

Variation in the persistence and effects of Argentine ants throughout their
invaded range in New Zealand

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Abstract

Invasive ants are a serious ecological problem around the world. The Argentine ant has had devastating effects on resident ant communities and may negatively impact other invertebrates in its introduced range. First detected in Auckland in 1990, this invader has since spread widely around the country. The effect of Argentine ants on invertebrates in New Zealand was investigated by comparing ground-dwelling arthropod species richness and abundance between and among paired uninvaded and invaded sites in seven cities across this invader's New Zealand range. In order to study density-dependent effects, invaded sites were chosen so as to differ in Argentine ant population density. The effects of rainfall and mean maximum temperature on Argentine ant abundance and the species richness and abundance were also examined. Argentine ant population persistence in New Zealand was examined by re-surveying sites of past infestation across this species range. The influence of climate on population persistence was investigated, and how this effect may vary after climate change. Additionally, the potential of community recovery after invasion was also examined. Epigaeic (above ground foraging) ant species richness and abundance was negatively associated with Argentine ant abundance; however, no discernable impact was found on hypogaeic (below ground foraging) ant species. The effect of Argentine ant abundance on non-ant arthropod species richness and abundance was mixed, with most arthropod orders being unaffected. Diplopoda was negatively influenced by Argentine ant abundance while Hemiptera was positively influenced. Annual rainfall and mean maximum temperature were found to have no effect on Argentine ant abundance or resident ant species richness and abundance, though these variables did help explain the distribution of several non-ant arthropod orders. Argentine ant populations appear to be collapsing in New Zealand. Populations had a mean survival time of 14.1 years (95% CI= 12.9- 15.3 years). Climate change may prolong population survival, as survival time increased with increasing temperature and decreasing rainfall, but only by a few years. Formerly invaded Auckland ant communities were indistinguishable from those that had never been invaded, suggesting ant communities will recover after Argentine ant collapse.

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Chapter 1:

General Introduction

Biological invasions contribute significantly to the current biodiversity crisis (Vitousek, 1997). Invasive species threaten native species and ecosystem function all over the world, and also have significant economic impacts in their new regions (Lockwood *et al.*, 2009). Invasive species may change ecosystem function by displacing other species through predation or competition (Christian, 2001; O'Dowd, 2003). The outcomes of biological invasions vary widely; indeed, the majority of species transported to new areas fail to establish (Allendorf and Lundquist, 2003). Of those species that do establish, some introduced species will become innocuous members of their new community (Lockwood *et al.*, 2009). However, a minority of introduced species not only successfully establish and spread, but go on to have serious widespread environmental and economic impacts (Vitousek, 1997). Consequently, considerable resources are frequently applied to invasive species management. For example, in the United States, introduced species are estimated to cost the country almost \$120 billion per year in environmental damages and control (Pimentel *et al.*, 2005). The calculated cost for the control and management of imported red fire ant (*Solenopsis invicta*) populations in five major cities in Texas alone was estimated to be \$581 million a year in 2000 (Salin *et al.*, 2000). Another invasive ant species, the Argentine ant (*Linepithema humile*), is predicted to eventually cost New Zealand \$68 million a year in treatment and management expenditure (Anonymous, 2002).

Introduced ant species are often particularly successful invaders (Holway *et al.*, 2002a), as exemplified by the presence of five species of ant on the “100 of the world’s worst invasive alien species list” (Lowe *et al.*, 2000). Most widely-established, ecologically and economically damaging invasive ant species share a number of characteristics that are thought to aid in their success. They are often polygynous, with multiple queens per colony, which increases reproductive output and leads to larger colony size (Tsutsui and Suarez, 2003). Colony reproduction is often by budding, a process in which queens do not participate in mating flights; instead they walk away from their natal nest with a small

group of workers and establish new colonies nearby. Invasive ants are also closely associated with humans and disturbance, which enables them to be dispersed by humans rapidly and easily (Passera, 1994; Holway *et al.*, 2002a). Polygyny and budding also both increase the chances of these ants being spread to new locations by humans because colony fragments are more likely to have an impregnated queen in them (Tsutsui and Suarez, 2003). Perhaps most importantly to the success of these ants, they are usually unicolonial, meaning there is no intraspecific aggression between workers of different colonies. Thus energy that would have been spent defending territorial boundaries can be used for foraging and reproduction (Thomas *et al.*, 2006). The above traits lead to these ants forming massive supercolonies (a polydomous colony with high nest density and an expansive spatial scale such that worker exchange between all parts of the colony is unlikely), with enormous numbers of workers. It is this huge worker abundance that may explain the success of invasive ants (Human and Gordon, 1999; Holway *et al.*, 2002a).

Five of the most notorious and damaging ant invaders are the Argentine ant (*Linepithema humile*), the imported red fire ant (*Solenopsis invicta*), the yellow crazy ant (*Anoplolepis gracilipes*), the African big-headed ant (*Pheidole megacephala*), and the little fire ant (*Wasmannia auropunctata*) (Lowe *et al.*, 2000; Holway *et al.*, 2002a). These five species are considered among the world's worst invasive species (Lowe *et al.*, 2000). They are distinguished from other ant species easily spread by humans because once they are established in urban areas they are able to spread into undisturbed habitat where they may cause severe ecological damage (Holway *et al.*, 2002a).

Invasive ant species have had major impacts on native species. The following are just a few examples of the harm these invaders may cause. Argentine ants have been documented to disrupt seed-dispersal and pollination of plants in California, South Africa, and Spain (Bond and Slingsby, 1984; Christian, 2001; Carney *et al.*, 2003; Blancafort and Gomez, 2005). Yellow crazy ants are annihilating red land crabs on Christmas Island, thereby causing an "invasional meltdown" of the forest ecosystem on that island (O'Dowd *et al.*, 2003). Red imported fire ants have been implicated in the decline of many different vertebrate groups, including birds and lizards in the United

States (Allen *et al.*, 2001; Wojcik *et al.*, 2001). African big-headed ants have been shown to cause significant declines in invertebrate abundance, such as termites, where they occur in Australia and Mexico (Hoffmann *et al.*, 1999; Dejean *et al.*, 2007). Little fire ants have been known to blind domestic and wild animals with their sting (Wetterer and Porter, 2003). All of these ant species have been associated with the decline of various invertebrate species (Human and Gordon, 1997; Holway *et al.*, 2002a), but frequently the most devastating impact invasive ants have is on other ant species (Porter and Savignano, 1990; Holway, 1998; Hoffmann, 2009; Hoffmann and Saul, 2010).

Scientists suggest invasive ants displace other ant species by excelling at both exploitative and interference competition (Human and Gordon, 1996; Holway, 1999). However, this superior competitive ability may actually be a result of numerical supremacy, and perhaps not behavioural dominance *per se*. The colony size of invasive ants often greatly exceeds that of other ant species (Holway and Case, 2001), but population densities of ants may vary temporally and spatially due to biotic or abiotic factors, such as rainfall and temperature (Holway and Case, 2001; Palmer, 2004). Thus, the impact of invasive ants on resident ant species has been observed to vary depending on invasive ant densities (Helm and Vinson, 2001; Abbott, 2007) and time since the initial invasion (Morrison, 2002; Heller *et al.*, 2008).

The Argentine ant is one of the most notorious and widespread ant invaders (Krushelnycky *et al.*, 2010). Native to northern Argentina and surrounding regions, this ant has invaded Mediterranean-type ecosystems worldwide, and now occurs on all continents except Antarctica (Wetterer *et al.*, 2009). Introduced populations of this ant form high-density, widespread, highly aggressive colonies and can negatively impact native communities (Holway *et al.*, 2002a). Argentine ants have been associated with reductions in ground-dwelling arthropod diversity, though different studies have had mixed results (Cole *et al.*, 1992; Human and Gordon, 1997; Holway, 1998). Argentine ants are omnivores and therefore may affect ground-dwelling arthropods by direct predation or competition (Human and Gordon, 1997; Holway, 1998). Introduced populations of Argentine ants also commonly displace most native ant species where they

occur (Human and Gordon, 1997; Holway *et al.*, 2002a; Krushelnycky *et al.*, 2005). Argentine ants, like other invasive ants, possess traits that appear to make them superior competitors to native ants. They discover and recruit to resources faster than native ants (Human and Gordon, 1996), and once resources are found, keep native ants away through behavioural and numerical dominance (Holway, 1999). However, in their native range Argentine ants are not behaviourally dominant (LeBrun *et al.*, 2007). Furthermore, where Argentine ants are not able to maintain high population densities in their introduced range they are often replaced by other, better armed ant species (Lester and Sagata, 2003; Walters and MacKay, 2005; Blight *et al.*, 2010).

Small populations of colonists often impose a genetic bottleneck, due to small founding population size, resulting in significantly reduced genetic diversity compared to that of the parent population (Allendorf and Lundquist, 2003). Inbreeding depression can limit population growth, and reduce the likelihood of population persistence (Sakai *et al.*, 2001). Low genetic diversity interferes with the species' ability to adapt to its new environment (Allendorf and Lundquist, 2003). Due to these factors, invasive species may be prone to population crashes (Sakai *et al.*, 2001). For example, low genetic diversity may interfere with workers' ability to detect and respond to pathogens, leaving the colony vulnerable to infection (Ugelvig *et al.*, 2010). Tsutsui and colleagues (2000, 2001, 2003) suggest the unicolonial behaviour Argentine ants display is a consequence of low genetic diversity among founding individuals. Californian Argentine ant populations were compared to native South American populations, and it was found that nearly half of the native alleles were missing, with heterozygosity reduced by over 60% (Tsutsui *et al.*, 2000). Argentine ants recognize nestmates using genetically based cues (Holway *et al.*, 2002a). In their native range an encounter between individuals from different colonies would result in fighting and probably death. This lack of nestmate recognition is hypothesized to be due to a genetic bottleneck during founding (Tsutsui and Suarez, 2003), or possibly a genetic cleansing of recognition alleles after founding (Giraud *et al.*, 2002). While the mechanism resulting in unicoloniality and co-operation is unknown, the results are that large populations frequently occur. These large populations mean that Argentine ants often vastly outnumber resident ant species (Holway and Case, 2001).

When the Argentine ant was first observed in Auckland in 1990 (Green, 1990), there was serious concern about the impact this invader could have on New Zealand's economy and biodiversity (Harris, 2002). Despite this worry, the decision was made not to eradicate (Charles *et al.*, 2002), and as a result Argentine ants have since spread widely around the North Island of New Zealand, assisted by human-mediated dispersal. This ant is also now found in Blenheim, Nelson and Christchurch on the South Island (Lester *et al.*, 2003). However, despite a widespread distribution and 20 years of establishment, the Argentine ant is still very patchily distributed in New Zealand, forming many discrete, non-continuous populations (Corin *et al.*, 2007a). It is also confined to urban areas, having not yet spread into natural ecosystems (Ward *et al.*, 2010).

The distribution and spread of this invader have been found to be governed by environmental factors such as temperature and rainfall (Roura-Pascual *et al.*, 2004). In California, for example, the Argentine ant is absent from cold temperature and xeric environments (Holway *et al.*, 2002b). In New Zealand this ant has established in areas where the climate is considered to be suitable (Hartley *et al.*, 2006), and climate change is predicted to increase its range within the country (Roura-Pascual, 2004).

Previous observations suggest that not all Argentine ant populations are persisting in New Zealand. For example, Hartley and Chandy (unpublished data) monitored a large infestation of this ant in Wellington over 5 years (Fig. 1). Initially this was a high-density, widespread population covering many blocks. However, over several years Hartley and Chandy observed a fairly rapid contraction of this population until it existed as only a few nests. The return of resident ant species to the areas that were formerly dominated by Argentine ants was also observed. Interviews with the local residents indicated that no chemical control attempts had been made in the area.

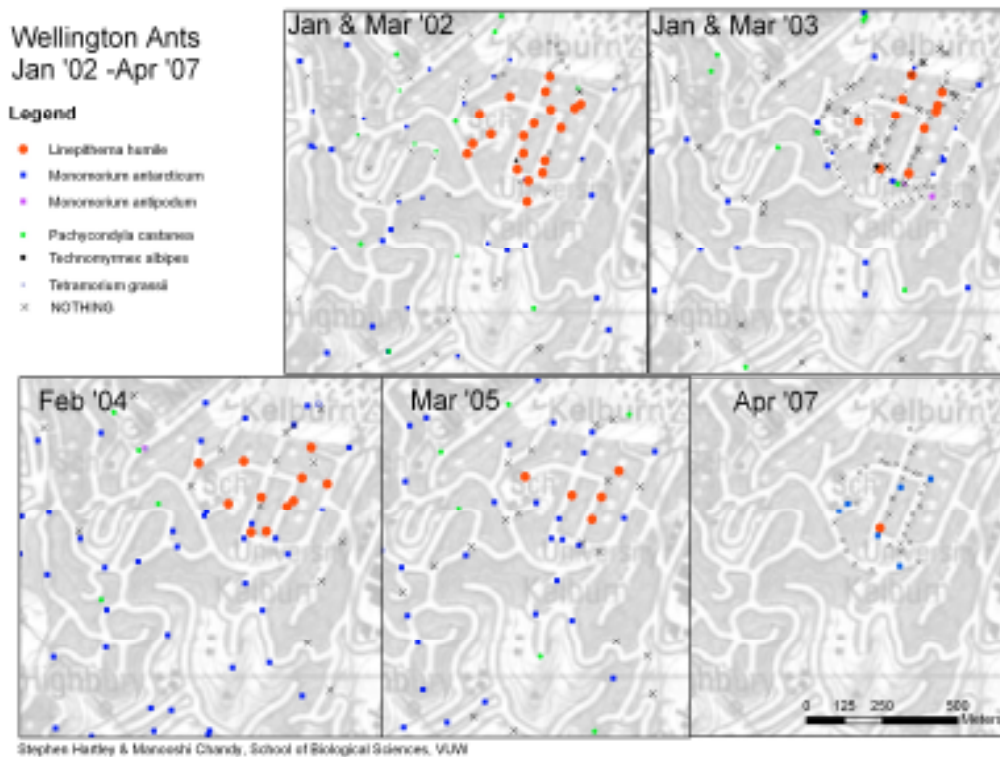


Figure 1.1. Long-term monitoring of an Argentine ant population in Kelburn, Wellington from January 2002 to April 2007. The red dots indicate Argentine ant presence. Please note that only the area previously recorded to be infested with Argentine ants was surveyed in April 2007.

Though there have been a number of studies examining the spread and potential distribution of this species in New Zealand (Hartley and Lester, 2003; Ward and Harris, 2005; Ward *et al.*, 2005), there have been few investigations into its long-term persistence, or the impact it has on resident ant species and other invertebrates in this country (Haw, 2006).

Research Aims

This study was conducted to assess the impact Argentine ants have on ground-dwelling arthropods in New Zealand and to see if the effects of this ant are likely to continue in the long-term. I studied the population persistence of this invader, as well as examining the

effect Argentine ants have on resident ant species richness, abundance and community structure. I also investigated the impact this invader has on non-ant arthropod species richness and abundance. My study sites were across this ant's New Zealand range, from Kaitaia in the north of the North Island to Christchurch on the South Island.

Firstly, in Chapter 2, I examined the effect of Argentine ants on resident ant species and other ground-dwelling arthropods. I investigated whether or not these effects, if any, are density-dependent. I compared resident arthropod species richness and abundance between sites that were uninvaded by Argentine ants and sites that were invaded by Argentine ants. The invaded sites were chosen so as to encompass the natural variation in abundance found between Argentine ant populations.

In Chapter 3 I investigated the population persistence of Argentine ant populations in New Zealand using visual surveys. I examined how temperature and rainfall influenced their persistence, and what effect climate change will have on their survival. In addition, I studied the effect their presence has on resident ant communities, and whether or not these communities are able to recover after Argentine ant populations collapse.

Finally, in Chapter 4 I discuss my findings and their implications.

Please note that Chapters 2 and 3 have been written as individual research papers, so there is inevitable repetition between the introductions and discussions of these chapters.

Chapter 2:

The effect of Argentine ants (*Linepithema humile*) on ground-dwelling arthropods is density-dependent

Abstract

The Argentine ant (*Linepithema humile*) is well known to displace resident ant species where it occurs at high population densities, and may also reduce densities of other ground-dwelling arthropods. However, few studies have examined if the effect of this invader on resident species is density-dependent. I investigated the effect of varying Argentine ant abundance on resident ant and non-ant arthropod species richness and abundance in seven cities across this ant's range in New Zealand. Pitfall traps were used to compare four uninvaded and four invaded sites in each city, with invaded sites being chosen based on natural varying abundance of Argentine ant populations. As in other parts of its introduced range, Argentine ant density had a significant negative effect on epigaeic (above ground foraging) ant species richness and abundance. Hypogaeic (below ground foraging) ant species were not significantly affected by Argentine ant abundance. Diplopoda species richness and abundance decreased with increasing Argentine ant abundance, while Hemiptera abundance increased. Other non-ant arthropods were not affected by Argentine ant abundance, suggesting these ants may not be having a deleterious influence on all non-ant arthropods in urban areas of New Zealand.

Keywords: biological invasions, Argentine ant, *Linepithema humile*, impact, abundance, density-dependent effects, ground-dwelling arthropods, New Zealand

Introduction

Invasive species are widely considered to be a serious threat to ecosystems and biodiversity around the world (Vitousek, 1997). However, only a fraction of the species that are introduced to a place will go on to become sufficiently widespread and abundant to cause ecological or economic damage (Lockwood *et al.*, 2009). It is frequently assumed that because a species is ecologically or economically damaging in one country, it will inevitably be so in a new environment. This assumption may lead to inappropriate and unnecessary management decisions.

Ants are among the world's worst invasive species (Lowe *et al.*, 2000; Holway *et al.*, 2002a). There are several ant species that have become widely established, cosmopolitan invaders, which are referred to as "tramp" ants. Passera (1994) describes tramp ant species as being polygynous (having multiple queens), unicolonial, reproducing by budding, and closely associated with humans and disturbance. Due to introduced populations of tramp ants attaining extremely high densities, invasive ants have had devastating effects on native ant communities (Bond and Slingsby, 1984; Porter and Savignano, 1990; Holway, 1999). The Argentine ant (*Linepithema humile*) is one such invasive tramp ant species. Listed among 100 of the world's worst invasive species (Lowe *et al.*, 2000), this invader is native to South America. It has invaded sub-tropical and Mediterranean regions worldwide, and is now established on six continents (Wetterer *et al.*, 2009). Introduced populations of this ant form high-density, widespread, highly aggressive colonies and can deleteriously influence native communities (Holway *et al.*, 2002a). In California and Hawaii, invasion and proliferation of Argentine ants are associated with the destruction of resident ant populations, reductions in ground-dwelling arthropod diversity, declines in vertebrate populations, and damage to crops (Human and Gordon, 1997; Suarez *et al.*, 2000; Holway *et al.*, 2002a; Krushelnycky *et al.*, 2005).

