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Ant dominance in urban areas

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Abstract A survey was conducted to determine the distribution of dominant ants and factors that may influence their dominance in New Zealand cities. A new method of active ant trapping combining aspects of pitfall trapping and attraction to food baits was used to capture a sample of all ant species that attended baits. Fifty eight percent of the ant species present in New Zealand were recovered from 2202 traps, with multiple species catches in 245 traps. There was a strong latitudinal relationship in the distribution of ant species, with the proportion of native to introduced species increasing in favour of the native species as latitude increased (south). The presence of *Linepithema humile,* the Argentine ant, a numerically dominant species was associated with a significant reduction in the number of other ant species captured. With increased urbanisation, providing refugia at times of cool temperatures for warm temperate-sub tropical introduced ant species, their range may extend into the higher latitudes, further displacing native ants from New Zealand cities.

Keywords Introduced species · Latitudinal gradient · Species co-occurrence · *Linepithema humile* · *Paratrechina* · *Monomorium*

Introduction

Many introduced ant species are nuisance pests in urban and natural environments and can have negative impacts on local invertebrate and vertebrate populations (Holway et al. 2002),

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whereas other species may have little or no impact beyond nuisance value (Passera 1994). Some studies have investigated the ecology of ants in urban environments showing differences between ant communities with different dominant species (Heterick et al. 2000) and different habitats within the environments (Pacheco and Vasconcelos 2007). These urban environments may provide a diverse range of habitats from residential to parks and industrial areas facilitating species co-existence (Palmer 2003; Sarty et al. 2006).

Species that do not show invasive traits are often ignored, especially if they are not considered invasive elsewhere in the world. As a result there are small populations of introduced species in many countries for which the benefits of eradication are not considered sufficiently high, even though the cost of eradication at the present stage may be relatively low. However, there is a risk associated with doing nothing: some introduced species have been shown to increase suddenly and spread, despite having remained localised for a substantial period of time (Crooks and Soulé 1999; Groves 2006). With climate change and other forms of disturbance, the potential for currently innocuous species to become a major problem seems great.

In order to assess the current distribution of dominant ants in New Zealand cities, particularly the Argentine ant, *Linepithema humile* (Mayr), a survey was conducted throughout the country (Charles et al. 2002). The Argentine ant is established in New Zealand (Green 1990) and is predicted to be a key driver behind future change in ant community composition, because of its influence in other parts of the world (Holway et al. 2002). The survey was conducted in a manner to obtain the maximum amount of information about this highly invasive species and other likely competitors based on dominance at food resources. The results allowed us to identify some factors that are likely to be driving community dominance.

We considered three key determinants for the likelihood of ant presence in an area. Firstly, we anticipated that would be a latitudinal gradient in the distribution of native and introduced ants with a greater likelihood of trapping introduced species in the north of the country, where temperatures are warmer, the majority of New Zealand's ports are located and where human population pressure is greater, all of which potentially increase the chance of human-mediated arrival and/or establishment of ant species. Secondly, we considered whether ant community dominance changes with habitat. We predicted that a greater number of species and more native species would be trapped in structurally diverse environments, as these habitats are likely to provide a more heterogeneous environment, promoting species co-existence (Palmer 2003). Thirdly, we considered interactions among various ant species. We predicted that the presence of *L. humile* would have a negative impact on the presence of other ant species.

Methods

Survey methods

Pitfall traps are not practical in areas with paved surfaces. As such, we developed a new method of trapping ants. We modified bait vials by inserting a 15 mm × 120 mm strip of yellow double-sided sticky fly-trap into an open-ended 150 mm length of soft clear plastic tubing with an internal diameter of 19 mm. The sticky fly-trap insertions provided a surface on which specimens of all species that attended the bait could be captured, reducing the influence of bait dominance on the number of species detected in an area. The tubes were placed directly on the surface and were fixed to the ground where possible, although, the weight and shape of the tubing prevented them from being easily disturbed by wind (Fig. 1c).

