, 2006	5-33	Canning Highway / Kwinana Freeway	(not available)

19B	1982	29	Leach Highway / Albany Highway	<i>Acacia</i> spp., <i>Adenanthos cygnorum</i> , <i>Adriana quadripartita</i> , <i>Allocasuarina fraseriana</i> , <i>Banksia</i> spp., <i>Calothamnus quadrifidus</i> , <i>Chamelaucium</i> spp., <i>Corymbia calophylla</i> , 14 <i>Eucalyptus</i> spp., <i>Hakea</i> spp., <i>Hardenbergia comptoniana</i> , <i>Hovea trisperma</i> , <i>Kennedia prostrata</i> , <i>Kunzea ericifolia</i> , <i>Macrozamia riedlei</i> , <i>Melaleuca</i> spp., <i>Nuytsia floribunda</i> , <i>Xanthorrhoea preissii</i>
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. Ant species collected from 20 Perth gardens for the Garden study. *denotes an introduced species. Letters in square brackets refer to Ant Functional Group (Andersen, 1995): [CS] = Cryptic species, [DD] = Dominant Dolichoderinae, [GM] = Generalised myrmicines, [HCS] = Hot climate specialists, [O] = Opportunists, [SC] = Subordinate Camponotini. Watering regime: ‘W’ denotes regular watering by reticulation or hand.

Variable	NW1	NW2	NW3	NW4	NW5	NE1	NE2	NE3	NE4	NE5	SW1	SW2	SW3	SW4	SW5	SE1	SE2	SE3	SE4	SE5
Property size	447	456	729	447	823	519	372	215	348	1006	453	492	636	346	418	531	327	246	416	515
Garden/Lawn size	65	191	258	68	332	112	94	43	178	246	95	88	291	75	158	101	92	56	48	186
Plant Richness (Approximate)	2	7	5	5	1	1	1	6	9	1	3	5	1	5	3	5	2	3	2	2
Watering Regime	U	U	U	U	W	W	W	U	W	W	U	U	W	W	W	W	W	U	U	U
Taxon																				
Dolichoderinae																				
<i>Iridomyrmex bicknelli</i> Emery [DD]	2	2		9	9											1	1			
<i>Iridomyrmex chasei</i> Forel [DD]	129	357	74	255		789		1	528	1713				55			23	1		
<i>Iridomyrmex suchieri</i> Forel [DD]	9		71		15		5									39	2	26		
<i>Iridomyrmex suchieroides</i> Heterick & Shattuck [DD]	23		5			6			66	12							48	24		
<i>Linepithema humile</i> (Mayr)*					26		77									47				
<i>Ochetellus glaber</i> gp. sp. JDM 19 [O]			16	3							4	8	1				6		1	
Ectatomminae																				
<i>Rhytidoponera metallica</i> (F. Smith) [O]			8																	
Formicinae																				
<i>Camponotus claripes nudimalis</i> Forel [SC]										1										
<i>Camponotus gasseri</i> (Forel) [SC]		1		1																
<i>Camponotus minimus</i> Crawley [SC]		3																		
<i>Melophorus turneri perthensis</i> Wheeler [HCS]		2	6						35											
<i>Nyländeria glabrior</i> (Forel) [O]					45															
Myrmicinae																				
<i>Cardiocondyla atalanta</i> Forel	1	7	114			187				17							334	1		
<i>Cardiocondyla nuda</i> (Mayr)*					9		1			16				1					3	
<i>Carebara</i> sp. 1								1											1	
<i>Crematogaster laeviceps chasei</i> Forel [GM]	1	2																		
<i>Monomorium 'sydneyense'</i> (10-seg. antenna) [GM]												5								
<i>Pheidole ampla perthensis</i> Crawley [GM]			208						2											
<i>Pheidole megacephala</i> (Fabricius)*	1										1028	497	2409	136	1641			272	1122	4670
<i>Pheidole vigilans</i> (F. Smith)*	10				40															
<i>Solenopsis clarki</i> Crawley [CS]	3			6		2	1	4		3		5					2	1		1