The distribution of the Argentine ant has been found to be limited by environmental variables such as temperature and rainfall (Roura-Pascual *et al.*, 2004), but much of the

New Zealand climate is considered suitable for this invader (Hartley and Lester, 2003). Given its high impact in other parts of the world (Holway *et al.*, 2002a) the Argentine ant is a good candidate for becoming a successful invasive species in New Zealand. However, that it will have similar ecologically and economically deleterious effects here as it does elsewhere is not a foregone conclusion.

There are at least two common explanations for the high densities that Argentine ants attain. Firstly, introduced ants have escaped the competitors and predators found within their native range. In South America natural enemies and competitors appear to regulate Argentine ant populations (LeBrun *et al.*, 2007). Secondly, introduced populations frequently form supercolonies (a polydomous colony with high nest density and an expansive spatial scale such that worker exchange between all parts of the colony is unlikely), with multiple queens over wide spatial areas with no intraspecific aggression within the supercolony (Pedersen *et al.*, 2006). The supercolonies found in this ant's introduced range may stretch for hundreds of kilometers (Vogel, 2010). However, population densities of invasive ants may vary spatially and temporally (Abbott, 2006; Heller *et al.*, 2008). Where invasive ants exist at lower population densities, their impact on resident ant species and other arthropods may be reduced (see Chapter 3; Morrison, 2002; Lester *et al.*, 2009).

The displacement of native ant species by Argentine ants has been well documented (Erickson, 1971; Holway, 1998; DiGirolamo and Fox, 2006; Heller *et al.*, 2008). However, its effect on non-ant arthropods is less clear. Studies investigating the impact of Argentine ants on non-ant invertebrates have produced mixed results. Cole *et al.* (1992) reported a significant decline in a number of invertebrate orders, the most severe effect being on two endemic pollinators, as a consequence of Argentine ant invasion in Hawaii. Human and Gordon (1997), working in California, also found a decrease in species richness and abundance in certain groups, though other groups, most notably scavengers, increased in the presence of Argentine ants. In contrast, Holway (1998) found no differences in non-ant arthropod diversity between invaded and uninvaded sites in

California, perhaps because Argentine ants interacted with ground-dwelling arthropods in a similar way as native ants.

First observed in Auckland in 1990 (Green, 1990), Argentine ants have since spread widely around the North Island of New Zealand, assisted by human-mediated dispersal. This ant is also now found in Blenheim, Nelson and Christchurch on the South Island (Lester *et al.*, 2003). It is still largely confined to urban areas (Ward *et al.*, 2010). There has only been one previous study investigating the impact of Argentine ants on other species in New Zealand. Haw (2006) looked at their effect on ground-dwelling invertebrates in remnant patches of native Auckland forests in urban areas but found few differences in species richness or abundance between invaded and uninvaded sites. Here, I have investigated the effect of Argentine ants on ground-dwelling arthropod communities in seven cities spanning the range of the Argentine ant in New Zealand. In order to examine the impact these ants are having in New Zealand, I posed three questions. Firstly, are Argentine ants associated with a reduction in ant species richness and abundance? Secondly, is non-ant arthropod species richness and abundance negatively associated with Argentine ants? Finally, if the previous associations do exist, what effect does variation in Argentine ant abundance have on the impact of this invader?

Materials and Methods

Study Sites

This study was conducted from January - March of 2011 in seven different localities throughout the Argentine ant's New Zealand range (Fig. 2.1). Sites were located in Russell, Auckland, Morrinsville, Wellington, Blenheim, Nelson and Christchurch. I had four paired study sites, four uninvaded by Argentine ants and four invaded by Argentine ants in each city or township. The Russell and Auckland sites were sampled in January, and the Wellington, Blenheim, Nelson and Christchurch sites were sampled in February. The Morrinsville sites were sampled in early March due to extremely heavy rains during the January sampling period. All sites were sampled a single time. See Table 2.1 for the

geographical coordinates, description, vegetation characteristics and climate of each site. Invaded sites were chosen so as to have differing Argentine ant abundances between cities. These varying abundances allowed me to investigate the effect of varying Argentine ant abundance on ground-dwelling arthropod abundance and diversity instead of simply the effect of Argentine ant presence or absence. Uninvaded and invaded sites within each city were chosen so as to have similar vegetation, cover, and level of disturbance. In order to investigate the effect of differing Argentine ant abundance on other ground-dwelling invertebrates within each city, four sites were chosen based on differences in Argentine ant abundance as well as substrate, cover, and vegetation. Sites were also paired between uninvaded and invaded sites. Sites were chosen, and Argentine ant abundance determined by baiting.

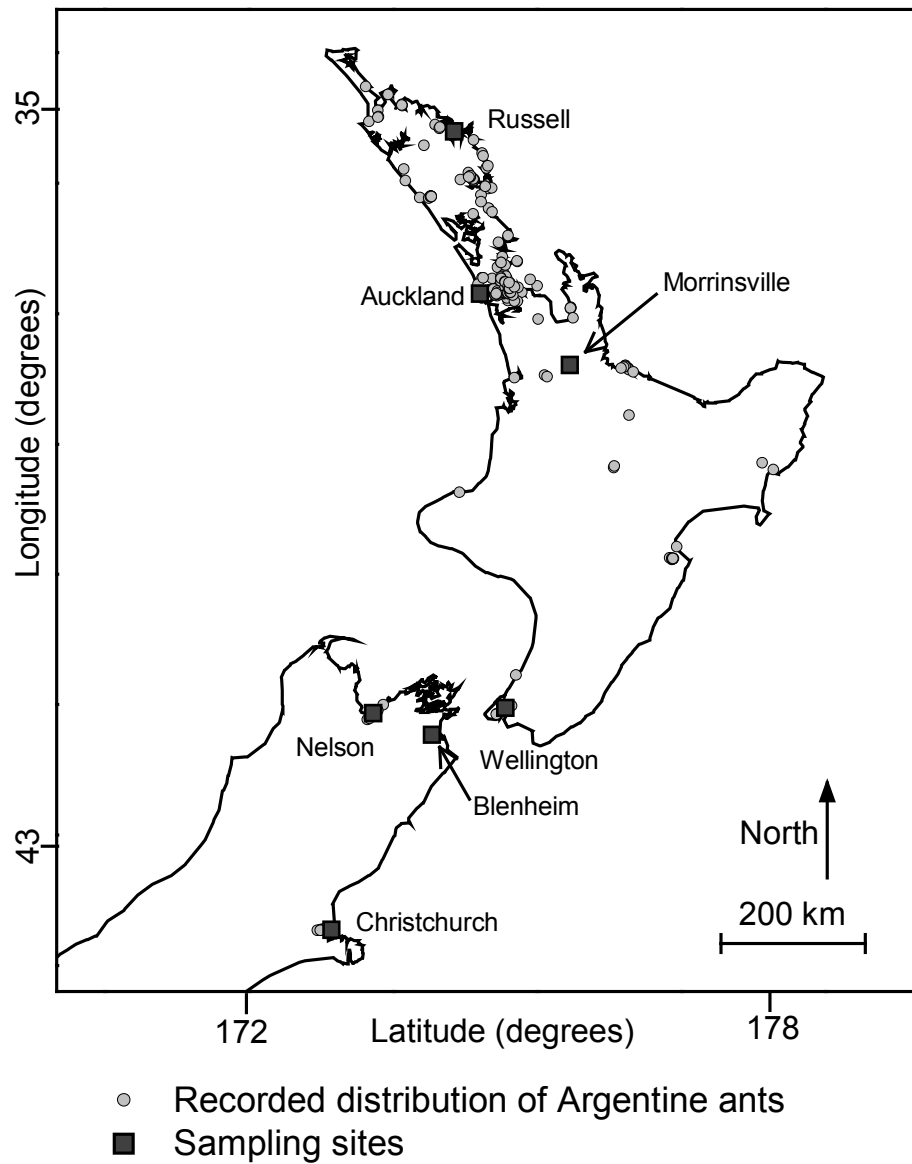


Figure 2.1. Location of study sites in New Zealand. Sites were sampled during January-March, 2011.

Table 2.1. Study site characteristics for uninvaded and invaded sites in seven cities across New Zealand. The four uninvaded or invaded sites in each city shared the same general characteristics. Location coordinates are easting and northing. The “year invaded” is the year Argentine ants were first recorded in the area. The “type” describes the location of the sites, and the plant species listed are the dominant vegetation in the area. The climate data is from weather stations within 20km of the sites, obtained from <http://cliflo.niwa.co.nz>.

	Site					
	Russell		Auckland		Morrinsville	
	U	I	U	I	U	I
Location	2613500E		2640500E		2734000E	2734000E
	6659600N		6472800N		6391000N	6391000N
Year Invaded	2002		2005		2001	
Type	Cemetery grounds		Forest remnant		Park	
Vegetation	<i>Coprosma</i> sp. <i>Leptospermum scoparium</i>	<i>Coprosma</i> sp. <i>Pinus</i> sp. <i>Populus</i> sp.	<i>Metrosideros excelsa</i> <i>Macropiper excelsum</i>		<i>Quercus</i> spp. <i>Sequoia</i> sp. <i>Platanus</i> sp.	
						<i>Coprosma</i> sp. <i>Populus</i> sp.
Mean Temp. (°C)	15.8		15.2		14.5	12.8
Mean Max. Temp. (°C)	19.3		18.9		19.6	15.7
Mean Min. Temp. (°C)	12.2		11.4		9.4	9.9
Rainfall (mm)	1183.1		1345.3		1035.7	1416.6
Sunshine Hours	1973		2060		2009	2065
	Site					
	Blenheim		Nelson		Christchurch	
	U	I	U	I	U	I
Location	2590400E		2529400E		2485800E	
	5965500N		5990000N		5740900N	
Year Invaded	2006		2009		2007	
Type	School garden	Business garden	Riverside garden		Park garden	Business garden
Vegetation	<i>Pittosporum</i> spp. <i>Acer</i> sp.	<i>Pittosporum</i> spp. Cycad	<i>Phormium</i> sp. <i>Coprosma</i> sp.		<i>Phormium</i> sp.	
Mean Temp. (°C)	13.2		13.1		12.3	
Mean Max. Temp. (°C)	18.6		17.8		17.2	
Mean Min. Temp. (°C)	7.9		8.4		7.4	
Rainfall (mm)	673.6		920.8		651.0	
Sunshine Hours	2409		2405		2100	

Ant Sampling

First, in order to find sites with varying Argentine ant abundance, I used bait traps. Within each city, 30 bait stations were set up around 6 potential sites (5 bait stations per site). In Russell and Blenheim only 4 sites were baited (5 bait stations per site) due to space constraints. Bait stations consisted of half a cue card (3" X 4" Office Line System Cards, Ruled) and approximately 2.5mL of Arataki Honey ("Squeeze Me" bottle) placed in the centre. Stations were checked in order of set-up every 15 minutes for 3 hours. The number of Argentine ants on each bait card was counted at every sampling time. When the number of ants on each card became too numerous to accurately count, a photograph was taken for future analysis. Ants that were clearly trapped in the honey were not counted. After baiting, bait cards were removed and 4 sites chosen based on differing Argentine ant abundance. Sites were approximately 5m X 5m and approximately 10m from each other (except in Blenheim, which was less, due to space constraints). Due to the very different shapes and sizes of sites, I was not able to lay out traps in a standard pattern; instead, pitfall traps were arranged in a haphazard fashion so that they were at least 1m apart and fit within the site.

I used pitfall traps to investigate the effect of Argentine ants on New Zealand's ground-dwelling invertebrate fauna. Five pitfall traps were used at each site for a total of 20 per uninvaded and invaded sites. Pitfall traps consisted of 225mL clear plastic cups, 65mm in diameter at the mouth, tapering to 43mm at the base and 90mm deep (Deeko Everyday Plastic Cups). Cups were filled with 50ml of preservative (1:1 mixture of propylene glycol and water) and a drop of dish detergent (Sunlight Dishwashing Liquid) to decrease surface tension. Bulb diggers were used to remove soil with as little disturbance as possible and traps were set flush with the ground. Traps were collected after 72 hours. Pitfall traps are a common method of trapping ground-dwelling invertebrates, including ants (Human and Gordon, 1997; Holway, 1998). However, pitfall traps may give biased estimates of species richness and abundance as some species are more likely to be caught than others (Gotelli *et al.*, 2011). Additionally, the number of workers caught in pitfall traps is not always a surrogate for the relative abundance of species in an area due to

large differences in colony size and foraging patterns between species (Anderson, 1991; Olson, 1991). The ant species collected may not represent the entire ant community present. These potential biases should be kept in mind when interpreting the results of this study.

Invertebrate Identification

All ants were identified to species after Don (2007). Other invertebrates were identified to order, and more precisely where possible using Grant (1999), Crowe (2002), and Parkinson (2007). Invertebrates that could not be identified to species were sorted into morphospecies as laid out by Oliver and Beattie (1995). The use of morphospecies may artificially increase or decrease estimates of richness, depending on the degree of splitting and/or lumping that occurs (Oliver and Beattie, 1995); however, Krell, (2004) suggests that the use of morphospecies give adequate estimates of species diversity when comparing diversity between sites (impact assessment). After identification all specimens were stored in 70% ethanol.

Statistical Analysis

The climate data, annual rainfall (mm) and mean maximum daily temperature (°C), were obtained from <http://cliflo.niwa.co.nz>. The nearest weather station to each sampling site was within ~20 km of each location. These climate variables were chosen because previous studies have shown temperature and rainfall to constrain Argentine ant occurrence at regional scales (Roura-Pascual *et al.*, 2011). I used univariate general linear models (GLM) to test the influence of the two climate variables, Argentine ant abundance and their interaction terms on the number of ant species, ant worker abundance, number of non-ant arthropod morphospecies and non-ant arthropod abundance. All dependent variables were log-transformed prior to analysis to meet assumptions of normality (Kolmogorov-Smirnov and Shapiro-Wilks). The best fitting model using R^2 goodness-of-fit criterion included rainfall, maximum temperature, and Argentine ant abundance as

independent/predictor variables. The interaction terms were not significant and so were omitted. Both GLMs with the number of species (or morphospecies), or abundance as the dependant variable used means (within a site) as data points. I did not use the sequential Bonferroni technique to correct for multiple comparisons, as it has been shown to substantially increase the chance of a making a Type II error (failing to reject a false null hypothesis) (Nakagawa, 2004). For presentation, I performed multiple individual Spearman rank correlations, which do not assume linearity or normality, on total abundance and morphospecies diversity, ant species abundance and diversity and non-ant arthropod order abundance and morphospecies richness as a function of Argentine ant abundance by city. The lines of fit on the graphs are linear regressions for ease of interpretation. All statistical analyses were performed in PASW Statistics 18 (SPSS Inc. 2009).

Results

Effects of Argentine ant abundance, rainfall, and temperature on resident ants

Epigaeic ant species became significantly less abundant as Argentine ant abundance increased ($F_{1,52} = 8.77$, $P = 0.01$) (Table 2.2 ant 2.3, Fig. 2.2, Appendix 1 and 2). The GLM model predicted that with each increase of ten Argentine ants, epigaeic ant abundance would decrease by 1.05 ants, on a log-linear scale. Consequently, a city might have an abundance of 300 ants with 10 Argentine ants, but this abundance would decline to 152 ants with 1000 Argentine ants. The abundance of hypogaeic ant species was not affected by Argentine ant abundance ($F_{1,52} = 0.78$, $P = 0.38$), rainfall ($F_{1,52} = 1.38$, $P = 0.25$) or maximum temperature ($F_{1,52} = 2.68$, $P = 0.11$). Rainfall and maximum temperature had no significant effect on epigaeic ant abundance ($F_{1,52} = 0.59$, $P = 0.44$; $F_{1,52} = 3.68$, $P = 0.06$). Argentine ant abundance was also not associated with rainfall ($F_{1,52} = 0.25$, $P = 0.62$) or maximum temperature ($F_{1,52} = 0.08$, $P = 0.79$). These results are in contrast to those from Chapter 3. Only 8.2% of ant workers caught at invaded sites belonged to other ant species. Native species made up only 9.0% of captured ant workers in uninvaded sites

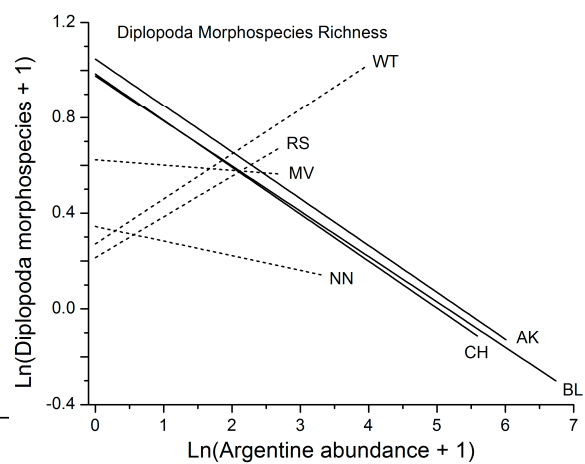
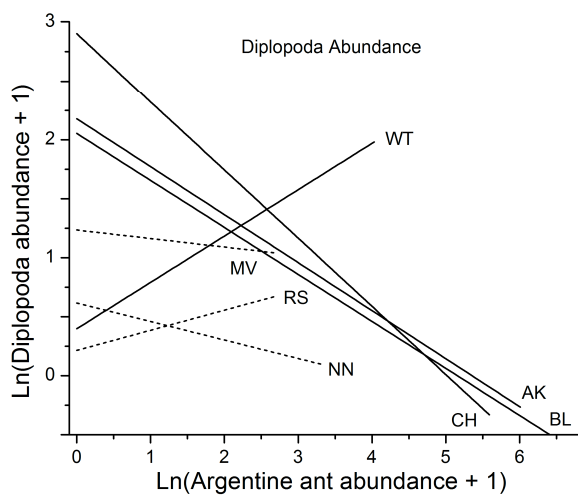
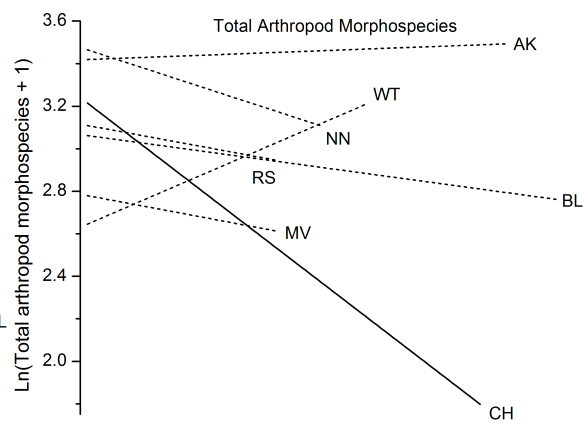
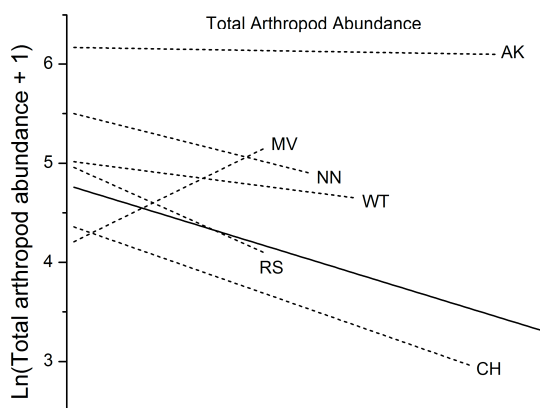
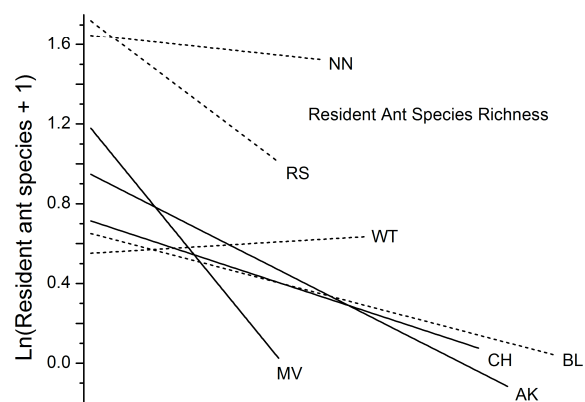
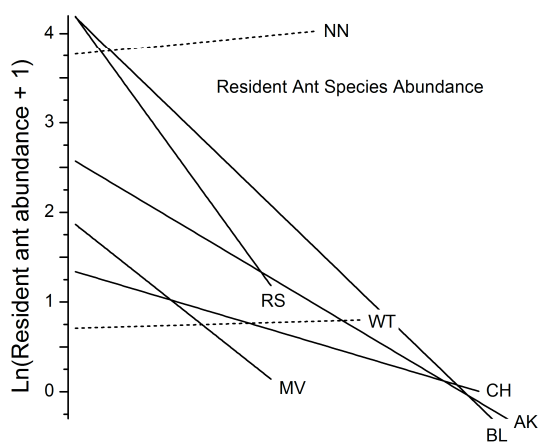
compared to 4.2% in invaded sites (excluding Argentine ant workers). Argentine ant workers outnumbered all other ant species workers combined in Auckland, Wellington, Blenheim and Christchurch. Argentine ant workers were more than twice as abundant as all other ant species workers combined across all cities (2958 Argentine ant workers versus 1340 non-Argentine workers).