Trapping was conducted in two ways; starburst arrays (Fig. 1b) and hotspot trapping. Starburst arrays were employed in previously known centres of *L. humile* infestation (unpublished surveys). Traps were placed approximately 100 m, 200 m, 400 m and 800 m from the central point along eight radiating transects, dictated by street layout, giving a maximum of 33 traps per starburst. Hotspot trapping was done by placing traps outside of high traffic areas such as ports, railway yards, commercial transfer stations, commercial trading centres and hospitals in cities with a population greater than 35,000 people ($n=69$) and at sites where there had been anecdotal evidence of *L. humile* presence. Trapping commenced in southern (temperate) New Zealand in late March (late summer) and finished in northern (sub-tropical) New Zealand in late May (autumn) 2001 (Fig. 1a).

Traps were baited with 1 cm^3 of jam (variable flavours) and placed on the ground in areas likely to have ants (eg. along edges of buildings and at the bases of trees), on warm (air temperature 15–20°C) sunny days where possible. After approximately 24 h, samples were retrieved. Ant collection data also included GPS readings, habitat placement and weather details. (Fig. 1a). Samples of each ant species were removed from the sticky bases using kerosene, stored in vials containing 75% ethanol and identified to species (Landcare Research 2008). Native and introduced species-status was determined following Ward

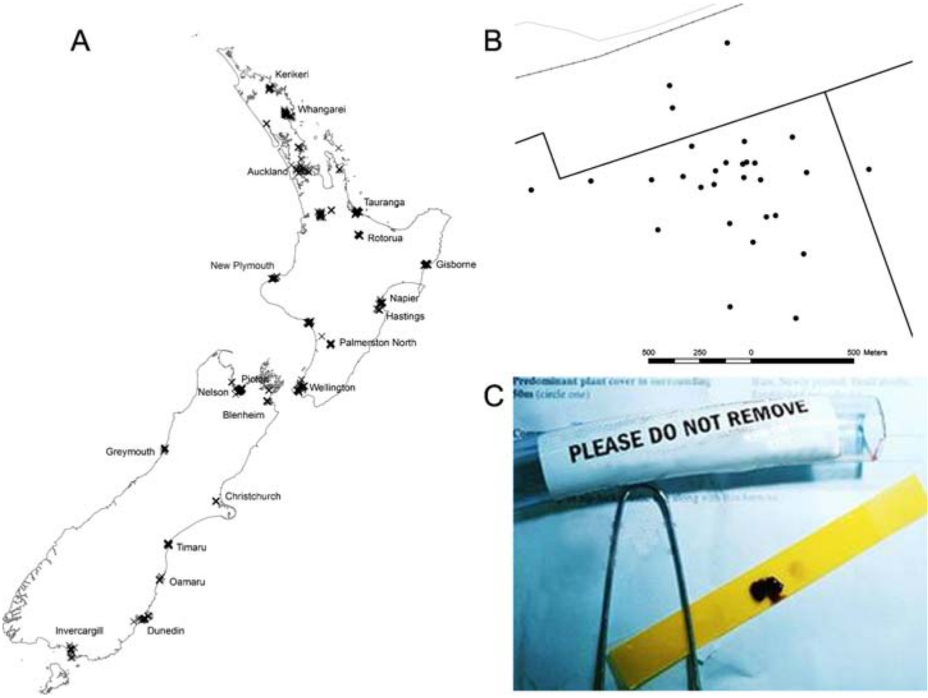

Fig. 1 Location of ant traps in New Zealand cities (**a**) and examples of the starburst array (**b**) and trap setup showing the tube, sticky fly trap with bait in the centre (**c**)

(2005). Voucher specimens were deposited in the New Zealand Arthropod Collection (NZAC) at Landcare Research, Mount Albert.