<i>Strumigenys perplexa</i> (F. Smith) [CS]																				2
<i>Tetramorium bicarinatum</i> (Nylander)*					305					441										
<i>Tetramorium impressum</i> (Viehmeyer) [O]										1										
<i>Tetramorium simillimum</i> (Mayr)*	184	161	33	166	62	102		7	87	564			26		137	23	23		6	
Ponerinae																				
<i>Pachycondyla (Brachyponera) lutea</i> (Mayr) [CS]	1		23	17		19			28	59					1	83	1			
Abundance	364	535	558	457	511	1106	84	456	746	2385	1032	515	2410	218	1641	225	522	353	1129	4671
Species richness	11	8	10	7	8	7	4	6	6	8	2	4	2	4	1	5	9	10	3	2
Shannon index (H')	0.53	0.34	0.77	0.43	0.60	0.38	0.15	0.08	0.43	0.34	0.01	0.08	0.00	0.40	0.00	0.43	0.51	0.38	0.02	0.00
Fisher alpha index	2.14	1.33	1.73	1.17	1.35	0.83	0.87	0.98	0.89	1.03	0.24	0.59	0.21	0.70	0.10	0.91	1.55	1.92	0.37	0.20
Evenness (J')	0.50	0.38	0.77	0.51	0.66	0.45	0.25	0.11	0.55	0.37	0.04	0.14	0.01	0.66	0.00	0.61	0.54	0.38	0.04	0.00

Table 3. Ant species collected from a bush control site and 13 regrowth sites (12 along the Kwinana freeway and one beside Leach Hwy) for the Freeway study. *denotes an introduced species. Ant Functional Group symbols as for Table 2 with the following additional groups: [CCS] = Cold climate specialists, [SP] = Solitary predators.

Variable	0	1	2	3	4	6A	6B	6C	6D	6E	6F	19A	19B	C
Size of quadrant (m ²)		5281	5782	4287	10728	13388	8971	7149	5315	6470	5921	7239	5040	7915
Revegetation age (years)	0	1	2	3	4	6	6	6	6	6	6	19	19	
Taxon														
Dolichoderinae														
<i>Anonychomyrma iterans perthensis</i> (Forel) [DD]														13
<i>Doleromyrma rotnestensis</i> (Wheeler) [O]					19	2	1							2
<i>Dolichoderus clusor</i> Forel [CCS]														1
<i>Dolichoderus glauerti</i> Wheeler [CCS]			8								1			
<i>Dolichoderus</i> sp. JDM 513 [CCS]			1				1							
<i>Iridomyrmex bicknelli</i> Emery [DD]	1	5	114	3	398	21	79	72	31	25	13	15	46	
<i>Iridomyrmex chasei</i> Forel [DD]	4	158	112	420	36	5	32	532	8	23	3	37		
<i>Iridomyrmex discors</i> Forel [DD]			43	1	148	42	84	1	3	14		29		
<i>Iridomyrmex dromus</i> Clark [DD]			1		2			1	2					1
<i>Iridomyrmex longisoma</i> Heterick & Shattuck [DD]									2	1				1
<i>Iridomyrmex mjobergi</i> Forel [DD]									1		8			
<i>Iridomyrmex purpureus</i> (F. Smith) [DD]			30						57					
<i>Iridomyrmex suchieri</i> Forel [DD]		59	3	199									21	41
<i>Iridomyrmex suchieroides</i> Heterick & Shattuck [DD]		6		19			1	63	11		3			
<i>Ochetellus glaber</i> sp. JDM 19 [O]										1		3	3	
<i>Tapinoma</i> sp. JDM 78 [O]				1										
<i>Technomyrmex jocosus</i> Forel [O]														7
Ectatomminae														
<i>Rhytidoponera inornata</i> Crawley [O]														5
<i>Rhytidoponera metallica</i> (F. Smith) [O]				2			2				80		38	
<i>Rhytidoponera violacea</i> (Forel) [O]	1					6			40	4	6	10		6
Formicinae														
<i>Camponotus minimus</i> Crawley [SC]				1	7	1				1				
<i>Camponotus scratius</i> Forel [SC]				2	1		2		1			4	9	