Table 2.2. Results of univariate GLM of total arthropod abundance, total species richness, and abundance and species (or morphospecies) richness within various arthropod orders as a function of Argentine ant abundance, rainfall and maximum temperature.

Variable	Argentine ant abundance				Rainfall				Maximum Temperature			
Abundance	Coeff.	SE	F _{1,52}	P	Coeff.	SE	F _{1,52}	P	Coeff.	SE	F _{1,52}	P
Epigaeic ants	-0.005	0.002	8.774	0.005	-0.001	0.001	0.590	0.446	0.504	0.263	3.679	0.061
Hypogaeic ants	0	0.001	0.776	0.382	0	0	1.377	0.246	-0.139	0.085	2.684	0.107
Amphipoda	0	0.002	0.031	0.861	0.008	0.001	35.713	0.001	-0.863	0.291	8.808	0.005
Araneae	0	0.001	0.490	0.487	0	0	0.119	0.732	-0.161	0.107	2.251	0.140
Coleoptera	0.001	0.001	0.672	0.416	0.002	0.001	8.764	0.005	-0.033	0.151	0.047	0.829
Diplopoda	-0.002	0.001	5.246	0.026	-0.001	0.001	1.221	0.274	0.029	0.169	0.029	0.867
Diptera	0	0.001	0.001	0.974	0.001	0.001	1.734	0.194	-0.115	0.116	0.981	0.327
Hemiptera	0.002	0.001	4.304	0.043	-0.002	0.001	11.774	0.001	0.161	0.114	1.987	0.165
Hymenoptera (no ants)	-0.001	0.001	0.935	0.338	0.001	0	4.651	0.036	-0.295	0.099	8.850	0.004
Isopoda	0.001	0.001	0.953	0.333	0.005	0.001	44.553	0.001	0.077	0.183	0.174	0.678
Orthoptera	0.001	0.001	1.713	0.196	0.002	0.001	12.956	0.001	0.145	0.128	1.285	0.262
Total arthropods (excl. AA)	0	0.001	0.124	0.726	0.003	0.001	19.456	0.001	-0.144	0.143	1.008	0.320
Richness												
Epigaeic ants	-0.002	0.001	10.346	0.002	0	0	0.181	0.672	0.132	0.089	2.208	0.143
Hypogaeic ants	0	0	0.661	0.420	0	0	2.026	0.161	-0.092	0.051	3.250	0.077
Araneae	0	0	0.042	0.838	0	0	0.989	0.324	-0.099	0.077	1.632	0.207
Coleoptera	0	0.001	0.334	0.566	0.001	0	3.015	0.088	0.068	0.100	0.465	0.498
Diplopoda	-0.001	0.001	5.258	0.026	0	0	0.140	0.710	0.022	0.081	0.076	0.783
Diptera	0	0.001	0.012	0.913	0	0	0.765	0.386	-0.145	0.083	3.046	0.087
Hemiptera	0	0.001	0.192	0.663	-0.001	0	11.827	0.001	0.092	0.087	1.106	0.298
Hymenoptera (no ants)	-0.001	0.001	1.207	0.277	0.001	0	2.670	0.108	-0.166	0.081	4.241	0.044
Orthoptera	0	0	1.361	0.249	0.001	0	10.623	0.002	0.062	0.064	0.949	0.335
Total arthropods	0	0	0.321	0.573	0.001	0	5.959	0.018	-0.020	0.073	0.078	0.782

Table 2.3. Species of ants captured in pitfall traps. Numbers are the numerical abundance of each species summed across sites in each city and one total for abundance summed across all cities (NZ). Species with a (h) are hypogaeic.

Species	Uninvaded sites per city								Invaded sites per city							
	RS	AK	MV	WT	BL	NN	CH	NZ	RS	AK	MV	WT	BL	NN	CH	NZ
<i>Introduced:</i>																
<i>Linepithema humile</i>	-	-	-	-	-	-	-	-	26	984	36	112	1091	66	643	2958
<i>Amblypone australis</i> (h)	-	2	-	-	-	-	-	2	-	-	-	-	-	-	-	-
<i>Doleromyrma darwiniana</i>	-	-	-	-	348	-	-	348	-	-	-	-	-	-	-	-
<i>Hypoponera eduardi</i>	6	-	1	-	-	6	15	28	8	-	-	-	-	9	1	18
<i>Iridomyrmex</i> sp.	125	-	-	-	-	-	-	125	-	-	-	-	-	-	-	-
<i>Monomorium antipodum</i>	2	-	-	-	-	10	-	12	2	-	-	-	-	-	-	2
<i>Paratrechina</i> sp.	128	-	16	-	-	247	-	391	3	-	3	-	-	184	-	190
<i>Pheidole rugosula</i>	1	12	15	-	-	-	-	28	-	-	-	-	-	-	-	-
<i>Ponera leae</i>	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	1
<i>Strumigenys perplexa</i> (h)	1	-	-	-	-	12	-	13	2	-	-	4	1	10	-	17
<i>Technomyrmex albipes</i>	-	-	1	4	-	-	-	5	-	-	-	-	-	-	-	-
<i>Tetramorium grassii</i>	218	50	-	-	-	-	-	268	32	-	-	-	-	-	-	32
<i>Native:</i>																
<i>Amblypone sandersi</i> (h)	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	2
<i>Monomorium antarcticum</i>	34	-	1	1	-	43	-	79	-	-	-	-	-	7	-	7
<i>Monomorium smithii</i>	2	5	-	-	-	31	-	38	-	-	-	-	-	2	-	2
<i>Pachycondyla castanea</i> (h)	1	-	2	1	-	-	-	4	-	-	-	-	-	-	-	-
Totals	517	69	36	6	348	349	15	1340	74	984	39	118	1092	269	644	3220



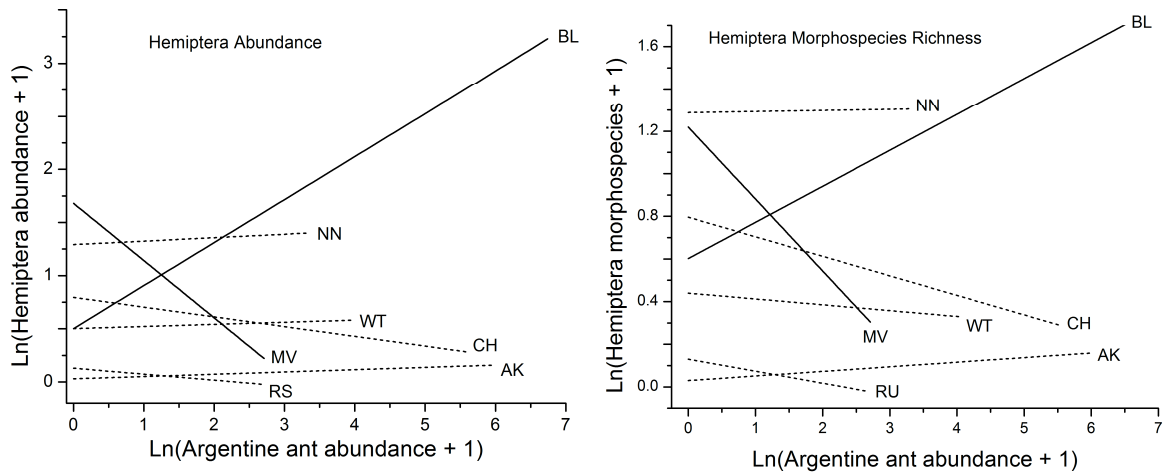


Figure 2.2. Linear regressions of the natural log of order abundance and morphospecies richness as a function of the natural log of Argentine ant abundance for Russell (RS), Auckland (AK), Morrinsville (MV), Wellington (WT), Blenheim (BL), Nelson (NN) and Christchurch (CH). Solid lines indicate a significant relationship and dashed lines a non-significant relationship using a Spearman rank correlation.

Epigaeic ant species richness also decreased significantly with increasing Argentine ant abundance ($F_{1,52} = 10.35$, $P = 0.01$), while hypogaeic ant species richness was unaffected ($F_{1,52} = 0.66$, $P = 0.42$) (Table 2.2 and 2.3, Fig. 2.2, Appendix 1 and 2). The GLM model predicted that with each increase of ten Argentine ants, epigaeic ant species richness would decrease by 1.02 ants, on a log-linear scale. In this case, a New Zealand ant community may have 10 different ant species in the presence of 10 Argentine ants, but this species richness would decline to 3 species in the presence of 1000 Argentine ants. Epigaeic and hypogaeic ant species richness were not correlated with rainfall ($F_{1,52} = 0.18$, $P = 0.67$; $F_{1,52} = 2.03$, $P = 0.16$) or maximum temperature ($F_{1,52} = 2.21$, $P = 0.14$; $F_{1,52} = 3.35$, $P = 0.08$). Russell and Nelson had the highest ant species richness and abundance in both their uninvaded and invaded sites that I examined. These cities also had among the lowest abundance of Argentine ants; only Morrinsville had a lower Argentine ant abundance than Nelson. Morrinsville had an equally high ant species richness to Nelson (6 species), but a low abundance of resident ant species. *Paratrechina* spp. were the most common epigaeic ant species in both uninvaded and invaded sites. It was found in Russell, Morrinsville, and Nelson, with a total of 391 workers in invaded sites and 190 workers in uninvaded sites. *Strumigenys perplexa* was the most common hypogaeic ant

species in invaded sites, present in Russell, Wellington, Blenheim and Nelson (total of 17 workers). It was the only ant species found to co-occur in the heavily Argentine ant infested Blenheim site. *Strumigenys perplexa* was also found in uninvaded sites in Russell and Nelson (a total of 13 workers). *Pachycondyla castanea* was the most commonly found hypogaeic species in uninvaded sites. It was found in uninvaded sites in Russell, Morrinsville, and Wellington (total of 4 workers) but was not found in any invaded sites. Other ant species that were never found co-existing with Argentine ants were *Amblyopone australis*, *Doleromyrma darwiniana*, *Iridomyrmex* spp., *Pheidole rugosula*, and *Technomyrmex albipes*.

Effects of Argentine ant abundance, rainfall, and temperature on non-ant arthropods

Results for the effect of Argentine ant abundance on non-ant arthropods were mixed, both for abundance and morphospecies richness (Table 2.2 and 2.4, Appendix 1 and 2). Total abundance and species richness across all orders did not change significantly ($F_{1,52}=0.12$, $P=0.73$; $F_{1,52}=0.32$, $P=0.57$) with increasing Argentine ant abundance (Figure 2.2). However, there was a slightly greater abundance of non-ant arthropods in the uninvaded sites than invaded sites for every city except Morrinsville. Morrinsville had the greatest difference in abundance between uninvaded and invaded sites with a total of 456 arthropods in the uninvaded sites and 1478 arthropods in the invaded sites (94% of which were Amphipoda) (Table 2.4). Diplopoda showed a decreasing abundance and morphospecies number with increasing Argentine ant abundance ($F_{1,52}=5.25$, $P=0.03$; $F_{1,52}=5.26$, $P=0.03$). The GLM model predicted that with an increase of 10 Argentine ants, Diplopoda abundance would decrease by 1.02 individuals and Diplopoda morphospecies richness would decrease by 1.01 morphospecies, on a log-linear scale. Auckland, Blenheim and Christchurch had the highest abundances of Diplopoda in their uninvaded sites but zero Diplopoda in their invaded sites. Argentine ant abundance was associated with an increased hemipteran abundance ($F_{1,52}=4.30$, $P=0.04$) but did not affect hemipteran morphospecies number ($F_{1,52}=0.19$, $P=0.66$). The GLM model predicted that with an increase of 10 Argentine ants, Hemiptera abundance would

increase by 1.01 individuals on a log-linear scale. Hemipteran abundances were low in uninvaded and invaded sites in most cities with the exception of Blenheim, which had 61 individuals in its invaded sites, versus 4 in its uninvaded. These low abundances are probably due to the arboreal habits of most hemipterans, which make pitfall traps an unsuitable method of collection for this order.

Table 2.4. Non-ant arthropod orders captured in pitfall traps. Numbers are the numerical abundance of each order summed across sites in each city.

Taxa	Uninvaded sites per city							Invaded sites per city						
	RS	AK	MV	WT	BL	NN	CH	RS	AK	MV	WT	BL	NN	CH
Abundance														
Amphipoda	-	889	303	885	-	451	-	5	1019	1387	219	-	253	-
Araneae	29	32	15	24	34	42	110	16	42	13	34	38	22	9
Coleoptera	75	166	17	14	60	103	23	45	241	25	83	27	118	22
Diplopoda	2	47	24	4	34	6	74	3	-	17	21	-	1	-
Diptera	57	34	8	12	13	16	25	27	24	9	22	14	16	66
Hemiptera	1	-	19	4	4	15	5	-	-	3	5	61	18	2
Hymenoptera	11	8	6	10	6	12	5	18	2	5	36	2	6	6
Isopoda	3	739	21	7	-	16	12	180	478	13	3	-	53	-
Orthoptera	49	4	7	1	-	-	3	7	80	3	-	-	1	-
Total arthropods	227	1919	420	961	151	661	257	301	1886	1475	423	142	498	105
Morphospecies diversity														
Araneae	35	16	11	15	14	29	27	32	24	11	12	16	13	7
Coleoptera	21	30	9	7	17	22	15	22	26	11	24	17	22	5
Diplopoda	2	3	5	2	3	2	2	3	-	3	3	-	1	-
Diptera	6	14	5	9	12	13	9	8	9	6	12	10	9	6
Hemiptera	1	-	8	3	3	14	2	-	-	3	2	10	12	2
Hymenoptera	5	6	4	10	3	11	4	8	2	5	5	2	6	5
Orthoptera	5	1	1	1	-	-	1	1	3	2	-	-	1	-
Total arthropods	75	70	43	48	52	91	60	74	54	41	58	55	64	25

Other orders such as Amphipoda, Araneae, Coleoptera, Diptera, Isopoda and Orthoptera showed no significant effects of changing Argentine ant abundance. Total abundance (of all orders pooled) and total morphospecies diversity were significantly and positively associated with annual rainfall. Rainfall had a significant, positive effect on abundance and morphospecies richness of Coleoptera and Orthoptera. Amphipoda and Isopoda abundance were also significantly and positively influenced by rainfall. Amphipoda was positively influenced by maximum temperature as well. Hemiptera abundance and morphospecies richness was negatively affected by rainfall (Table 2.2). Non-ant Hymenoptera abundance and morphospecies richness were negatively affected by maximum temperature.

Discussion

The strongest influence of Argentine ants appeared to be on ants. Most epigaeic ant species were not able to co-exist with Argentine ants. Epigaeic ant species richness and abundance was negatively correlated with Argentine ant abundance. The exclusion of many resident ant species by Argentine ants has been well-documented (Erickson, 1971; Human and Gordon, 1997; Holway 1998). However, at sites where Argentine ant abundance was low, such as in Russell and Nelson, resident ant species were able to co-exist at levels similar to those at uninvaded sites. Invaded sites in Russell showed a decline in ant abundance, but ant species richness was not significantly different from uninvaded sites. In Nelson there was no difference in resident ant species richness and abundance between invaded and uninvaded sites. The GLM model predicted that with each increase of 10 Argentine ants, epigaeic ant abundance would decrease by 1.05 ants and species richness would decrease by 1.02 species, on a log-linear scale. This same pattern of exclusion when Argentine ants were at high abundance, and co-existence when they were at low is observed in Chapter 3. These results suggest that the effect of Argentine ants on resident ants is density-dependent.

Argentine ants may competitively exclude other ant species by a combination of swift location of and recruitment to resources, followed by fierce defense of that resource (Rowles and O'Dowd, 2007), thereby breaking the trade-off between discovery and dominance commonly observed in ants (Fellers, 1987). However, there is evidence that Argentine ants are only able to break this trade-off due to numerical, not behavioural superiority (Holway 1999; Human and Gordon, 1999; Walters and MacKay, 2005). Behavioural dominance has been shown to be linked with numerical dominance in ant communities (Feller, 1987; Palmer, 2004). Laboratory experiments manipulating colony size showed Argentine ants were only able to dominate resources and overwhelm native ant species when they vastly outnumbered the other species (Holway and Case, 2001; Walters and MacKay, 2005; Sagata and Lester, 2009).