Statistics

Ant species analysis was conducted on all ant species captured in traps except where otherwise indicated. Presence, rather than abundance, data were recorded, because abundance as measured by ants per trap may be biased by species foraging method or size (Suarez et al. 1998) Analyses investigated the effect of latitudinal gradient, habitat and community composition on the species of trapped ants. Additionally, the effects of latitudinal gradient and habitat on species presence were analysed for *L. humile* (invasive), *Monomorium antarcticum* (Fr. Smith) (native) and *Paratrechina* sp.a (introduced). This was to compare the role of invasiveness of different (representative) ant species. In this context, ‘invasive’ means that there is evidence from the literature that it has a negative effect in its introduced range, while ‘introduced’ means the species has been introduced into the country and little known about its effect in its introduced range. *Monomorium antarcticum* was selected as it was the most abundant native species (Table 1).

Latitudinal gradients

To determine impacts of latitudinal gradients on ant distributions we followed the New Zealand map grid, a projection unique to New Zealand, whereby by the units represent distances measured in metres. The maximum and minimum northing values where traps were placed were 6666871N (35`11.69°S) in the north of New Zealand and 5391296N (46`35.79°S) in the south (Fig. 1a). We compared the mean northings co-ordinate value of traps that contained ants with those that did not with a Student’s t-test. A Student’s t-test was used to determine whether there was a difference in bait dominance, by comparing the mean northings value of native and introduced trapped species (excluding the empty trap data). We determined whether the average northings value could explain the number of introduced ant species found in a trap, through ANOVA followed where appropriate by Fisher’s LSD, with northings as the response variable. The median northing value of the three case study species was examined using a Kruskal-Wallis test. Furthermore, we carried out a non-metric multidimensional scaling analysis (nmds) on the similarity of the ant communities and the individual ant species from the survey.

Habitat

Habitat was divided into 11 categories: airport, commercial, horticultural, hospital, industrial, port, railway, recreation area, residential, rural, and transport depot. A Chi-square test was conducted to determine whether the presence of native and introduced ants trapped varied by habitat. Following this, an ANOVA was conducted on square-root transformed presence data of the number of species caught in each trap within the habitat type to determine whether habitat influenced the number of ant species captured. As the survey effort (the number of time that a habitat was surveyed) was not consistent between habitat types, we ran a linear regression comparing species presence and survey effort. A Chi-square was performed on the presence of each of the three case study species in traps in the habitat types, to determine whether each species was evenly trapped between the habitat types. Analyses included all traps that captured at least one ant species and did not include empty traps.

Table 1 The number of trapping occurrences of ant species during the survey of New Zealand urban areas. '*' denotes native species (Ward 2005)

Species	Number of times trapped	Trapped with another species
Subfamily Dolichoderinae		
Doleromyrma darwiniana (Forel)	11	Y
Iridomyrmex sp.	69	Y
Linepithema humile (Mayr)	86	Y
Ochetellus glaber (Mayr)	38	Y
Technomyrmex albipes (Smith)	74	Y
Subfamily Ectatomminae		
Rhytidoponera sp.	1	N
Subfamily Formicinae		
Paratrechina sp.a	446	Y
*Prolasius advena** (Fr. Smith)	3	Y
Subfamily Myrmicinae		
Cardiocondyla minutior Forel	4	Y
*Huberia striata** (Fr. Smith)	10	N
Mayriella abstinens Forel	1	Y
Monomorium fieldi Forel	13	Y
*Monomorium antarcticum** (Fr. Smith)	204	Y
Pheidole rugosula Forel	76	Y
Pheidole megacephala (Fabricius)	1	Y
Pheidole vigilans Fr. Smith	12	Y
Strumigenys perplexa (Smith)	3	Y
Tetramorium bicarinatum (Nylander)	19	Y
Tetramorium grassii Emery	204	Y
Subfamily Ponerinae		
Hypoponera eduardi (Forel)	1	N
*Pachycondyla castanea** (Mayr)	18	Y
*Pachycondyla casteneicolor** (Dalla Torre)	1	Y

Presence of Linepithema humile

We used a Student's t-test to compare the number of ant species (including *L. humile*) in traps in the presence or absence of *L. humile*. We ran a regression analysis to determine whether species co-occurrence was related to the number of times the species occurred in the survey.