<i>Camponotus terebrans</i> (Lowne) [SC]	2		1	45					9	2	2	
<i>Camponotus walkeri</i> Forel [SC]	2				1							1
<i>Melophorus insularis</i> Wheeler [HCS]									1			4
<i>Melophorus ladius</i> Forel [HCS]			6		1						3	12
<i>Melophorus turneri perthensis</i> Wheeler [HCS]	49	7	14	62	44	130	80	55	30	18	88	9
<i>Melophorus</i> sp. JDM 28 [HCS]		11		63		8						
<i>Melophorus</i> sp. JDM 500 [HCS]				3								
<i>Melophorus</i> sp. JDM 520 [HCS]								5	2			
<i>Melophorus</i> sp. JDM 783 [HCS]	9	3	1	2	5	1	1	5	3	14	10	
<i>Melophorus</i> sp. JDM 1221 [HCS]												1
<i>Notoncus gilberi</i> Forel [CCS]				3							1	
<i>Stigmatoceros aemula</i> Forel [CCS]			1		11	8		4	1			3
<i>Stigmatoceros reticulata</i> Clark [CCS]				12		4		1				
Myrmeciinae												
<i>Myrmecia clarki</i> Crawley [SP]												1
<i>Myrmecia urens</i> complex sp. JDM 1 [SP]									2			
Myrmicinae												
<i>Austromyrmex flavigaster</i> (Clark) [GM]							1					
<i>Cardiocondyla atalanta</i> Forel	7	3	1					3	2		34	
<i>Crematogaster laeviceps chasei</i> Forel [GM]	5		1136								1	1
<i>Meranoplus rugosus</i> Crawley [HCS]	4		22		5			4	6			35
<i>Monomorium fieldi</i> Forel [GM]						4		1				13
<i>Monomorium laeve</i> Mayr [GM]										6		
<i>Monomorium sordidum</i> Forel [GM]	30				1	46		4	24		73	329
<i>Monomorium sydneyense</i> Forel [GM]	4		11	6	4						1	12
<i>Monomorium</i> 'sydneyense' (10-seg. antenna) [GM]				1								37
<i>Monomorium sydneyense</i> complex sp. JDM 101 [GM]	1											
<i>Pheidole ampla perthensis</i> Crawley [GM]			2		68	8	4	5	8		9	25
<i>Pheidole megacephala</i> (Fabricius)*			1	1								
<i>Pheidole</i> sp. JDM 164 [GM]						14						
<i>Solenopsis clarki</i> Crawley [CS]			1			1	1					

<i>Strumigenys perplexa</i> (F. Smith) [CS]														1
<i>Tetramorium impressum</i> (Viehmeyer) [O]	1	34	4		6	13	7	17	1		6			
<i>Tetramorium simillimum</i> (Mayr)*	91		14						4		14	4		
Ponerinae														
<i>Hypoponera congrua</i> (Wheeler) [CS]				2										
<i>Pachycondyla (Brachyponera) lutea</i> (Mayr) [CS]	1		3	3	2	18	2	2	4	4			4	
Abundance	18	425	368	1872	812	221	458	771	259	175	142	340	596	101
Species richness	6	15	13	26	17	17	21	12	22	20	10	18	21	12
Shannon index (H')	0.61	0.79	0.79	0.52	0.73	0.88	0.93	0.47	1.00	1.07	0.67	0.97	0.77	0.83
Fisher alpha index	3.15	3.03	2.63	4.27	3.04	4.29	4.54	2.02	5.74	5.82	2.45	5.82	4.05	4.24
Evenness (J')	0.79	0.67	0.71	0.37	0.60	0.71	0.70	0.44	0.75	0.82	0.67	0.77	0.62	0.77