Argentine ants are highly aggressive (Buczkowski and Bennett, 2008) and often use physical and chemical defenses simultaneously while fighting (Human and Gordon, 1996; Rowles and O'Dowd, 2007). However, they are weak individually and do not win more often than other ant species in one-on-one encounters against enemy workers (Holway, 1999; Holway and Case, 2001). The impact of Argentine ants on other ant species may be small where Argentine ants can not maintain high abundances (Heller *et al.*, 2008; Sanders and Suarez, 2011). This inability to maintain high population densities may be due to unsuitable abiotic conditions in some sites (Menke and Holway, 2006; Heller *et al.*, 2008), or a result of population decline, which has been observed for many Argentine ant populations in New Zealand (Chapter 3).

Only in Morrinsville and Wellington was low epigaeic ant species richness not linked to high Argentine ant abundance. Wellington had very low ant species richness and abundance in all sites, regardless of whether Argentine ants invaded them or not. Morrinsville had significantly reduced ant species richness in its invaded sites compared to uninvaded sites despite a low overall abundance of Argentine ants. Morrinsville was sampled later than the other cities, in early March, due to heavy rains during the original sampling period in January. I noticed significantly less Argentine ant activity in March compared to January, suggesting the seemingly low Argentine ant abundance at these

sites was actually due to seasonal differences in foraging activity instead of a lack of Argentine ants.

Ant species richness did not increase in the absence of Argentine ants in Blenheim, possibly because the uninvaded sites there had been colonized by *Doleromyrma darwiniana*, another introduced pest species. The effect of *D. darwiniana* on other ant species and non-ant arthropods is unknown. However, the total lack of co-existing ant species in Blenheim's uninvaded sites suggests its impact on other ant species may be comparable to that of the Argentine ant.

Other studies have shown hypogaeic ant species to be less effected by Argentine ant presence than epigaeic species (Ward, 1987; Human and Gordon, 1997; Holway, 1998). My results support this observation. Hypogaeic ant abundance and species richness was unaffected by Argentine ant abundance. The mechanisms that enable hypogaeic ant species to co-exist with Argentine ants are as yet unknown, though it may simply be due to the lack of interaction between hypogaeic species and the epigaeic Argentine ant (Human and Gordon, 1997). However, there is also evidence that it is the small size (Suarez *et al.*, 1998; Touyama *et al.*, 2003) of many hypogaeic ant species, not their foraging behaviour per se, that allows them to co-exist with invasive ant species. The relatively small (2.2-2.7mm) *Strumigenys perplexa*, a hypogaeic ant species, was the only ant species found to co-occur in the heavily invaded Blenheim site. The much larger (4.9-6.1mm) hypogaeic *Pachycondyla castanea* was the most common hypogaeic species found in uninvaded sites, but it was not found to coexist with Argentine ants. Sarty *et al.* (2006) invoked the size-grain hypothesis, which proposes ants of different sizes may be able to co-exist due to differential use of habitat, to explain the co-occurrence of multiple ant species with high densities of the yellow crazy ant on Tokelau.

Ant species richness and abundance was not correlated with rainfall or temperature. Many ant species, including Argentine ants, are moisture-limited (Menke and Holway, 2006). Heller *et al.* (2008) found that native ant distribution was only affected by rainfall in invaded plots, most likely due to the spread of Argentine ants with increasing rainfall. This is unlikely to be a factor in New Zealand's wet climate, where the driest site receives

about 649.1mm of rain per year. Rainfall has been found to decrease the long-term persistence of Argentine ants in New Zealand, but not their establishment (Chapter 3).

Results for non-ant arthropod orders were mixed. Diplopoda abundance and morphospecies richness were negatively associated with Argentine ant abundance and Diplopoda were completely absent from invaded sites in the three most heavily invaded cities (Auckland, Blenheim and Christchurch). Previous studies found Diplopoda to be positively associated with Argentine ant presence (Cole *et al.*, 1992; Haw, 2006). Cole *et al.* (1992) hypothesized that the scavenging behaviour of Diplopoda was responsible for the higher population abundance in invaded areas, as the corpses of Argentine ants would represent a plentiful food source. It is possible Diplopoda compete with Argentine ants for space under rocks and dead wood, where Argentine ants may prefer to nest (personal observation).

Hemiptera abundance in Blenheim increased significantly with increasing Argentine ant abundance. This has been observed previously in New Zealand. For example, Haw (2006) found hemipteran abundance was significantly greater in Argentine ant invaded sites in Auckland native forest remnants in urban areas. Other studies have found that hemipteran abundance was lower in the presence of Argentine ants (Cole *et al.*, 1992; Human and Gordon, 1997; Bolger *et al.*, 2000). However, this positive correlation has been well-documented in New Zealand agricultural systems and others such systems around the world (Way, 1963; Lester *et al.*, 2003; Mgocheki and Addison, 2009).

Argentine ants are well known to tend honeydew producing hemipterans (Holway *et al.*, 2002a). This mutualism gives Argentine ants access to carbohydrate-rich honeydew, an important food source, and in return the ants protect the hemipterans from their natural enemies (Way, 1963). It has been suggested that access to, and the ability to utilize, carbohydrate-rich exudates leads to ecological dominance in ant communities by fueling high worker abundance and a high rate of activity and aggression (Davidson 1997, 1998; Holways *et al.*, 2002a). Rowles and Silverman (2009) found that the presence of carbohydrate food sources facilitated the invasion of natural habitat by Argentine ants in North Carolina. Tending ants are often a limiting resource for hemipterans, so the

presence of the highly abundant Argentine ant can result in irruptions of hemipteran populations (Holway *et al.*, 2002a). Lester *et al.* (2003) found Argentine ants tending 15 species of hemipteran on 15 kinds of agricultural crop across its range in New Zealand. The presence of particular species of hemipteran amenable to being tended by ants may explain why this positive correlation was found only in Blenheim. Additionally, pitfall traps are not an ideal method for sampling hemipterans, which are usually found on plants.

Argentine ants did not appear to affect most of the non-ant arthropod orders sampled. There was no association between Argentine ant abundance and the abundance and morphospecies richness of Amphipoda, Araneae, Coleoptera, Diptera, non-ant Hymenoptera, Isopoda and Orthoptera. Differing results have been found previously for Araneae. Cole *et al.* (1992) and Human and Gordon (1997) found a negative association, Holway (1998) and Haw (2006) found no association, and Bolger *et al.* (2000) found a positive association between Araneae and Argentine ants. Cole *et al.* (1992) and Bolger *et al.* (2000) found a negative association for Coleoptera overall, though conflicting results have been found for the family Carabidae (Cole *et al.*, 1992; Human and Gordon, 1997; Holway, 1998; Bolger *et al.*, 2000). Not enough carabids were caught in this study to investigate the effect of Argentine ant abundance on them separately from the rest of the Coleoptera. The hard exoskeleton of most Coleoptera may protect them from being killed and eaten by Argentine ants (Human and Gordon, 1997). For Diptera and non-ant Hymenoptera, adult individuals of these orders may be mobile enough to avoid Argentine ants.

This study provides a snapshot look at the effect of varying Argentine ant abundance on ground-dwelling arthropods at a single point in time. Impact of invasive species may interact with abiotic factors (Heller *et al.*, 2008). Hence, it is possible that temporal variation in climate or Argentine ant foraging activity would result in different patterns than those I observed. However, Mathieson (2011) observed that, in New Zealand, Argentine ants are most active foraging in the summer and fall, which is when this study occurred. Additionally, having a range of different Argentine ant abundance across cities

negates the hazard of temporal variation to some degree, as the most likely temporal variation to take place at these sites is the varying abundance of Argentine ants.

As shown elsewhere, Argentine ants negatively impact resident epigaeic ant species in New Zealand. This impact may be mitigated, however, by low Argentine ant abundance. Otherwise, in this experiment, the effect of Argentine ants on non-ant arthropods in New Zealand was mixed.

Chapter 3:

The widespread collapse of an invasive species: Argentine ants (*Linepithema humile*) in New Zealand

Abstract

The Argentine ant (*Linepithema humile*) is a widespread invasive species and can deleteriously influence native communities. In its introduced range it is well known to displace resident ant species where it occurs. First detected in Auckland in 1990, this invasive has since spread widely around New Zealand. However, like many invasive organisms, little research has investigated their long-term persistence. I surveyed 150 sites throughout the known distribution range of Argentine ants within the country and recorded the presence of these and other ant species. Argentine ant populations were found to have collapsed at 40% of surveyed sites across this range. Populations had a mean survival time of 14.1 years (95% CI= 12.9- 15.3 years). Models suggest that climate change will delay their collapse, as increasing temperature and decreasing rainfall significantly increased their longevity, but only by a few years. Ant species richness was significantly reduced at currently invaded sites compared to uninvaded; however, resident ant communities appeared to recover after the collapse of Argentine ant incursions. In Auckland, formerly invaded community composition was indistinguishable from those which had never been invaded. This study demonstrates the widespread collapse of an invasive species and the recovery of resident communities, suggesting that the Argentine ant, though devastating elsewhere, may not be a long-term threat to New Zealand's ant communities.

Keywords: biological invasions, population persistence, climate change, community recovery, Argentine ant, *Linepithema humile*, New Zealand

Introduction

The combined influence of invasive species and climate change may be harmful for economies and human health, and may cause extinction or change evolutionary pathways (Vitousek *et al.*, 1997). Consequently, considerable resources are frequently applied to invasive species management (Pimentel *et al.*, 2005). Invasive species have, however, been hypothesized to be susceptible to population crashes (Sakai *et al.*, 2001) irrespective of management approaches.

Introduced ant species are often particularly successful invaders (Holway *et al.*, 2002a). There are several ant species that have become widely established, cosmopolitan pests. These species share a number of characteristics that are thought to contribute to their success. They are polygynous (having multiple queens), unicolonial, reproduce by budding and are closely associated with humans and disturbance (Passera, 1994). Due to introduced populations attaining extremely high densities, invasive ants have had devastating effects on native ant communities (Porter and Savignano, 1990; Holway, 1998, Holway *et al.*, 2002a). The Argentine ant (*Linepithema humile*) is a typical example of a destructive invasive ant species. This ant is listed amongst 100 of the world's worst invasive species (Lowe *et al.*, 2000). Native to northern Argentina and surrounding regions, the Argentine ant has invaded sub-tropical and temperate regions and is now established on 6 continents (Wetterer *et al.*, 2009). Introduced populations of this ant form high-density, widespread, highly aggressive colonies and can deleteriously influence native communities. In California and Hawaii, invasion and proliferation of Argentine ants are associated with destruction of resident ant populations, reductions in ground-dwelling arthropod diversity, decline in vertebrate populations and damage to crops (Human and Gordon, 1997; Suarez *et al.*, 2000; Holway *et al.*, 2002a; Krushelnycky *et al.*, 2005).

There are at least 2 common explanations for the high densities that Argentine ants attain. Firstly, introduced ants are able to escape the competitors and predators found within their native range. In South America natural enemies and competitors appear to regulate

Argentine ant populations (Holway, 1998). For example, they must compete with a number of behaviourally dominant ant species in their native range (LeBrun *et al.*, 2007). Secondly, like native populations, introduced populations form supercolonies (a polydomous colony with high nest density and an expansive spatial scale such that worker exchange between all parts of the colony is unlikely) with multiple queens over wide spatial areas with no intraspecific aggression within the supercolony (Pedersen *et al.*, 2006). However, in their native range, a single supercolony controls a territory of between 25-500m, with many competing supercolonies in an area (Pedersen *et al.*, 2006). This area is several orders of magnitude smaller than the supercolonies found in this ant's introduced range where the largest known colony stretches over 6000km from Italy to the Spanish Atlantic coast (Giraud *et al.*, 2002).

Tsutsui and colleagues (2000, 2001, 2003) suggest this extreme supercolony behaviour is a consequence of low genetic diversity among founding individuals (Suarez *et al.*, 2008). Due to the genetic bottleneck of founding individuals it is believed that within closely interrelated populations, such as those in California, ants recognize each other as nestmates even though they may be from distant nests. This lack of intraspecific aggression means energy that would have otherwise been spent on fighting and defense can be used for foraging and reproduction (Thomas *et al.*, 2006).

First observed in Auckland in 1990 (Green, 1990), the species has since spread widely around the North Island of New Zealand, assisted by human-mediated dispersal, and is also found in Blenheim, Nelson and Christchurch on the south island (Ward *et al.*, 2005). The dates and locations of newly observed infestations have been recorded for populations (Roura-Pascual *et al.*, 2011), typically ranging in size from a few to several hundred hectares. Environmental variables such as temperature and rainfall have previously been suggested to help limit the distribution of this ant (Roura-Pascual *et al.*, 2004). Consequently, this invasive species is expected to expand its range with climate change, particularly in higher latitude regions such as New Zealand.

Invasive ants are a substantial global problem for biodiversity (Holway *et al.*, 2002a). However, populations of other invasive ant species have occasionally been known to collapse (Haines and Haines, 1978; Wetterer, 2006; Wetterer, *in press*). Similarly, long-term observations of local Argentine ant infestations also suggest that not all populations are persisting within New Zealand (Phil Lester, unpublished data). In order to assess the threat these ants pose to New Zealand, I asked three questions. Firstly, are Argentine ant infestations persisting, and if not, how is the collapse of these populations influenced by temperature and rainfall? Secondly, how might climate change affect the survival of Argentine ant populations? Finally, do Argentine ants reduce species richness and change resident ant communities, and do these communities recover after Argentine ant population collapse?

Materials and Methods

Argentine ant sampling

I surveyed ant communities for the presence of Argentine ants and estimated overall ant species richness on North and South Island, New Zealand in January and February 2011. Using records of first recorded Argentine ant presence (Roura-Pascual *et al.*, 2011), I examined 150 locations across this ant's range using similar methods as the original surveys. Sampling sites were located in non-natural areas in Northland, Auckland, Raglan, Hamilton, Morrinsville, Thames, Tauranga, Rotorua, Taupo, Napier, Hastings, Paraparaumu, Wellington, Blenheim, Nelson and Christchurch (Fig. 3.1, Appendix 3). A GPS unit (Garmin GPS 60) was used to navigate to the original location ($\pm 10\text{m}$) where the surrounding area of approximately $200 \times 200 \text{ m}^2$ was hand-searched for ants. Visual surveys involved turning over objects and examining the ground and vegetation for thirty minutes. Such survey methods are considered effective for ant sampling (Gotelli *et al.*, 2011). Thirty minutes was deemed sufficient due to the simplified urban environment and conspicuous nature of Argentine ant infestations (Ward and Harris, 2005). Argentine ant presence was determined and ants were collected with aspirators and preserved for identification. Climate data (annual rainfall (mm), mean temperature ($^{\circ}\text{C}$), mean

maximum daily temperature (°C) and mean minimum daily temperature (°C)) were obtained from <http://cliflo.niwa.co.nz> for the nearest weather station to each sampling site, which was generally within 20 km of each sampling location. These climate variables were chosen because previous studies have shown temperature and rainfall to constrain Argentine ant occurrence at regional scales (Roura-Pascual *et al.*, 2011). Weather stations are maintained by the National Institute of Water & Atmospheric Research.

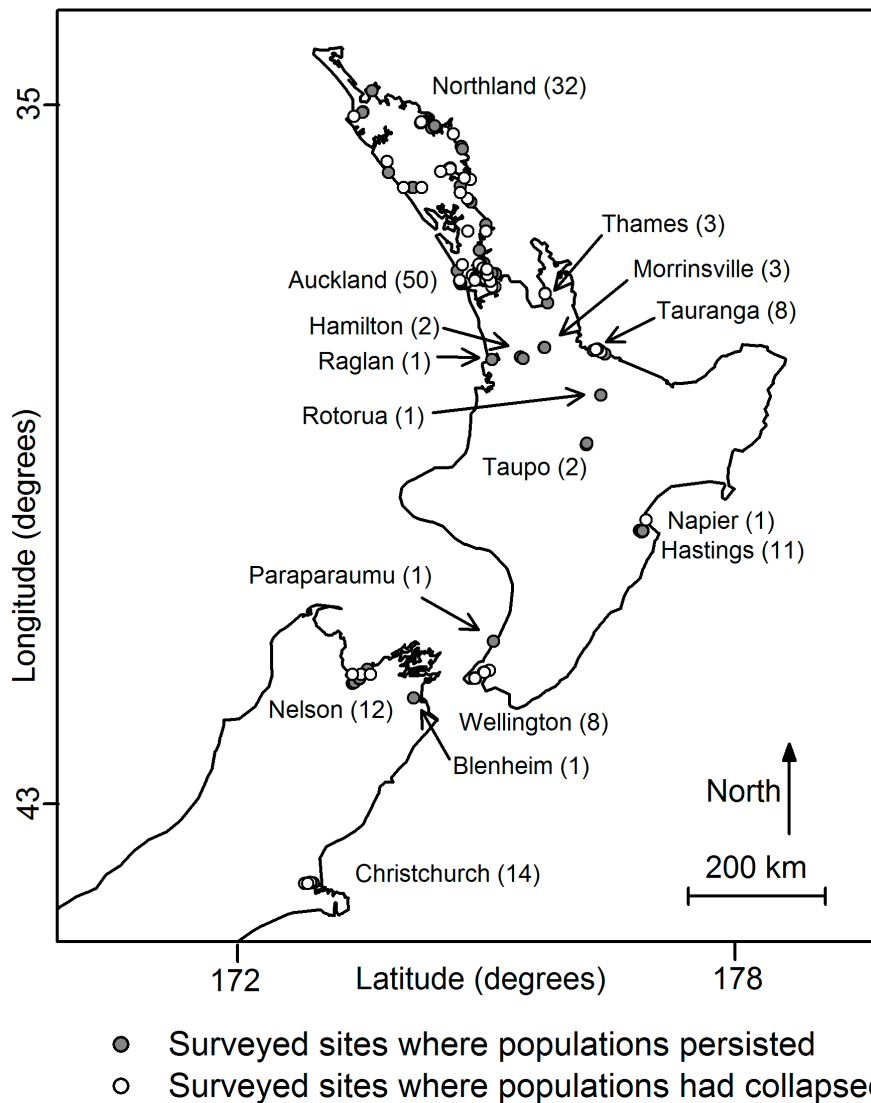


Figure 3.1. The location of surveyed sites of past known infestation and the number of sites surveyed in each city or region during January and February 2002.