Analyses were conducted using Minitab (2006) and the nmds was run in R- vegan: community ecology (Oksanen et al. 2008).

Results

Of the 2850 traps that were placed out for the survey, 2202 (705 starburst and 1497 hotspot) were recovered for analysis. Of those, 1293 contained ants. Twenty-two of the 38 ant species in New Zealand were trapped (Table 1). Five of these species are present in New

Zealand (Ward 2005). Overall, 236 traps contained native ant species, 1059 traps contained introduced species, and of those traps 245 captured more than one ant species, with a maximum of four species trapped together on nine occasions. All but three of the species trapped in the survey were captured with another ant species (Table 1).

Latitudinal gradients

Traps were more likely to contain an ant the further north samples were taken (two-sample t-test $t = -21.17$ $P<0.001$ df=1961); the average northings of traps that contained ants was 6301915 (38’22.83°S), while the average northings of traps that did not contain ants was 6015756 (40’57.17°S).

Native ants were more commonly found in southern areas, i.e. at sites with a lower northings value, (Fig. 2a; $t=16.03$ $P<0.001$ df=251) while the likelihood of trapping introduced species increased as the trapping moved from south to north (Fig. 2b; ANOVA $F=76.81_{4,848}$, $P<0.001$).

The northern ant communities were grouped separate to the southern communities with exception to the ‘nelson area’ in the nmds (Fig. 3), with the majority of the introduced ant species were placed near the northern ant communities. One exception to this was *Doleromyrma darwiniana* (Forel) which was placed closer to the southern ant communities. Two native species; *Pachycondyla castanea* (Mayr) and *Prolasius advena* (Fr. Smith) were grouped with the northern ant communities.

Further analysis conducted on three species, *L. humile*, *M. antarcticum* and *Paratrechina* sp.a indicated that there were significant differences in the median northing value where the ants were trapped throughout New Zealand ($P<0.001$), with the median value of *M. antarcticum* further south (lower northing value) than the other two species. Additionally,

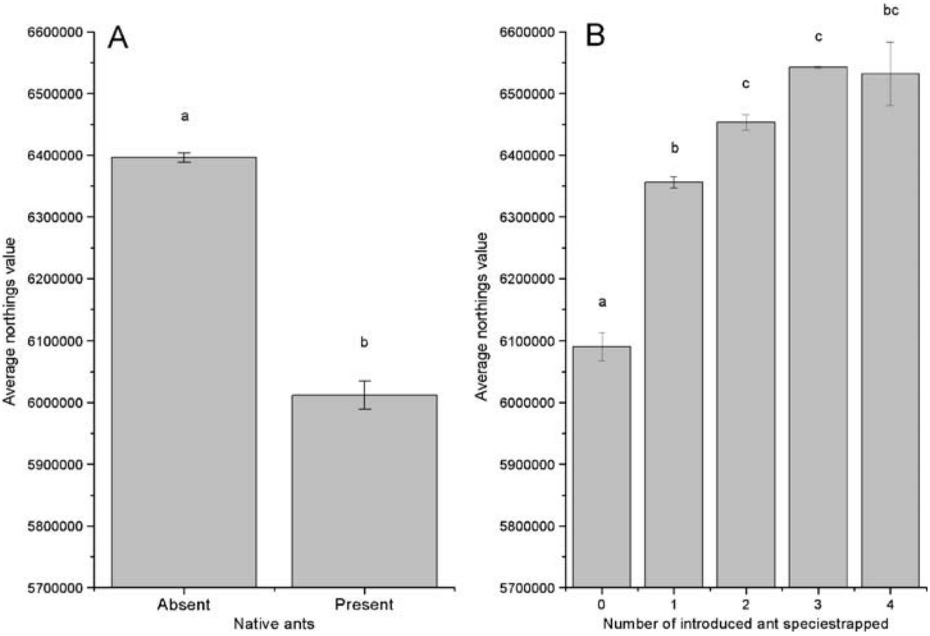

Fig. 2 Average (±SEM) NZMG northings of ant-infested sites that contained (**a**), native ant species and (**b**), invasive ant species. Bars with the same letter are not significantly different ($\alpha=0.05$)