A Cox's Proportional Hazards (PH) model, which is used to test the effects of covariates on the rate of death, was used to test the influence of the four climate variables on the rate of death of Argentine ant populations. Two parsimonious models were suggested by a forward stepwise model selection algorithm. Model 1 had 2 main effects: total rainfall and mean maximum daily temperature. Model 2 included the same variables and an interaction term between the 2 variables. The Goodness of Fit measure ($-2 \times \log$ likelihood) decreased from 468.6 (2 df) for Model 1 to 462.7 (3 df) for Model 2. Though this difference was significant ($P = 0.011$), I decided to use Model 1 for 2 reasons: (1) Model 1 gave biologically reasonable predictions of Argentine ant survival under different climatic conditions while Model 2 did not (for example it predicted very high survival rates in cold-wet locations such as the mountainous Southern Alps). This result may be partially due to the fact Argentine ant populations were not observed under some types of climatic conditions. And (2) the difference in model fit was not numerically large. For presentation, the survival data was organized into 4 groups based on the medians for rainfall and mean maximum temperature: high rainfall-high temperature, high rainfall-low temperature, low rainfall-high temperature and low rainfall-low temperature where low rainfall was 619-1163mm; high rainfall was 1167-1845mm; low temperature was 15.7-18.9°C and high temperature was 19.0-20.5°C. A Kaplan-Meier Survival Curve and Logrank statistic were used to estimate survival and compare groups.

Climate change model

To create the climate change model I applied the Cox's PH survival model fitted to current and future climate data to estimate probabilities of colony persistence under local conditions of rainfall and mean maximum daily temperature. Data regarding the climate across all of New Zealand were obtained from www.worldclim.org. Current climate was described by the 1950-2000 monthly averages at 2.5 minute resolution, while for future climate I used predictions for 2050 generated by the CSIRO A2 model. The CSIRO A2 projected data set for 2050 climate predicts an average increase in maximum temperature across all New Zealand of 1.4°C (from 15.0 to 16.4°C) and an average increase in rainfall

of 70mm per year (from 1670 to 1740mm per year) relative to the Worldclim 1950-2000 norm (Collier *et al.*, 2008). The CSIRO A2 scenario was chosen for future climate predictions because it represents a business as usual scenario with continued reliance on fossil fuels, continued population growth, and large differences in development between regions. Out of the six scenarios characterized in the 3rd Intergovernmental Panel on Climate Change report it predicts the second highest concentration of atmospheric CO₂ by 2050 (~525ppm, where other models predict between 550 and 450 ppm) and the fourth highest level of radiative forcing (Collier *et al.*, 2008).

Ant community surveys

Eleven additional sites in Auckland that had no record of ever being infested with Argentine ants were randomly selected and surveyed in April and May 2011 using identical methods. Auckland was selected due to the high diversity of its ant communities, the considerable length of time Argentine ants had been present in Auckland, and the large number of potential infested sites available. Three types of Auckland communities were assessed and compared for differences in species richness and community composition: (i) Communities currently with Argentine ants (note that some of these communities had large populations of Argentine ants, while others occupied less than 1% of the 40 000 m² study area); (ii) Communities where Argentine ant populations were no longer detected; and (iii) Communities where Argentine ants had never been recorded as present. The species richness of the 3 types of Auckland ant communities was examined using an ANOVA. To examine for differences in the species composition of these communities I used multivariate data analysis in PRIMER (Plymouth Routines in Multivariate Ecological Research, version 6.1.11, 2008: Plymouth Marine Laboratory, UK). An ordination analysis was conducted using non-metric Multidimensional Scaling (MDS) plots that score communities based on their similarity or dissimilarity. Stress values on MDS plots below 0.2 are an indication of a good fit. Analysis of Similarity (ANOSIM) test was used to assess the differences in species composition between the groups on the MDS plot. The resemblance matrix was derived using Jaccard similarity coefficients, which uses presence/ absence data. Comparisons

between communities were conducted using 9999 permutations. Global R values closer to or equal to zero indicate strong similarity between the test groups and those closer to or equal to one indicate large differences between the test groups.

Results

Argentine ant survival

Argentine ant populations were no longer detected in 40% of locations. Of the populations that did remain, many had shrunk from numerous nests covering multiple hectares with extremely high abundances of workers to just one or two nests covering a very small area with low worker densities. In these cases other ant species were present in the area. Every site Argentine ants had disappeared from had been recolonized by other ant species (with the exception of 3 sites which had no ant species present). A Kaplan-Meier estimator found the time to collapse was negatively influenced by mean maximum daily temperature and positively influenced by total annual rainfall ($P \leq 0.001$). Mean time to population collapse of these ants ranged from 10.48 years (10.10 – 10.86 years; 95% CI) in conditions of low rainfall and low temperature, to 17.80 years (15.59 – 20.01 years) under conditions of low rainfall and high temperature (Fig. 3.2a, Table 1).

Effect of climate change on Argentine ant survival

Climate change was predicted to increase the probability of Argentine ant survival in many regions (Fig. 3.2b). Under the CSIRO A2a model, the total New Zealand area with a higher than 80% chance of having populations persist for 15 years or more increases from 0.26% to 1.29%. Nowhere did survival probability decrease with climate change.

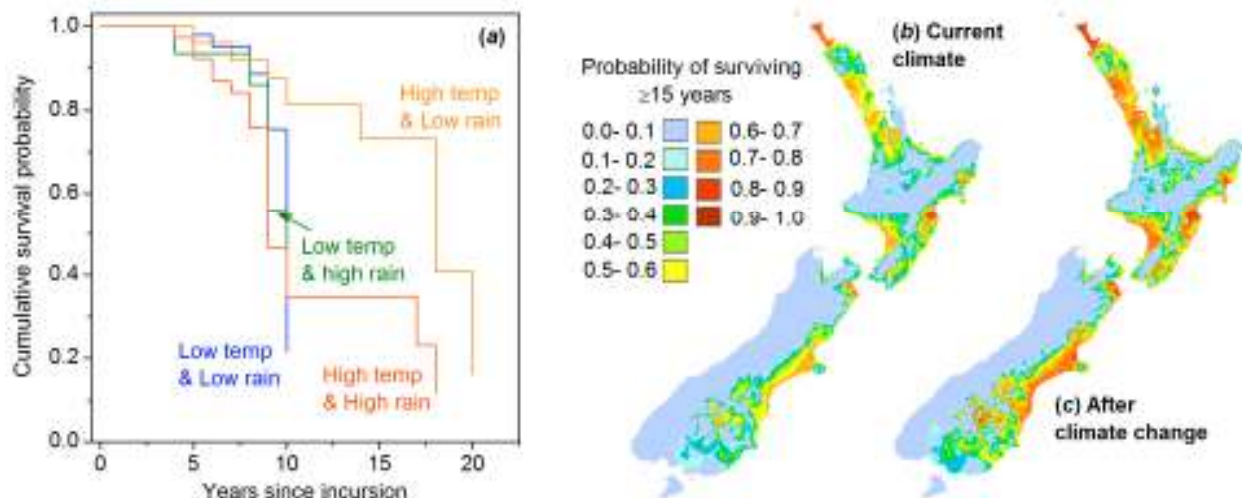


Figure 3.2. (a) Survivorship curves from sampling sites, with data divided into subsets of high and low temperature and rainfall conditions. (b) Probability of Argentine ant incursions surviving for ≥ 15 years under current climate conditions, and (c) after the CSIRO A2 climate change predictions.

Table 3.1. Kaplan-Meier estimates of survival time of Argentine ant populations under 4 different climate regimes.

Climate regime	N	Time (years)	95% CI
low rainfall – low temperature	50	10.5	10.1-10.9
high rainfall – low temperature	34	12.4	11.0-13.7
low rainfall – high temperature	22	17.8	15.6-20.0
high rainfall – high temperature	44	13.0	11.0-15.0
overall	150	14.1	12.9-15.3

Effect of invasion on resident ant communities

Ant species richness was significantly different by community type ($F_{2, 58} = 6.041$, $P = 0.004$, Fig. 3.3a). Post Hoc Tukey tests showed that ant communities with Argentine ants had significantly fewer ant species than communities without Argentine ants. The species richness of ant communities after Argentine ant collapse was intermediate, likely indicating that communities were at various stages of recovery post Argentine ant collapse. Communities with Argentine ants had significantly different community composition from those without Argentine ants present (ANOSIM; $R = 0.343$, $P = 0.001$) and from communities where populations had collapsed (ANOSIM; $R = 0.369$, $P =$

0.001) (Fig. 3b, Table 2). In contrast, communities in Auckland where Argentine ants had collapsed were indistinguishable from those which had never been invaded (ANOSIM; $R = 0.043$, $P = 0.749$). However, formerly invaded communities did have a much wider spread in the MDS plot, indicating more variability in their ant community composition, than uninvaded communities, which were tightly clustered.

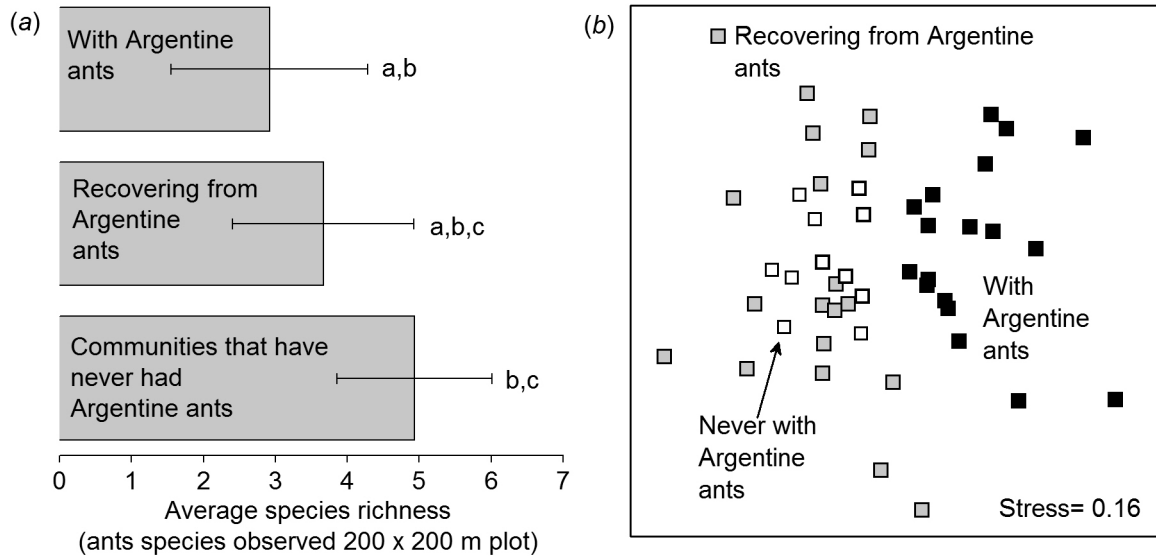


Figure 3.3. (a) The influence of Argentine ants on mean species richness of ant communities in Auckland (\pm SE). The recovering community probably has intermediate richness due to varying time since Argentine ant collapse. Letters represent results from post-hoc Tukey test groupings. (b) A multi-dimensional scaling analysis of Auckland ant communities currently with Argentine ants ($n=23$), without ever having Argentine ants ($n=11$), or communities recovering from incursions ($n=27$).

Discussion

Argentine ants had disappeared from 40% of the sampling sites. In many other sites, Argentine ant populations had been reduced from occupying multiple nests encompassing large areas to one or two small nests in a few square meters. These results are consistent with previous observations of the slow shrinkage and disappearance of large Argentine ant infestations in areas such as Wellington (Phil Lester, unpublished data). They do not

appear to move and to my knowledge are not managed by humans in any way that might reduce their abundance.

The shrinking and eventual disappearance of invasive species populations, including invasive ant populations, has historically been observed elsewhere (Simberloff and Gibbons, 2004). For example, yellow crazy ant (*Anoplolepis gracilipes*) populations in the Seychelles have declined dramatically over time and in some areas disappeared (Haines and Haines, 1978; Haines *et al.*, 1994). This has also been recorded for big-headed ant (*Pheidole megacephala*) populations on Madeira (Wetterer, *in press*). The reasons for this widespread population collapse of these species or Argentine ant populations are not yet known. However, population genetics predicts that invasive species might collapse due to inbreeding depression or an inability to adapt to their new environment (Sakai *et al.*, 2001). Previous genetic and behavioural assays have revealed that the New Zealand population of Argentine ants has amongst the lowest recorded genetic diversity of any introduced Argentine ant population worldwide, functionally forming a single unicolonial population over both islands (Corin *et al.*, 2007a; Suarez *et al.*, 2008). This low diversity is indicative of the entire supercolony arising from an incursion of just one nest (Vogel *et al.*, 2010), probably from Australia (Corin *et al.*, 2007b). Low genetic diversity, perhaps in combination with native pathogens (Vogel *et al.*, 2009) or a depletion of local resources (Haines and Haines, 1978), is a candidate mechanism for these collapses.

Abiotic conditions constrain Argentine ant spread in other parts of the world (Roura-Pascual *et al.*, 2011). New Zealand's climate is at the extreme end of what this species can tolerate, with the majority of the country being too cold. However, studies investigating the climatic suitability of New Zealand for this species predicted much of the northern half of the North Island and many cities around the country, due to their warmer microclimates, would be suitable for colonization (Hartley and Lester, 2003; Hartley *et al.*, 2006; Ward *et al.*, 2010). The Cox's PH model found total annual rainfall to have a negative effect on Argentine ant survival. This may seem to conflict with the results of other studies showing these ants are often moisture limited (Menke and

Holway, 2006), but the “low rainfall” category in this study is 619-1163mm, the lower end of which is still more rainfall than the areas where these other studies took place in California often receive (Holway *et al.*, 2002b). It is possible that excessive rainfall limits this ant’s range, as was found in Hawaii, by depressing soil temperature in the nest (Krushelnycky *et al.*, 2005). The survival analysis estimated population survival would be longest in areas of low rainfall and high temperature. This result is consistent with previous findings, as these conditions most closely match the Mediterranean-type habitat the Argentine ant prefers (Hartley *et al.*, 2006). The future climate model, based on rainfall and mean maximum daily temperature, indicates increased survival times in some parts of the country. In most cases, the model predicts a simple increase of probability in areas that are already suitable, though some areas, like the east coast of the South Island may become suitable. The total New Zealand area with a higher than 80% chance of having populations survive for 15 years or more substantially increases from 0.26% (69 685km²) to 1.29% (345 747 km²) under the climate change scenario. However, it should be noted that even under a scenario of high temperatures and low rainfall, the probability of Argentine ants persisting for more than 20 years was less than 20%. Thus the model predicts that while climate change may increase persistence, this increase in persistence is not dramatic.

Argentine ants are well known to competitively displace other ant species where they occur (Erickson, 1971; Human and Gordon, 1997; Holway 1998), but I found 61% of sites where Argentine ants were still present to have other co-occurring ant species. In some of these sites, previous surveys had shown highly abundant, widespread Argentine ant populations with no co-occurring ant species (Phil Lester, unpublished data). Many of these populations had shrunk to tiny remnant populations with multiple ant species present at the same site. In places where Argentine ants were at very high abundances there were very few or no co-occurring ant species, but at sites where Argentine ant densities were low there were many other ant species. When present in low abundance, Argentine ants are less competitive and prone to local extinction (Sagata and Lester, 2009). Thus any process that reduces Argentine ant densities (such as pathogens) is likely to have compounding effects on the ability of these invasive ants to compete and persist.

This pattern is explained by knowing the mechanisms by which Argentine ants dominate and exclude other ant species. Argentine ants out-compete other ant species by swiftly locating and recruiting to resources, then fiercely defending those resources against other ant species (Rowles and O'Dowd, 2007). In this way they break the usual evolutionary trade-off between resource discovery and resource domination as described by Fellers (1987). However, the breaking of this trade-off may be due to their numerical superiority, not their behavioural superiority (Holway 1999; Walters and MacKay, 2005; Human and Gordon, 1999). Laboratory experiments manipulating colony size showed Argentine ants were only able to dominate resources and overwhelm a native ant species when they vastly outnumbered the other species (Holway and Case, 2001; Walters and MacKay, 2005; Sagata and Lester, 2009). It was also observed during field studies showing the superior competitive abilities of these ants that their populations outnumbered the native ant species they were competing against by several fold (Holway, 1999; Human and Gordon 1999).

Though Argentine ants are intensely aggressive fighters, (Human and Gordon, 1996; Rowles and O'Dowd, 2007) often using both physical and chemical defenses simultaneously (Buczkowski and Bennett, 2008), in one on one encounters against other ant species workers they do not win more often than other species (Holway, 1999; Holway and Case, 2001). Argentine ants are group hunters; working together they can overwhelm and kill larger species (Buczkowski and Bennett, 2008; Sagata and Lester, 2009). Sagata and Lester (2009) showed Argentine ants were able to modify their behaviour based on how high their own worker abundances were. Their laboratory studies show that when worker abundances are low, Argentine ants will display increased avoidance and escape behaviours instead of responding to other ant species aggressively as they are likely to do when their own worker abundances are high. This behaviour may explain how newly established Argentine ant populations are able to persist while the population is still small. Where Argentine ants cannot maintain high worker densities their negative impact on other ant species lessens over time (Heller *et al.*, 2008; Sanders and Suarez, 2011). Morrison (2002) re-surveyed an area 12 years after the red imported fire ant had been documented to significantly decrease ant and other arthropod abundance

(Porter and Savignano, 1990). He found that all measures of ant and other arthropod species richness had returned to pre-invasion levels after the 12 years. He also noted population abundances of the red imported fire ant, though still high, had decreased significantly since they initially invaded. Morrison (2002) suggested the impact of such invasive ant species might be greatest during and shortly after the initial invasion phase.

Other ant species recolonized all areas where Argentine ant populations had collapsed. The community analysis indicated invaded communities had a significantly different composition than did either formerly invaded and uninvaded communities, which did not differ from each other. Sanders *et al.* (2003) compared the composition of ant communities pre and post Argentine ant invasion and found pre-invasion ant communities to be highly structured while invaded ant communities had a more random species composition. This result suggests ant communities that were formerly invaded by Argentine ants are recovering and regaining their pre-invasion structure. However, the formerly invaded communities had a wider spread on the MDS plot, indicating higher variability, than did the uninvaded communities, which were quite similar in composition. This pattern may be explained by the fact that the formerly invaded communities are likely all at different stages of recovery, as the number of years since Argentine ants disappeared from these communities is not known.

Uninvaded communities had significantly more ant species than either formerly invaded and invaded communities. The lower species number of the formerly invaded communities may also be explained by the different amounts of time the communities at each site may have had to recover, such as seen in ant community recovery after a toxic spill (Luque *et al.*, 2007). Of course, ant communities may be expected to recolonize areas an invasive species has disappeared from faster than those affected by an environmental disaster or mining because the invasive species does not affect the land itself (at least in the case of Argentine ants). Anderson *et al.* (2003) monitored ant community recovery after mine site restoration in Queensland and found in a case where the site vegetation and shade conditions were similar to reference sites the ant community had returned to pre-mining composition and species richness. Hoffmann (2009) showed

ant communities in Northern Australia to recover completely following the eradication of the big-headed ant.

Other factors such as colony migration or human management are alternative explanations to population collapse. However, I attempted to control for colony migration by searching a wide area (200 X 200m) around each original site. Though Argentine ants do move nests easily in response to disturbance and abiotic factors, they usually only move a few meters (Heller and Gordon, 2006). Human management by toxic baiting is another possibility, but Argentine ant control measures have been very limited in New Zealand (Charles *et al.*, 2002) and Argentine ants are notoriously difficult to eradicate due to their polygynous colony structure (Mathieson, 2011). Therefore, though human management is a possible explanation for population disappearance at some sites, it is unlikely to account for disappearance at all of the sites. In addition, long-term monitoring has revealed Argentine ant populations to decline in areas where colonies did not simply move away and were not managed by humans (Figure 1.1).

Given the local presence of this invasive species for short durations such as 10–20 years, and the apparent recovery of the resident communities after their collapse, it seems unlikely that Argentine ants will have any major long-term ecological or evolutionary effects in New Zealand. Other invasive species and climate change clearly contribute to the current global biodiversity crisis (Vitousek *et al.*, 1997), and their costs may be substantial. The control of Argentine ants was predicted to cost New Zealand up to \$68 million per year (Anonymous, 2002). Such economic and environmental costs will be considerably smaller in this and other countries, however, if populations collapse of their own accord.

Chapter 4:

General Discussion

In this thesis I investigated the effect of Argentine ants on other invertebrates. I measured ant and non-ant arthropod species richness and abundance in uninvaded and invaded sites in cities across this species range. In order to examine density-dependent effects more closely, I chose invaded sites that varied naturally in Argentine ant abundance between each city. I also looked at the effect rainfall and temperature had on arthropod species richness and abundance. Additionally, I examined the population persistence of Argentine ant populations in New Zealand by re-surveying sites of past infestation throughout this species' New Zealand range. I investigated the influence that climate variables, such as rainfall and temperature, have on population persistence, and how this effect might differ after climate change. In order to examine if resident ant communities could recover after Argentine ant invasion, I surveyed the resident communities at each Auckland site of known past infestation. I then compared community structure and ant species richness between Auckland sites currently infested with Argentine ants and those formerly infested with Argentine ants with control plots that had no record of ever being invaded.

The influence of Argentine ant presence and abundance on resident ant species

Argentine ants are known to eliminate most other ant species in the areas they invade (Erickson, 1971; Human and Gordon, 1997; Holway, 1998; Holway *et al.*, 2002a). However, this impact may be less severe when Argentine ant densities are low (Sanders and Suarez, 2011). As discussed in Chapters 2 and 3, I observed a wide range of natural variation in Argentine ant abundance between invaded sites. Population densities of invasive ants may vary spatially and temporally (Abbott, 2006; Heller *et al.*, 2008). The MDS plot (Chapter 3) showed that invaded communities had a lot of variation in their composition, indicative of communities in different states of invasion due to varying densities of Argentine ants. In Chapter 2, epigaieic ant species richness and abundance was negatively influenced by Argentine ant abundance. Very few ant species were able to

co-exist with high densities of Argentine ants. This same pattern was observed in Chapter 3. At sites where Argentine ant abundance was high, very few or no other ant species were found, but where local Argentine ant densities were low, there were many other ant species present. Hypogaieic species were unaffected by Argentine ant abundance, a pattern that has been documented in other studies (Human and Gordon, 1997; Holway, 1998). The tolerance of hypogaieic species to Argentine ants or other invasive ant species may be due to their having different foraging methods than these invaders (Sarty *et al.*, 2007).

Ant communities have been observed to recover after invasion, though it may take time (Morrison, 2002; Hoffmann, 2009). Ant communities in Auckland appeared to return to their pre-invasion structure after Argentine ant populations collapsed. At formerly invaded sites, community structure was identical to that of communities that had never been invaded (uninvaded), though the spread observed in the MDS plot indicates there was more variation in community composition in formerly invaded sites than uninvaded sites. Ant species richness of formerly invaded sites was intermediate between that of invaded and uninvaded sites. The greater variability in community composition and intermediacy in species richness between formerly invaded and uninvaded sites are probably both due to differing amounts of time since Argentine ant collapse between formerly invaded sites. Formerly invaded sites are likely at various stages of recovery.

The influence of Argentine ant abundance on non-ant arthropods

Ground-dwelling arthropods may be affected by invasive ants in a number of different ways. Arthropods may be preyed upon by invasive ants, compete with them, depend on organisms displaced by invasive ants, or be released from competition with organisms displaced by invasive ants (Human and Gordon, 1997). Previous studies of the impact Argentine ants have on non-ant arthropods have had differing results, from no discernable effect (Holway, 1998), to population and species declines in multiple invertebrate orders (Cole *et al.*, 1992; Human and Gordon, 1997). For the majority of non-ant arthropod orders sampled in Chapter 2, Argentine ant abundance had no effect on morphospecies

richness or abundance. The exceptions to this were Diplopoda and Hemiptera. Argentine ant abundance had a negative effect on Diplopoda morphospecies richness and abundance, with this order being completely absent from the most heavily infested sites. However, Diplopoda populations may recover if Argentine ant populations collapse, as was observed with the Auckland ant communities in Chapter 3. Hemiptera, on the other hand, had a positive association with Argentine ant abundance, though this relationship was mostly due to an extremely strong positive correlation in Blenheim's highly invaded sites. The strong relationship that Argentine ants, like many other invasive ant species (Holway *et al.*, 2002a), have with Hemiptera species has been extensively documented (Way, 1963; Holway *et al.*, 2002a, Lester *et al.*, 2003; Mgocheki and Addison, 2009).

The influence of rainfall and mean maximum temperature

The influence of rainfall and mean maximum temperature on arthropod morphospecies richness and abundance was mixed. This study detected no influence of rainfall or maximum temperature on Argentine ant abundance, or resident ant species richness and abundance. However, these climate variables did help explain patterns of variation in abundance and morphospecies richness in some orders of non-ant arthropods. Morphospecies richness and abundance of several non-ant arthropod orders were positively correlated with rainfall. Hemiptera was negatively associated with rainfall. Amphipoda abundance was positively influenced by both rainfall and maximum temperature, while non-ant Hymenoptera morphospecies richness and abundance was negatively influenced by maximum temperature.

As rainfall and maximum temperature were found to influence survival time of Argentine ant populations (Chapter 3) I would have expected these variables to influence Argentine ant abundance as well. However, the study sites in a city did not necessarily reflect the "typical" Argentine ant population density of a region. For example, just because the invaded sites in Christchurch had very high densities of Argentine ants does not mean that all Christchurch Argentine ant populations are high-density. More Argentine ant population densities would have to be measured in each region in order to detect the

possible influence of climate. There have been multiple previous studies investigating the potential range of Argentine ants in New Zealand (Harris, 2002; Hartley and Lester, 2003; Harris and Barker, 2007). These researchers used multiple methods for their predictions, including degree-day models and climate matching, but they all agree that the cities in which I did my pitfall trapping (Chapter 2) are within this invader's climatic tolerances. Thus, Argentine ants physiologically should be able to establish and spread in these cities. In Chapter 3, however, the Cox's proportional hazards model found that rainfall and maximum temperature had significant effects on Argentine ant survival time. Rainfall negatively influenced survival time of populations, while maximum temperature positively influenced survival time. These results are in agreement with previous studies (Roura-Pascual *et al.*, 2004; Roura-Pascual *et al.*, 2011).

Population persistence of the Argentine ant in New Zealand

Populations of invasive ants have been observed to boom and bust (Wetterer, 2006; Abbott, 2007; Wetterer, *in press*). Forty percent of Argentine ant populations surveyed had either disappeared or were at such low population densities so as to escape detection. Many of the remaining populations had declined to very low densities. A Cox's proportional hazards model estimated the mean time to collapse of Argentine ant populations to be 10.5 to 17.8 years depending on climate variables. Survival was positively associated with mean maximum temperature and negatively associated with annual rainfall. Climate change was predicted to increase the survival time of populations in many areas of New Zealand, but only by a few years.

Overall the results of this study suggest that the impact of the Argentine ant in New Zealand may not end up being as dire as in other parts of its introduced range. Morrison (2002) suggested invasive ant populations may be "tamed" over time. That is, population densities peak during and shortly after the initial invasion, but then decline significantly over time (Morrison, 2002; Abbott *et al.*, 2007). This decline in population abundance may leave Argentine ants vulnerable to other processes, such as competition.

Argentine ants may not be very competitive when they occur in low abundance (Walters and MacKay, 2005; Lester *et al.*, 2009; Blight *et al.*, 2010), and thus may be unable to displace other ant species. In their native range they are only mid-way up the dominance hierarchy (LeBrun *et al.*, 2007) and colony turnover is high (Vogel *et al.*, 2009). In Chapter 2 Argentine ants had the most severe impact on epigaeic ant species richness and abundance when they were in high densities. As discussed in Chapter 3 it was observed during visual surveys that there were more resident ant species present when Argentine ants were at low local abundance. Argentine ants rely on numerical dominance to overwhelm and displace other ant species. Studies investigating this question have found that Argentine ants could only exclude other ants from baits when they outnumbered the other species at least 2 to 1 (Holway and Case, 2001; Walters and MacKay, 2005; Sagata and Lester, 2009). In addition, there is evidence that Argentine ants are less aggressive when in low abundance (Sagata and Lester, 2009). Therefore, any process that results in a decline in population density (e.g. pathogens) may decrease this invader's ability to compete and persist. This low population density may leave Argentine ant populations vulnerable to more aggressive, highly armed ant species, such as the New Zealand endemic *Monomorium antarcticum* (Sagata and Lester, 2009; Blight *et al.*, 2010).

Populations of Argentine ants appear to be collapsing in New Zealand. A large number of populations of this invasive appeared to have disappeared completely, and many others had declined from widespread, high-density, colonies covering many hectares to remnant populations occupying only a few nests. In the latter case, other ant species had recolonized the area. This sudden disappearance of populations has been observed periodically, not only with other invasive species populations (Simberloff and Gibbons, 2004), but other species of invasive ants (Wetterer, 2006). Haines and Haines (1978) noted the decline and disappearance of local populations of yellow crazy ants (*Anoplolepis gracilipes*) on the Seychelles. Abbott *et al.* (2006) also noticed local declines in some populations of this species on Christmas Island, though overall populations of yellow crazy ants have been increasing on that island. Big-headed ant (*Pheidole megacephala*) populations have been observed to go through boom and bust phases throughout their introduced range (Wetterer, *in press*). The reasons for the

population declines of these species and Argentine ants are not known. However, population genetics predict that invasive species might collapse due to inbreeding depression or an inability to adapt to their new environment (Sakai *et al.*, 2001). The New Zealand population of Argentine ants is amongst the lowest in terms of recorded genetic diversity of any introduced Argentine ant population worldwide, functionally forming a single unicolonial population over both islands (Corin *et al.*, 2007a; Suarez *et al.*, 2008). This low diversity infers that the entire supercolony arose from the introduction of a single nest (Corin *et al.*, 2007a; Vogel *et al.*, 2010). Low genetic diversity, perhaps in combination with native pathogens (Vogel *et al.*, 2009) or a depletion of local resources (Haines and Haines, 1978), are candidate mechanisms for these collapses.

The impact of disease and parasites may be especially high in social animals, due to increased transmission rates (Hughes and Boomsma, 2004). The polygynous colony structure of Argentine ants could make them particularly vulnerable to disease. Valles *et al.* (2010) found that the unicolonial polygynous form of the red imported fire ant was more likely to be infected with pathogens than the monocolonial monogynous form, probably due to the high levels of intermixing individuals found in unicolonial colonies. Low genetic diversity may result in lowered resistance to disease and reduced anti-pathogen response in ants (Ugelvig *et al.*, 2010). Genetic diversity was found to increase colony resistance to parasitic infection in leaf-cutting ants (Hughes and Boomsma, 2004). Pedersen *et al.* (2006) suggest decreased competition between supercolonies and increased supercolony size may lead to the proliferation of selfish mutants and thus form an unstable system over evolutionary time (Helanterä *et al.*, 2009).

Haines *et al.* (1994) hypothesized the crash of yellow crazy ant populations observed on the Seychelles was due to the ants over-exploiting local food resources. Depletion of local resources has been invoked as a reason for invasive species collapse before (Simberloff and Gibbons, 2004). However, if Argentine ants were causing declines in ground-dwelling invertebrate populations, I would have expected to see differences in arthropod abundance between uninvaded and invaded sites. No such difference in

arthropod abundance was observed even in the sites with very high densities of Argentine ants.

Argentine ants are omnivores (DiGirolamo and Fox, 2006), though one of their primary sources of carbohydrates may be exudate collected from Hemiptera (Human and Gordon, 1997). Many invasive ant species tend Hemiptera (Holway *et al.*, 2002a), and it has been suggested that the presence of honey-dew producing Hemiptera facilitates invasion by invasive ants by fuelling the ants' high worker numbers (Davidson, 1998; Rowles and Silverman, 2009). The positive association between Argentine ant abundance and hemipteran abundance in some of the most heavily infested sites in Blenheim supports this idea. The association between Argentine ants and Hemiptera in New Zealand has been previously examined (Lester *et al.*, 2003). However, further investigation of the possible facilitation of Argentine ant invasions by Hemiptera in New Zealand is needed.

This study gives a snapshot of communities at a single point in time. It is possible that other factors, such as seasonal variation in Argentine ant population densities explain the patterns observed. However, Mathieson (2011) observed that, in New Zealand, Argentine ants forage most actively in the summer and fall, which is when this study took place. Additionally, the variation of Argentine ant abundance in each city controls for this problem to a limited degree. Colony migration or human management could explain the observed collapse of Argentine ant populations. I tried to minimize the risk of colony migration by searching a wide area (200m X 200m) around each sample site. Human management (i.e. toxic baiting) may account for the collapse of populations at some sites, but is unlikely to explain the majority because Argentine ants are notoriously difficult to eradicate (Mathieson, 2011). Furthermore, long-term monitoring of Argentine ant populations around New Zealand has revealed that some populations are declining significantly without human management, and have not simply moved (Figure 1.1).

The lack of discernable impact on many arthropod orders and the lessening of impact with decreasing Argentine ant abundance, apparent community recovery of resident ant species after Argentine ant population collapse, combined with the short amount of time

individual populations are predicted to survive (10-20 years), strongly suggests that the Argentine ant will not have any long-term ecological or evolutionary consequences in New Zealand. This is not to say this ant will simply disappear from New Zealand, only that individual populations will not persist long enough to cause lasting ecological harm, for example by extirpating resident ant species.

Future directions

Ideally, continued long-term monitoring of the sites of known previous infestation I examined should occur. Sites that are currently invaded and formerly invaded should both continue to be monitored to look at the recovery of resident ant communities and the potential increase in small populations of Argentine ant populations that I may have failed to detect the first time.

The next step for future research is to discover why populations of Argentine ants are collapsing. One possibility is native pathogens, or parasites. There is currently little information about pathogens or parasites limiting Argentine ant populations in their native range (Holway *et al.*, 2002a; but see Reuters *et al.*, 2005). However, the red imported fire ant, which is native to the same area of South America as the Argentine ant, is limited by pathogens and parasites in its native range, and to a lesser extent its introduced range (Valles *et al.*, 2010). The presence of pathogens or parasites that cause population decline in New Zealand Argentine ant populations would have exciting implications for future bio-control of introduced Argentine ant populations world-wide.

It would be interesting to return to sites previously recorded to be infested with Argentine ants and document not only the presence/absence of populations but also the local population densities of this invader. Population densities could then be related to both the time since initial invasion and climatic factors such as rainfall and temperature. Such fine-scale knowledge would aid in management decisions and prediction of effects on resident ant species.

Further investigation into the Argentine ant/hemipteran mutualism in New Zealand is warranted. Whether Hemiptera facilitate Argentine ant invasions in this country has important implications for the potential survival times of this invader because any process which increases Argentine ant abundance or enables this ant to maintain high population densities could increase the survival time of populations.

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Appendix 1. Number of abundance and morphospecies per site for total arthropods, epigaeic and hypogaeic Formicidae, Amphipoda, Araneae, Coleoptera, Diplopoda, Diptera, Hemiptera, Isopoda and Orthoptera at uninhabited (U) and inhabited (I) sites across the seven cities and the total across New Zealand. The groups Formicidae and total Arthropods do not include Argentine ant numbers. Table entries are means (± 1 SE) of the 4 sites in each city (for New Zealand totals means (± 1 SE) of all 28 sites).