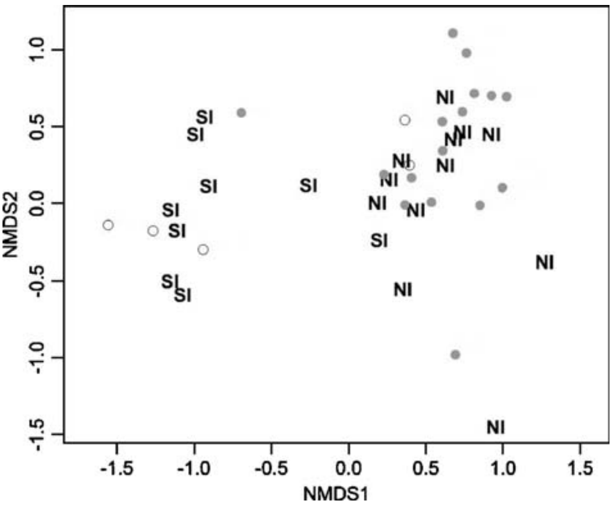

Fig. 3 A non-metric multidimensional scaling plot of ant communities and individual species similarity throughout New Zealand. NI=North Island, SI=South Island ant communities, ○= native and ●= introduced ant species

M. antarcticum was recovered from traps spanning the entire length of the survey area, while *Paratrechina* sp.a and *L. humile* were only found in northern New Zealand (Fig. 4).

Habitat

The number of species caught varied between the habitat types (ANOVA, $F=1.40_{10,945}$, $P=0.041$), but there was a significant relationship between the survey effort and the number of species captured within each habitat ($R^2=0.7604$, $P<0.001$). Native ants were trapped more frequently at airports, horticultural areas and industrial sites, and less frequently around hospitals and residential areas ($\chi^2=63.25$, df=10, $P<0.001$).

Linepithema humile was found in 86 sites in 22 cities and was present in 9% of the traps containing ants. The majority of these were from residential habitats (38%); however, in terms of survey effort, a greater percent were trapped in the transport depot (22%) than in the residential habitat (12%) (Fig. 5a). *Linepithema humile* was not trapped equally between the habitats (positive ant finds only, $\chi^2=33.23$, df=10, $P<0.001$). *Paratrechina* sp.a was trapped in 46% of the traps that caught ants. There was no significant difference in trap

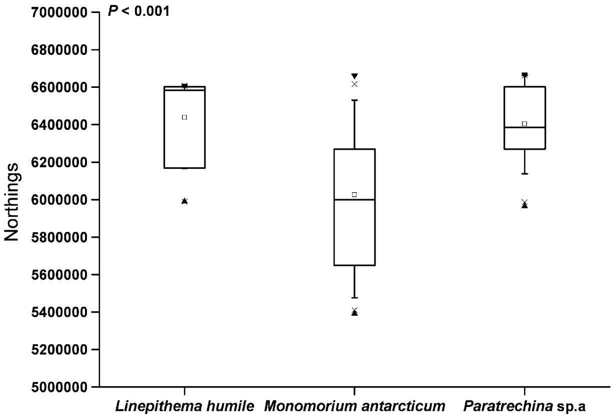

Fig. 4 Boxplots showing spread of positive finds of three ant species during the survey by latitudinal gradient. The *P*-value is a Kruskal-Wallis test comparing median northing value of the ant finds