Taxa	Sites							
	Russell		Auckland		Morrinsville		Wellington	
	U	I	U	I	U	I	U	I
Number per site								
Epigaeic Formicidae	129.0 \pm 24.8	11.5 \pm 3.1	16.8 \pm 2.6	0	16.5 \pm 7.3	0.8 \pm 0.4	1.3 \pm 0.4	0
Hypogaeic Formicidae	0.5 \pm 0.1	0.5 \pm 0.3	0.5 \pm 0.3	0	0.5 \pm 0.3	0	0.3 \pm 0.1	1.5 \pm 0.4
Amphipoda	-	1.3 \pm 0.5	222.3 \pm 39.0	254.8 \pm 39.2	75.8 \pm 23.6	346.8 \pm 139.8	221.3 \pm 66.3	54.8 \pm 0.5
Araneae	7.3 \pm 0.8	4.0 \pm 0.8	8.0 \pm 1.0	10.5 \pm 1.2	3.8 \pm 0.4	3.3 \pm 0.4	6.0 \pm 0.5	8.5 \pm 0.9
Coleoptera	18.8 \pm 1.0	11.3 \pm 2.2	41.5 \pm 3.0	60.3 \pm 3.8	4.3 \pm 0.4	6.3 \pm 1.1	3.5 \pm 1.4	20.8 \pm 2.7
Diplopoda	0.5 \pm 0.1	0.8 \pm 0.4	11.8 \pm 2.9	-	6.0 \pm 2.1	4.3 \pm 1.4	1.0 \pm 0.4	5.3 \pm 1.1
Diptera	14.3 \pm 1.5	6.8 \pm 0.9	8.5 \pm 1.4	6.0 \pm 1.0	2.0 \pm 0.4	2.3 \pm 0.7	3.0 \pm 0.2	5.5 \pm 1.1
Hemiptera	0.3 \pm 0.1	-	-	-	4.8 \pm 0.4	0.8 \pm 0.2	1.0 \pm 0.2	1.3 \pm 0.6
Hymenoptera	2.8 \pm 0.4	4.5 \pm 1.0	2.0 \pm 0.4	0.5 \pm 0.1	1.5 \pm 0.6	1.3 \pm 0.3	2.5 \pm 0.5	9.0 \pm 1.2
Isopoda	0.8 \pm 0.1	45.0 \pm 8.9	184.8 \pm 53.4	119.5 \pm 12.9	5.3 \pm 1.3	3.3 \pm 0.5	1.8 \pm 0.1	0.8 \pm 0.4
Orthoptera	12.3 \pm 2.2	1.8 \pm 0.3	1.0 \pm 0.5	20.0 \pm 3.5	1.8 \pm 0.9	0.8 \pm 0.2	0.3 \pm 0.1	-
Total Arthropods	191 \pm 25.9	88.0 \pm 14.5	547.0 \pm 93.4	482.3 \pm 45.7	122.8 \pm 24.5	369.8 \pm 140.4	243.8 \pm 66.3	108 \pm 9.6
Number of morphospecies								
Epigaeic Formicidae	5.8 \pm 0.4	2.0 \pm 0.4	1.5 \pm 0.3	0	2.3 \pm 0.1	0.3 \pm 0.1	0.8 \pm 0.2	0
Hypogaeic Formicidae	0.5 \pm 0.1	0.3 \pm 0.1	0.3 \pm 0.1	0	0.3 \pm 0.1	0	0.3 \pm 0.1	1.0 \pm 0.3
Araneae	4.5 \pm 0.3	3.3 \pm 0.7	5.0 \pm 0.4	8.0 \pm 0.7	2.8 \pm 0.2	3.0 \pm 0.3	4.5 \pm 0.3	4.3 \pm 0.3
Coleoptera	9.3 \pm 0.3	6.8 \pm 1.4	11.5 \pm 1.3	12.0 \pm 0.5	3.3 \pm 0.4	4.0 \pm 0.4	2.0 \pm 0.7	9.5 \pm 1.2
Diplopoda	0.5 \pm 0.1	0.8 \pm 0.4	2.0 \pm 0.2	-	1.3 \pm 0.5	1.3 \pm 0.4	0.5 \pm 0.1	1.5 \pm 0.3
Diptera	1.3 \pm 0.4	2.5 \pm 0.3	4.8 \pm 0.4	3.0 \pm 0.2	1.0 \pm 0.2	1.3 \pm 0.4	2.0 \pm 0.2	3.3 \pm 0.4
Hemiptera	0.3 \pm 0.1	-	-	-	2.5 \pm 0.1	0.8 \pm 0.2	0.8 \pm 0.1	0.5 \pm 0.3
Hymenoptera	2.3 \pm 0.3	3.3 \pm 0.4	2.0 \pm 0.4	0.5 \pm 0.1	1.0 \pm 0.4	1.3 \pm 0.3	2.5 \pm 0.5	2.5 \pm 0.1
Orthoptera	2.5 \pm 0.4	0.8 \pm 0.1	0.3 \pm 0.1	2.5 \pm 0.1	0.3 \pm 0.1	0.5 \pm 0.1	0.3 \pm 0.1	-
Total Arthropods	27.5 \pm 1.0	18.3 \pm 2.6	30.0 \pm 1.7	32.3 \pm 1.7	16.3 \pm 1.0	13.0 \pm 1.2	14.0 \pm 1.2	21.5 \pm 2.1

Appendix 2. Results of Spearman rank correlation of the natural log of total abundance, total arthropod and abundance and morphospecies richness within various arthropod orders as a function of the natural log of Argentine ant abundance and rainfall. N=8 for all tests.

	Coeff.	P
Resident ant abundance		
Russell	-0.85	0.01
Auckland	-0.87	0.01
Morrinsville	-0.58	0.13
Wellington	0.13	0.75
Blenheim	-0.81	0.02
Nelson	0.05	0.91
Christchurch	-0.89	0.01
Resident ant species		
Russell	-0.20	0.64
Auckland	0.22	0.60
Morrinsville	-0.20	0.64
Wellington	0.65	0.08
Blenheim	-0.71	0.05
Nelson	-0.43	0.29
Christchurch	-0.73	0.04
Total arthropod abundance		
Russell	-0.63	0.10
Auckland	-0.01	0.98
Morrinsville	0.33	0.43
Wellington	-0.07	0.87
Blenheim	-0.76	0.03
Nelson	-0.24	0.57
Christchurch	-0.71	0.05
Total arthropod morphospecies		
Russell	-0.20	0.64
Auckland	0.22	0.60
Morrinsville	-0.20	0.64
Wellington	0.65	0.08
Blenheim	-0.71	0.05
Nelson	-0.43	0.29
Christchurch	-0.73	0.04
Diplopoda abundance		
Russell	0.22	0.60
Auckland	-0.87	0.01
Morrinsville	-0.15	0.73
Wellington	0.74	0.04
Blenheim	-0.87	0.01
Nelson	-0.24	0.56
Christchurch	-0.87	0.01
Diplopoda morphospecies		
Russell	0.22	0.60

Auckland	-0.87	0.01
Morrinsville	-0.14	0.75
Wellington	0.64	0.09
Blenheim	-0.88	0.01
Nelson	-0.18	0.67
Christchurch	-0.89	0.01
Hemiptera abundance		
Russell	-0.28	0.50
Auckland	0.09	0.84
Morrinsville	-0.83	0.01
Wellington	-0.05	0.91
Blenheim	0.92	0.01
Nelson	0.16	0.71
Christchurch	-0.59	0.13
Hemiptera morphospecies		
Russell	-0.28	0.50
Auckland	0.09	0.84
Morrinsville	-0.76	0.03
Wellington	-0.05	0.91
Blenheim	0.88	0.04
Nelson	0.07	0.88
Christchurch	-0.59	0.13

Appendix 3. Location, coordinates, and year of initial invasion record for all surveyed sites of past known infestation. Invaded sites are those sites which are currently invaded by Argentine ants. Formerly invaded sites are those sites which used to have Argentine ants but the population has since collapsed. In Auckland uninvaded sites, reference sites which have no record of ever being invaded by Argentine ants, were also surveyed. The ant fauna found at each site can be found in Appendix 3. Site locations were obtained from the Landcare Research ant distribution database at

http://www.landcareresearch.co.nz/research/biocons/invertebrates/ants/distribution/distribution_details.asp

Region	#	Invasion Status	Site Location	Easting	Northing	Year
NL	1	Invaded	Dargaville, Parore St, Northland	2588865	6584635	2001
NL	2	Invaded	Dargaville, Victoria St, Northland	2589615	6584525	2001
NL	3	Invaded	Hatea Dr, Whangarei	2630650	6608400	2002
NL	4	Invaded	Kaitaia, West Coast Dental, Blencowe St, Northland	2534600	6676600	2001
NL	5	Invaded	Kaitaia, Puckey Ave, Pak'nSave, Northland	2534705	6676390	2001
NL	6	Invaded	Kaitaia, Worth St, Northland	2534495	6675965	2002
NL	7	Invaded	Kerikeri, Jacaranda Pl, Northland	2597800	6663465	2002
NL	8	Invaded	Mangawhai Heads, Northland	2653200	6567000	2002
NL	9	Invaded	Paihia, Bayview Rd, Swiss Chalet Motel (3 Bayview) & Dr Surgery, Northland	2609890	6657250	2002
NL	10	Invaded	Ruakaka, beach and dunes around township, Northland	2641600	6586700	2002
NL	11	Invaded	Russell, 46 Oneroa Rd, Northland	2613645	6659510	2002
NL	12	Invaded	Russell, Northland	2613200	6659000	2002
NL	13	Invaded	Russell, Russell Heights, Northland	2613655	6659385	2002
NL	14	Invaded	Tokerau Beach, Virtue Cres, Northland	2544900	6702200	2004
NL	15	Invaded	Whananaki North, Brookers Bay, last little beach on road, Northland	2642400	6634900	2002
NL	16	Invaded	Woodhill, Kauika Road, Whangarei	2629000	6607500	2001
NL	1	Formerly Invaded	Ahipara Beach, Northland	2524840	6671125	2002
NL	2	Formerly Invaded	Bank St outside building, Whangarei	2630300	6608400	2001
NL	3	Formerly Invaded	Bland Bay, Northland	2634000	6649600	2006
NL	4	Formerly Invaded	Dargaville, Gordon St, Northland	2589350	6584850	2001
NL	5	Formerly Invaded	Dargaville, Tirarau St, Northland	2589065	6584775	2001
NL	6	Formerly Invaded	Dent St, Whangarei	2630715	6607440	2001
NL	7	Formerly Invaded	Kerikeri, Landing Road (DOC office), Northland	2598400	6664700	2004
NL	8	Formerly Invaded	Langs Beach, forest remnant at end of Seacrest Rd, Northland	2649500	6571100	2002
NL	9	Formerly Invaded	Langs Beach, Northland	2649100	6571500	2001
NL	10	Formerly Invaded	Maungatapere, Whangarei	2619900	6604300	2004
NL	11	Formerly Invaded	Ocean Beach, Northland	2652500	6594600	2005
NL	12	Formerly Invaded	Waipoua Forest Headquarters, Northland	2561126	6616359	2006
NL	13	Formerly Invaded	Waipu township, Northland	2641300	6578500	2002
NL	14	Formerly Invaded	Whananaki, Northland	2643600	6631400	2001
NL	15	Formerly Invaded	Whangarei Heads, 114 Reotahi Rd, Whangarei	2645860	6596280	2001
AK	1	Invaded	Birkdale, 22 Bishopgate St, Auckland Birkenhead, 15 Rawene Rd, by tennis court, Auckland	2662550	6487535	2000
AK	2	Invaded		2664390	6486225	2000
AK	3	Invaded	Birkenhead, 33 Hebe Pl, Auckland	2662625	6486290	2005

			Blockhouse Bay, Te Whau Point,			
AK	4	Invaded	Auckland	2662000	6473100	2000
AK	5	Invaded	Bucklands Beach, Auckland	2680000	6480000	1992
AK	6	Invaded	Campbells Bay, Centennial Pl, Auckland	2667200	6493200	2002
AK	7	Invaded	Glenfield, 88 Lynn Rd, Auckland	2662355	6490480	2000
AK	8	Invaded	Hillsborough, 14 Goodall St, Auckland	2666565	6473720	2001
AK	9	Invaded	Karekare Rd, Karekare, Auckland	2642100	6467900	2002
AK	10	Invaded	Mt Eden, 37 Marsden Ave, Auckland	2666810	6477245	2003
AK	11	Invaded	Muriwai Beach, Auckland	2638000	6483900	2001
			Muriwai Beach, Waitea Rd housing,			
AK	12	Invaded	Auckland	2638100	6484000	2002
AK	13	Invaded	Newmarket, 371 Khyber Pass, Auckland	2668345	6480165	2001
			Northcote, Tarahanga St, Onepoto			
AK	14	Invaded	Domain, Auckland	2666504	6486397	2005
AK	15	Invaded	Omaha, Auckland	2669700	6539600	1998
AK	16	Invaded	Penrose, Mt Smart, Auckland	2671900	6474300	1990
AK	17	Invaded	Penrose, O'Rorke Rd, Auckland	2672400	6474500	1990
AK	18	Invaded	Piha, Auckland	2641200	6470500	1999
AK	19	Invaded	Piha, North Piha Rd, Auckland	2641157	6471857	2005
AK	20	Invaded	Piha, sand at top of beach, Auckland	2641100	6471300	1999
			Red Beach, 155 Whangaparaoa Rd,			
AK	21	Invaded	Auckland	2662550	6508560	2006
AK	22	Invaded	St Heliers, Dingle Dell Reserve, Auckland	2675900	6480900	2000
AK	23	Invaded	Titirangi, Daffodil Street, Auckland	2657400	6473200	2000
AK	1	Formerly Invaded	Albany, Upper Harbour Hwy, Auckland	2663486	6493016	2005
			Auckland Regional Botanic Gardens, north			
AK	2	Formerly Invaded	entrance, Totara Heights, Auckland	2679600	6464600	2002
			Cuthill, Wickham Ln, near Chester Park,			
AK	3	Formerly Invaded	Auckland	2661825	6492050	2000
AK	4	Formerly Invaded	Henderson, 5 Claret Pl, Auckland	2654610	6478440	2000
			Kelston, Westech Place at Great North Rd,			
AK	5	Formerly Invaded	Auckland	2658410	6475939	2005
AK	6	Formerly Invaded	Lynfield, Boundary Rd, Auckland	2663000	6474400	1995
			Manurewa, The Warehouse Distribution			
			Centre, Wiri 92 Langley Rd, Wiri,			
AK	7	Formerly Invaded	Auckland	2676300	6464200	2003
			Mount Roskill, Big King Reserve,			
AK	8	Formerly Invaded	Auckland	2666800	6476300	2000
AK	9	Formerly Invaded	Mt Eden Domain, Auckland	2667700	6479000	2000
AK	10	Formerly Invaded	Mt Roskill, Auckland	2665000	6475000	1992
			New Lynn, Willerton at Hutcheson Ave,			
AK	11	Formerly Invaded	Auckland	2659665	6474485	1995
			Newton, Johnston's Coachlines (445			
AK	12	Formerly Invaded	Karangahape Rd), Auckland	2666930	6481085	2001
			Northcote, Howard St, near Onepoto			
AK	13	Formerly Invaded	Domain, Auckland	2666300	6487000	2000
AK	14	Formerly Invaded	Onehunga, Auckland	2669000	6474000	1992
AK	15	Formerly Invaded	Onehunga Dump, Auckland	2670000	6473000	1996
AK	16	Formerly Invaded	Onehunga, Mt Smart Stadium, Auckland	2671900	6474400	1990
AK	17	Formerly Invaded	Onehunga, O'Rorke St, Auckland	2669370	6473425	1990
AK	18	Formerly Invaded	Otahuhu, Nikau Rd, Auckland	2674500	6471400	1990
AK	19	Formerly Invaded	Parnell, Auckland	2669400	6481400	1992
			Piha Beach, start of Marawhara walk,			
AK	20	Formerly Invaded	under grass on bridge concrete, Auckland	2641000	6472300	2000
AK	21	Formerly Invaded	Remuera, Auckland	2670700	6479100	1992
AK	22	Formerly Invaded	Remuera, Waiata Reserve, Auckland	2671000	6479000	2000

			Stanley Bay, North Shore City, Ngataranga			
AK	23	Formerly Invaded	Park walkway, Auckland	2670500	6485500	2002
AK	24	Formerly Invaded	Titirangi School, Auckland	2657600	6472500	1993
			Waimauku School, corner of State Hwy 16			
AK	25	Formerly Invaded	and Muriwai Rd, Auckland	2643455	6491345	2002
AK	26	Formerly Invaded	Warkworth, 10 Pound St, Auckland	2659540	6532155	2001
AK	27	Formerly Invaded	Warkworth, Auckland	2659800	6532000	2001
AK	1	Uninvaded	Oratia, Glengarry Rd, Auckland	2655366	6475365	
AK	2	Uninvaded	Albany, Oteha Valley Rd Ex, Auckland	2661889	6496034	
AK	3	Uninvaded	Avondale, Henry St, Auckland	2661700	6477576	
AK	4	Uninvaded	Glendene, Milwaukie Pl, Auckland	2657228	6478096	
AK	5	Uninvaded	Orakei, Martin Ave, Auckland	2671981	6479416	
AK	6	Uninvaded	Half Moon Bay, Gillis Rd, Auckland	2680096	6477270	
AK	7	Uninvaded	Massey, Killygordon Pl, Auckland	2653663	6483569	
AK	8	Uninvaded	Dannemora, Athenry Pl, Auckland	2681499	6472846	
AK	9	Uninvaded	Mangere, Wedgewood Ave, Auckland	2673565	6469009	
AK	10	Uninvaded	Mangere, Lawford Pl, Auckland	2669966	6468273	
AK	11	Uninvaded	Onehunga, Amaru Rd, Auckland	2669660	6475519	
CL	1	Invaded	Thames, 270 Coast Rd, RD5, Coromandel	2734620	6456445	2000
CL	2	Invaded	Totara, Coromandel	2737200	6445200	2001
CL	1	Formerly Invaded	Ngarimu Bay, 17 Patui Ave, Coromandel	2734525	6456095	2001
WO	1	Invaded	Morrinsville, Canada St, Waikato	2733505	6390815	2001
WO	2	Invaded	Morrinsville, Park St / Thames St, Waikato	2733630	6390965	2001
WO	3	Invaded	Morrinsville, Waverley Avenue, Waikato	2733930	6391045	2001
WO	4	Invaded	Raglan, 1a Daisy St, Waikato	2676025	6376485	2003
WO	1	Formerly Invaded	Avalon Drive, Hamilton	2707345	6379295	2001
WO	2	Formerly Invaded	Pak nSave, Mill St, Hamilton	2710400	6377800	2001
TA	1	Invaded	Rotorua Golf Course, Rotorua	2795200	6333200	2003
TA	2	Invaded	Otomoetai Rd, Tauranga	2787100	6387300	2001
			Papamoa Tavern, Domain Rd, Papamoa			
TA	3	Invaded	Beach, Tauranga	2799800	6383200	2003
TA	1	Formerly Invaded	Mt Maunganui, Bayfair Mall , Tauranga	2794700	6386800	2001
TA	2	Formerly Invaded	Mt Maunganui, Farm St, Tauranga	2794515	6387100	2001
TA	3	Formerly Invaded	Mt Maunganui, Newton St, Tauranga	2792700	6388600	2001
TA	4	Formerly Invaded	Mt Maunganui, Te Maunga, Tauranga	2795300	6385500	2000
TA	5	Formerly Invaded	Mt Maunganui, Totara St, Tauranga	2791350	6388955	1992
TA	6	Formerly Invaded	Mt. Maunganui, Sulphur Point, Tauranga	2789730	6388570	2003
TO	1	Invaded	10 Fairview Tce, Taupo	2779340	6272690	2003
TO	2	Invaded	22 Matai St, Taupo	2780055	6274875	2003
HA	1	Invaded	Kitchener St, Hastings	2840400	6167535	2001
HA	2	Invaded	A&P show grounds, Hastings	2841625	6168160	2001
HA	3	Invaded	Mayfair Ave at Caroline Rd, Hastings	2840985	6167670	2001
HA	4	Invaded	Coventry Rd, Hastings	2841150	6168385	2001
HA	5	Invaded	Harlech St, Hastings	2841255	6167980	2001
HA	6	Invaded	Hastings, juice producer, Hastings	2840000	6167000	2001
HA	7	Invaded	Omahu Rd, Hastings	2837835	6168815	2001
HA	8	Invaded	Rangiora St, Hastings	2840225	6168155	2001
HA	9	Invaded	Tomoana Rd, Hastings	2840085	6167815	2001
HA	10	Invaded	Warwick Pl, Hastings	2841250	6167720	2001
HA	11	Invaded	Williams St, Hastings	2840800	6168175	2001
HA	1	Formerly Invaded	Napier, Napier	2844900	6181700	2001
WN	1	Invaded	Kelburn, 9 Ngaio Rd, Wellington	2657745	5989675	2001
			Lower Hutt, Alicetown, 35 Fitzherbert St,			
WN	2	Invaded	Wellington	2668800	5997220	2006
			Paraparaumu Beach, 36 Arnold Grove,			
WN	3	Invaded	Wellington	2677895	6033995	2004