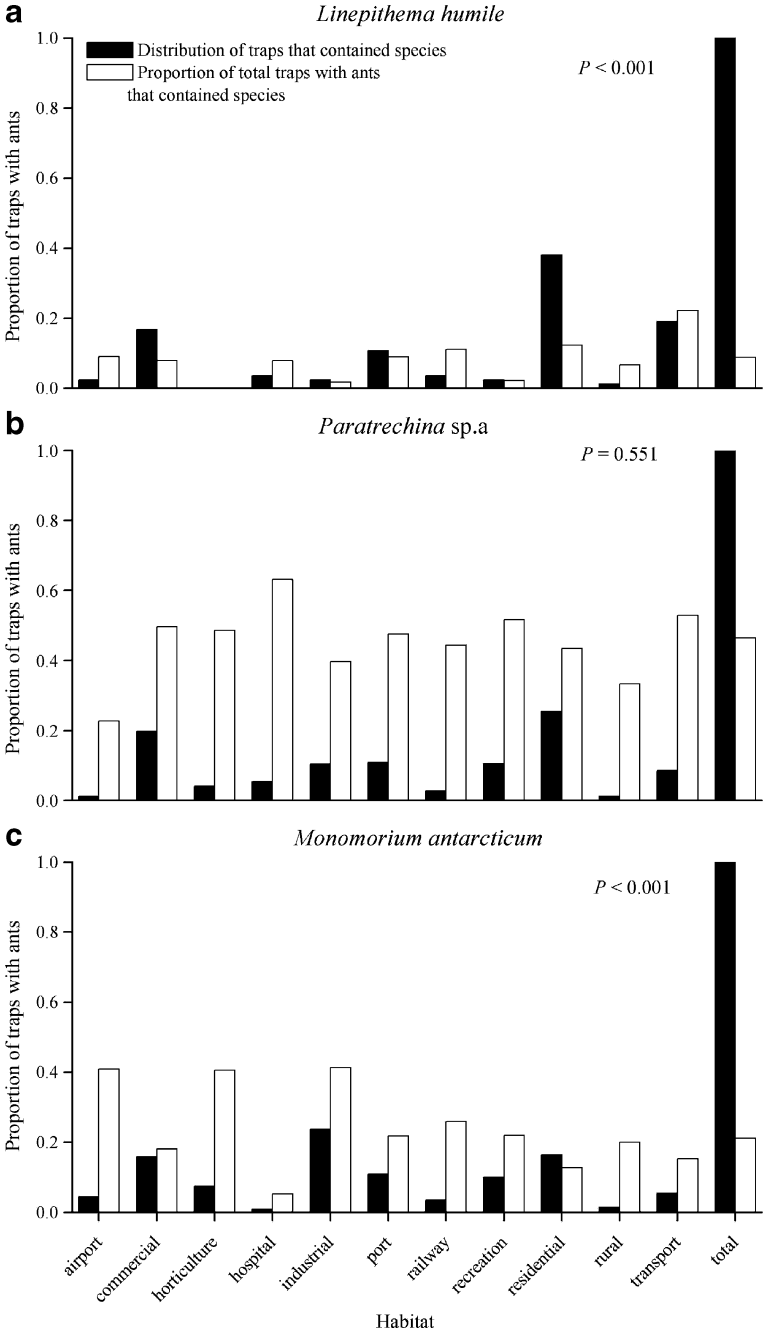

Fig. 5 Distribution of proportion of traps of each ant species trapped by habitat (black bars), capture by sampling effort on positive ant find data only (white bars). *P*- value on Chi-square analysis of number of traps ant trapped in each habitat on the sampling effort data (white bars)

catch between the habitats (positive ant finds only, $\chi^2=8.80$, df=10, $P=0.551$) (Fig. 5b). *Monomorium antarcticum* was found in 21% of the occupied traps. There was a significant difference (positive ant finds only, $\chi^2=48.77$, df=10, $P<0.001$) of trapping frequency between the different habitat types (Fig. 5c).

Presence of Linepithema humile

Significantly more species were found in traps when *L. humile* was absent (mean=1.371; SEM=0.023) than when it was present (mean=1.163; SEM=0.052, t-value=3.68, $P<0.001$, df=119). During the survey, *L. humile* was found together with another species 16.3% of the times it was trapped. In eight of the traps, it was found together with *Paratrechina* sp.a, four times with *Tetramorium grassii* Emery and once with both *Technomyrmex albipes* (Smith) and the native *M. antarcticum*. However, the number of times a species co-occurred with *L. humile* was related to the number of times that the species was found during the survey ($R^2=0.8849$, $P<0.001$).

Discussion

In this study, we developed a new method for trapping ants in urban areas where pitfall traps are not feasible. These traps use a food bait and capture multiple ant species attending food. Some of those that were not trapped have an extremely limited distribution in New Zealand (e.g. *Monomorium sydneyense* Forel; Stringer and Lester 2007). The traps have the advantage of being cheap and easy to assemble. They can be used on paved surfaces (unlike pitfall traps) and so are ideal for monitoring ant diversity in urban areas. Our survey design was biased towards catching ants with a carbohydrate food preference by using only one type of food (jam) and had a trap efficiency of 58%. This may not have been attractive to all species in the area (Sanders and Gordon 2003; Stringer and Lester 2007), such as *Huberia striata* (Fr. Smith) which had a limited range from this survey compared to historical data records (Landcare Research 2008). The food would have been attractive to other potential *L. humile* competitors such as *Iridomyrmex* sp. and other species with similar resource needs and tolerances to temperature stress and physical disturbance (Andersen 1995).

Different methods of assessing ant assemblages can give different pictures of the same ant assemblage (Schlick-Steiner et al. 2006). For example, pitfall traps give a better estimate of species composition than nest counts, but nest counts give a better estimate of density. Although we have not directly compared the number of species captured between baited traps with and without a sticky base, work comparing baited traps with and without a sticky base has shown a five times higher occurrence of multiple species catch in sticky base traps (Stringer et al. unpublished data). Our traps were designed to catch every ant that was attracted to the bait, in order to estimate community composition, although it is likely that we have still recorded species dominance. Work is continuing on trapping multiple species in baited traps.

While the likelihood of species co-occurrence was related to the number of times species were trapped in the survey, there was a significant latitudinal gradient component to the presence of ants in New Zealand. The further north traps were located, the greater the chance that they caught introduced ants with northern ant communities more similar to each other than to southern ones. There were some anomalies, with the nelson area ant community more similar to the northern assemblages. Nelson lies at a lower latitude than some north island areas and has a port, both of which could account for it grouping with the north island ant communities. The placement of the introduced *D. darwiniana* with the southern ant communities may be due to it's strong presence in the south island compared to many of the other introduced species. While the native *P. advena* and *P. castanea* were placed closer to the northern ant communities due to *P. advena* only being trapped on the north island (while present in the south) and *P. castanea* is only present on the north island (Landcare Research 2008).

Most of New Zealand's invasive ants have come from, or via, Australia (Green 1992; Ward 2005). These species are likely to be better adapted to the warmer, northern parts of New Zealand (Ward 2007), thus may not tolerate the cooler conditions further south. Climate change scenarios suggest that New Zealand will become increasingly suitable for tropical and subtropical species (Kriticos et al. 2007) including ants. With increasing temperatures and other anthropogenic changes, we may expect a further range restriction of native ants by introduced ant species to increase as many of the introduced species' ranges expand.

Traps containing *L. humile* contained significantly fewer competing species, native or introduced, than traps excluding *L. humile*. It appears that *L. humile* is having a significant effect on other ant species present in its range. A reduction in ant species diversity is a common response to the invasion of *L. humile* in both native and modified habitats (Holway et al. 2002; Rowles and O'Dowd 2007; Suarez et al. 1998; but see Clark et al. 2008). As the starburst layout primarily used in this survey places traps out from the assumed centre of the *L. humile* incursion, it is possible that traps crossed the *L. humile* invasion front. At the invasion front, resident species will be competing for resources and may not have been displaced from the area (Holway et al. 2002) allowing them to be detected. Potentially some species can co-exist with *L. humile* by foraging at temperatures outside of the range that *L. humile* forages (Andersen 1995; Cerdá et al. 1997) in or by exploiting different habitats or tolerating low resource levels within the *L. humile* invaded area (Palmer 2003). Alternatively, the New Zealand environment could be suboptimal (at the limits of the range of *L. humile*), reducing its competitive ability thus allowing some level of co-existence (Cerdá et al. 1997).

Our analysis found that the habitat type influenced the number of ant species trapped. However, there was a relationship between the number of species trapped and survey effort. Looking beyond any main effects, we expected a difference between the species dominance of ants trapped in the different habitats, specifically, that native ant species would be found in urban habitat types that are similar to natural habitats, such as recreational areas and horticultural plantings. Surprisingly, native species were found more often at airports, industrial sites and horticultural areas. Perhaps the disturbance regime (physical or chemical) is some what less in these areas than at the hospital and residential sites, allowing them to persist despite possible foraging pressure from introduced species. The proportion of traps that contained either *L. humile* or *M. antarcticum* were not spread evenly between the different habitats, suggesting a habitat effect on their capture rates, while there was no difference in capture rate for *Paratrechina* sp.a between the habitats. Andersen's (1995, 1997) categorising of ants into functional groups based primarily on thermal and physical disturbance tolerances may account for the observed differences among the three species. Ants in the genus *Paratrechina* are able to tolerate a large range of temperatures and disturbance regimes (Andersen 1997) and their large capture over all habitats reflects this.

While most *L. humile* were found in residential habitats, when we corrected for survey effort, transport depots are highlighted as potential hotspots for *L. humile*. This high level of occurrence in transport depots could suggest that these environments are the starting point of *L. humile* invasion in a new region and that human-assisted transport is moving these species around the country. Increased awareness of ant problems by transport operators may be necessary to reduce the spread of this species.

Ants in the genus *Monomorium* are also able to tolerate a range of environments and habitats (Andersen 1995). *Monomorium antarcticum* was most commonly found in airport, horticultural and industrial habitat types and was found throughout the latitudinal range of the survey. However, it was more common in southern areas where perhaps there is less competition for resources from other ants, suggesting that its range in urban areas has been restricted by introduced ants in northern areas. To determine the extent of its decline in urban areas, we would need to compare its abundance over the same latitudinal range in less modified areas, where introduced ants are likely to be less common.

While most of the current species in New Zealand have come from or via Australia (Green 1992; Ward 2005), most of the recent (2004–2005) interception records are from the Pacific Islands (Ward et al. 2006), where many of the ants are wide-ranging Pacific species. Most of these ants are likely to be tropical species and, as such, are unlikely to be a threat in southern New Zealand, although they may establish in the north. Lester (2006) found that mean temperature at the highest latitude of species that had established in New Zealand was significantly lower than temperatures at latitudes where species had only ephemerally established or failed to establish (despite records of interception). Species with a subtropical-warm temperate distribution such as red imported fire ant, *Solenopsis invicta* Buren (Sutherst and Maywald 2005) are likely to become a major part of the ant fauna in northern-coastal parts of New Zealand if they establish, while southern regions of New Zealand should be more concerned about ant species from cooler temperate regions such as *Camponotus* spp., which are structural pests in North America and Europe.

We anticipate that this work can be used as a base-line study from which future changes as a result of climate change or the addition of further invasive species can be monitored. Any ant species' dominance can be influenced by factors such as the presence of competitors and thermally optimal environments. As introduced ant ranges increase and new species are transported to New Zealand we expect to see a decrease in the native ant fauna due to competitive displacement in New Zealand cities. Subsequent to this survey, *L. humile* has further spread in New Zealand urban areas, predominantly through human-mediated dispersal (Ward et al. 2005).

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