WN	4	Invaded	Petone, 128 Jackson St, Wellington	2667020	5996435	2001
WN	5	Invaded	Petone, Jackson St, Hutt Valley Polytech butchery school, close to Pak'nSave, Wellington	2666925	5996470	2001
WN	1	Formerly Invaded	Kelburn, 24 Rimu Road, Wellington	2657730	5989550	2001
WN	2	Formerly Invaded	Kelburn, Wellington	2657500	5989000	2000
WN	3	Formerly Invaded	Lower Hutt, Naenae Rd, Wellington	2673190	5998705	2001
WN	4	Formerly Invaded	Petone, Jackson Street, Weltec Meat Training Facility, Wellington	2667780	5996160	2006
BL	1	Invaded	Park Terrace Motors, 30 Park Terrace, Blenheim	2590470	5965565	2006
NN	1	Invaded	406 Wakapuaka Rd, SH6, Nelson	2539895	6000251	2008
NN	2	Invaded	Hope, 293 Ranzau Rd East, Nelson	2523328	5983183	2008
NN	3	Invaded	Port Nelson, Rodgers St at Graham St, Nelson	2533100	5994000	2001
NN	4	Invaded	Port Nelson, Vickerman St, edge of infestation near slipway, Nelson	2533500	5994100	2001
NN	5	Invaded	Richmond CBD, Nelson	2525340	5985235	2005
NN	6	Invaded	Richmond, Olympus Way, Nelson	2525400	5983985	2005
NN	7	Invaded	The Ridgeway, 112 Arapiki Rd, Nelson	2530800	5988500	2004
NN	8	Invaded	The Wood, 27 Tasman St, Nelson	2534465	5993100	2006
NN	9	Invaded	Wakatu, 66 Waterhouse St, Nelson	2530985	5988990	2004
NN	1	Formerly Invaded	Port Nelson, Collins at Haven Rd, Nelson	2532800	5993700	2001
NN	2	Formerly Invaded	Port Nelson, Vickerman St at Carkeek St, Nelson	2533300	5993700	2001
NN	3	Formerly Invaded	Port Nelson, Rogers St, Nelson	2533300	5993900	2001
CH	1	Invaded	162 Tuam St, Christchurch	2480570	5741270	2005
CH	2	Invaded	166 St Asaph St, Christchurch	2480530	5741150	2005
CH	3	Invaded	197 Durham St, Brown Brothers Engineering, Christchurch	2480375	5741015	2005
CH	4	Invaded	Boise Office Products, Tuam St at Durham St, Christchurch	2480415	5741305	2005
CH	5	Invaded	General Cables, 75-89 Main South Rd, Christchurch	2474585	5741325	2005
CH	6	Invaded	Handmade Studio, 575 Colombo St, Christchurch	2480620	5741120	2005
CH	7	Invaded	Martin Car Company, 166 Tuam St, Christchurch	2480580	5741305	2005
CH	8	Invaded	Mastertrade, 146 Tuam St, Christchurch	2480500	5741265	2005
CH	9	Invaded	Mollett Ln, Flexi Lease, Christchurch	2480505	5741220	2005
CH	10	Invaded	Riccarton High School, Curletts Rd, Upper Riccarton, Christchurch	2474680	5741140	2005
CH	1	Formerly Invaded	Hornby Mall, Hornby, Christchurch	2471305	5740265	2004
CH	2	Formerly Invaded	Riccarton, 24 Wharenu Rd, Christchurch	2476550	5741530	2005
CH	3	Formerly Invaded	Riccarton, Broadbent St at Matipo St, Christchurch	2477500	5741500	2000
CH	4	Formerly Invaded	Wigram Park, Mainfreight International, 48 McAlpine St, Christchurch	2474485	5740550	2002

Appendix 4. Resident ant communities in surveyed sites of past known infestation. Invaded sites are those sites which are currently invaded by Argentine ants. Formerly invaded sites are those sites which used to have Argentine ants but the population has since collapsed. In Auckland uninvasion sites, reference sites which have no record of ever being invaded by Argentine ants, were also surveyed. The black squares indicate species presence. Native ant species are listed first, followed by introduced ant species. Location of each site can be found in Appendix 3.

Northland (NL)

	Invaded Sites															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
<i>Huberia brounii</i>																
<i>Monomorium antarcticum</i>																
<i>Pachycondyla castanea</i>																
<i>Prolasius advenus</i>																
<i>Cardiocondyla minutior</i>																
<i>Hypoponera eduardi</i>																
<i>Iridomyrmex</i> sp.																
<i>Mayriella abstinens</i>																
<i>Monomorium antipodum</i>																
<i>Ochetellus glaber</i>																
<i>Paratrechina</i> spp.																
<i>Pheidole megacephala</i>																
<i>Pheidole proxima</i>																
<i>Pheidole rugosula</i>																
<i>Rhytidoponera chalybaea</i>																
<i>Technomyrmex albipes</i>																
<i>Tetramorium bicarinatum</i>																
<i>Tetramorium grassii</i>																

	Formerly Invaded Sites														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
<i>Huberia brounii</i>															
<i>Monomorium antarcticum</i>															
<i>Pachycondyla castanea</i>															
<i>Prolasius advenus</i>															
<i>Cardiocondyla minutior</i>															
<i>Hypoconera eduardi</i>															
<i>Iridomyrmex</i> sp.															
<i>Mayriella abstinens</i>															
<i>Monomorium antipodum</i>															
<i>Ochetellus glaber</i>															
<i>Paratrechina</i> spp.															
<i>Pheidole megacephala</i>															
<i>Pheidole proxima</i>															
<i>Pheidole rugosula</i>															
<i>Rhytidoponera chalybaea</i>															
<i>Technomyrmex albipes</i>															
<i>Tetramorium bicarinatum</i>															
<i>Tetramorium grassii</i>															

Auckland (AK)

Invaded Sites

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	
<i>Monomorium antarcticum</i>																								
<i>Monomorium antipodum</i>																								
<i>Cardiocondyla minutior</i>																								
<i>Hypoponera eduardi</i>																								
<i>Iridomyrmex</i> sp.																								
<i>Mayriella abstinens</i>																								
<i>Ochetellus glaber</i>																								
<i>Paratrechina</i> sp.																								
<i>Pheidole megacephala</i>																								
<i>Pheidole proxima</i>																								
<i>Pheidole rugosula</i>																								
<i>Rhytidoponera chalybaea</i>																								
<i>Technomyrmex albipes</i>																								
<i>Tetramorium bicarinatum</i>																								
<i>Tetramorium grassii</i>																								

Formerly Invaded Sites

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
<i>Monomorium antarcticum</i>																											
<i>Monomorium antipodum</i>																											
<i>Cardiocondyla minutior</i>																											
<i>Hypoponera eduardi</i>																											
<i>Iridomyrmex</i> sp.																											
<i>Mayriella abstinens</i>																											
<i>Ochetellus glaber</i>																											
<i>Paratrechina</i> sp.																											
<i>Pheidole megacephala</i>																											
<i>Pheidole proxima</i>																											
<i>Pheidole rugosula</i>																											
<i>Rhytidoponera chalybaea</i>																											
<i>Technomyrmex albipes</i>																											
<i>Tetramorium bicarinatum</i>																											
<i>Tetramorium grassii</i>																											

Uninvaded Sites

	1	2	3	4	5	6	7	8	9	10	11
<i>Monomorium antarcticum</i>											
<i>Monomorium antipodum</i>											
<i>Cardiocondyla minutior</i>											
<i>Hypoponera eduardi</i>											
<i>Iridomyrmex</i> sp.											
<i>Mayriella abstinens</i>											
<i>Ochetellus glaber</i>											
<i>Paratrechina</i> sp.											
<i>Pheidole megacephala</i>											
<i>Pheidole proxima</i>											
<i>Pheidole rugosula</i>											
<i>Rhytidoponera chalybaea</i>											
<i>Technomyrmex albipes</i>											
<i>Tetramorium bicarinatum</i>											
<i>Tetramorium grassii</i>											

	Coromandel (CO)		Hamilton (WO)				Tauranga (TA)		
			Invaded Sites						
	1	2	1	2	3	4	1	2	3
<i>Huberia brounii</i>									
<i>Monomorium antarcticum</i>							■		■
<i>Pachycondyla castanea</i>									
<i>Prolasius advenus</i>							■		
<i>Cardiocondyla minutior</i>								■	■
<i>Hypoponera eduardi</i>								■	■
<i>Iridomyrmex</i> sp.		■					■	■	■
<i>Mayriella abstinens</i>									
<i>Monomorium antipodum</i>									
<i>Ochetellus glaber</i>	■	■					■	■	■
<i>Paratrechina</i> spp.	■	■		■			■	■	■
<i>Pheidole megacephala</i>									
<i>Pheidole proxima</i>									
<i>Pheidole rugosula</i>							■	■	
<i>Rhytidoponera chalybaea</i>									
<i>Technomyrmex albipes</i>									
<i>Tetramorium bicarinatum</i>		■							■
<i>Tetramorium grassii</i>	■	■							■

	Formerly Invaded Sites											
	1		1	2			1	2	3	4	5	6
<i>Huberia brounii</i>												
<i>Monomorium antarcticum</i>	■											
<i>Pachycondyla castanea</i>												
<i>Prolasius advenus</i>												
<i>Cardiocondyla minutior</i>												
<i>Hypoponera eduardi</i>												
<i>Iridomyrmex</i> sp.	■			■				■	■	■	■	■
<i>Mayriella abstinens</i>												
<i>Monomorium antipodum</i>	■	■										
<i>Ochetellus glaber</i>	■	■		■				■	■	■	■	■
<i>Paratrechina</i> spp.	■	■						■	■	■	■	■
<i>Pheidole megacephala</i>												
<i>Pheidole proxima</i>												
<i>Pheidole rugosula</i>	■							■	■	■		■
<i>Rhytidoponera chalybaea</i>												
<i>Technomyrmex albipes</i>				■								
<i>Tetramorium bicarinatum</i>								■		■		■
<i>Tetramorium grassii</i>	■											

	Taupo (TO)		Hastings (HA)										
			Invaded Sites										
	1	2	1	2	3	4	5	6	7	8	9	10	11
<i>Huberia brounii</i>													
<i>Monomorium antarcticum</i>	■		■										
<i>Pachycondyla castanea</i>													
<i>Prolasius advenus</i>													
<i>Cardiocondyla minutior</i>										■			
<i>Hypoponera eduardi</i>	■								■				
<i>Iridomyrmex</i> sp.			■	■	■	■	■		■	■			■
<i>Mayriella abstinens</i>													
<i>Monomorium antipodum</i>													
<i>Ochetellus glaber</i>	■		■	■									
<i>Paratrechina</i> spp.	■		■	■							■		
<i>Pheidole megacephala</i>													
<i>Pheidole proxima</i>													
<i>Pheidole rugosula</i>			■						■				
<i>Rhytidoponera chalybaea</i>													
<i>Technomyrmex albipes</i>					■				■		■		
<i>Tetramorium bicarinatum</i>													
<i>Tetramorium grassii</i>													
Formerly Invaded Sites													
			1										
<i>Huberia brounii</i>													
<i>Monomorium antarcticum</i>													
<i>Pachycondyla castanea</i>													
<i>Prolasius advenus</i>													
<i>Cardiocondyla minutior</i>													
<i>Hypoponera eduardi</i>													
<i>Iridomyrmex</i> sp.			■										
<i>Mayriella abstinens</i>													
<i>Monomorium antipodum</i>													
<i>Ochetellus glaber</i>			■	■									
<i>Paratrechina</i> spp.			■										
<i>Pheidole megacephala</i>													
<i>Pheidole proxima</i>													
<i>Pheidole rugosula</i>			■										
<i>Rhytidoponera chalybaea</i>													
<i>Technomyrmex albipes</i>			■										
<i>Tetramorium bicarinatum</i>													
<i>Tetramorium grassii</i>													

	Wellington (WT)					Nelson (NN)								
						Invaded Sites								
	1	2	3	4	5	1	2	3	4	5	6	7	8	9
<i>Huberia brounii</i>														
<i>Monomorium antarcticum</i>	■								■	■				
<i>Pachycondyla castanea</i>														
<i>Prolasius advenus</i>														
<i>Cardiocondyla minutior</i>														
<i>Hypoponera eduardi</i>														
<i>Iridomyrmex</i> sp.														
<i>Mayriella abstinens</i>														
<i>Monomorium antipodum</i>		■	■											
<i>Ochetellus glaber</i>											■	■		
<i>Paratrechina</i> spp.							■	■	■	■	■	■	■	
<i>Pheidole megacephala</i>														
<i>Pheidole proxima</i>														
<i>Pheidole rugosula</i>									■	■				
<i>Rhytidoponera chalybaea</i>														
<i>Technomyrmex albipes</i>														
<i>Tetramorium bicarinatum</i>														
<i>Tetramorium grassii</i>														
						Formerly Invaded Sites								
	1	2	3	4		1	2	3						
<i>Huberia brounii</i>														
<i>Monomorium antarcticum</i>	■		■	■		■	■	■						
<i>Pachycondyla castanea</i>	■		■	■		■	■	■						
<i>Prolasius advenus</i>														
<i>Cardiocondyla minutior</i>														
<i>Hypoponera eduardi</i>														
<i>Iridomyrmex</i> sp.														
<i>Mayriella abstinens</i>														
<i>Monomorium antipodum</i>														
<i>Ochetellus glaber</i>							■	■						
<i>Paratrechina</i> spp.			■	■		■	■	■						
<i>Pheidole megacephala</i>														
<i>Pheidole proxima</i>														
<i>Pheidole rugosula</i>							■	■						
<i>Rhytidoponera chalybaea</i>														
<i>Technomyrmex albipes</i>				■										
<i>Tetramorium bicarinatum</i>														
<i>Tetramorium grassii</i>														

Christchurch (CH)										
Invaded Sites										
	1	2	3	4	5	6	7	8	9	
<i>Huberia brounii</i>				■						
<i>Monomorium antarcticum</i>				■						
<i>Pachycondyla castanea</i>										
<i>Prolasius advenus</i>										
<i>Cardiocondyla minutior</i>										
<i>Hypoponera eduardi</i>										
<i>Iridomyrmex</i> sp.			■							
<i>Mayriella abstinens</i>										
<i>Monomorium antipodum</i>										
<i>Ochetellus glaber</i>										
<i>Paratrechina</i> spp.	■			■						
<i>Pheidole megacephala</i>										
<i>Pheidole proxima</i>										
<i>Pheidole rugosula</i>										
<i>Rhytidoponera chalybaea</i>										
<i>Technomyrmex albipes</i>										
<i>Tetramorium bicarinatum</i>										
<i>Tetramorium grassii</i>										
Formerly Invaded Sites										
	1	2	3	4						
<i>Huberia brounii</i>										
<i>Monomorium antarcticum</i>	■	■		■						
<i>Pachycondyla castanea</i>										
<i>Prolasius advenus</i>										
<i>Cardiocondyla minutior</i>										
<i>Hypoponera eduardi</i>										
<i>Iridomyrmex</i> sp.		■		■						
<i>Mayriella abstinens</i>										
<i>Monomorium antipodum</i>										
<i>Ochetellus glaber</i>		■	■	■						
<i>Paratrechina</i> spp.		■	■	■						
<i>Pheidole megacephala</i>										
<i>Pheidole proxima</i>										
<i>Pheidole rugosula</i>										
<i>Rhytidoponera chalybaea</i>										
<i>Technomyrmex albipes</i>										
<i>Tetramorium bicarinatum</i>										
<i>Tetramorium grassii</i>										

The widespread collapse of an invasive species: Argentine ants (*Linepithema humile*) in New Zealand

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Synergies between invasive species and climate change are widely considered to be a major biodiversity threat. However, invasive species are also hypothesized to be susceptible to population collapse, as we demonstrate for a globally important invasive species in New Zealand. We observed Argentine ant populations to have collapsed in 40 per cent of surveyed sites. Populations had a mean survival time of 14.1 years (95% CI = 12.9–15.3 years). Resident ant communities had recovered or partly recovered after their collapse. Our models suggest that climate change will delay colony collapse, as increasing temperature and decreasing rainfall significantly increased their longevity, but only by a few years. Economic and environmental costs of invasive species may be small if populations collapse on their own accord.

Keywords: biological invasions; persistence; ant community; long-term effects; climate change; Argentine ant

1. INTRODUCTION

The combined influence of invasive species and climate change may be harmful for economies and human health, and may cause extinctions or change evolutionary pathways [1]. Consequently, considerable resources are frequently applied to invasive species management [2]. Invasive species have, however, been hypothesized to be susceptible to population crashes [3] irrespective of management approaches.

The Argentine ant (*Linepithema humile*) is listed among 100 of the world's worst invasive species [4]. Originally from South America, this ant is known to invade sub-tropical and temperate regions and is established on six continents [5]. Introduced populations form high-density, widespread, highly aggressive, unicolonial populations and can deleteriously influence native communities [6]. First observed in New Zealand in Auckland during 1990, the species has since spread widely around the country assisted by human-mediated dispersal [7]. The dates and locations of newly observed infestations have been recorded for many populations

[5], which typically range in size from a few to several hundred hectares. Environmental variables, such as temperature and rainfall have previously been suggested to help limit the distribution of this ant [5,8]. Consequently, this invasive species is expected to expand its range with climate change, particularly, in regions of higher latitude such as New Zealand [9].

Invasive ants are a substantial global problem for biodiversity [6]. However, populations of other invasive ants have occasionally been known to collapse [10]. Similarly, our long-term personal observations of local Argentine ant infestations also suggested that not all populations are persisting within New Zealand. Here, we asked three questions. Firstly, are Argentine ant infestations persisting, and if not, how is the collapse of these populations influenced by temperature and rainfall? Secondly, how might climate change affect the survival of Argentine ant populations? Finally, do Argentine ants reduce species richness and change resident ant communities, and do these communities recover after the collapse of Argentine ant populations?

2. MATERIAL AND METHODS

Using records of first recorded Argentine ant presence [5], we examined 150 locations across this ant's range in New Zealand. Ant communities were surveyed on the North and South Islands in January and February 2011. Detail on the sampling sites is given in the electronic supplementary material, S1. A GPS unit was used to navigate to the original location (± 10 m) where the surrounding area of approximately 200×200 m was hand-searched for ants. Such survey methods are considered effective for ant sampling [11]. Ants were collected with aspirators and preserved for identification. Climate data (annual rainfall (millimetre), mean temperature ($^{\circ}\text{C}$), mean maximum daily temperature ($^{\circ}\text{C}$) and mean minimum daily temperature ($^{\circ}\text{C}$)) [5] were obtained from <http://cliflo.niwa.co.nz> for the nearest weather station to each sampling site, which was within approximately 20 km of each location. Cox's Proportional Hazards (PH) models were used to test the influence of the four climate variables on the rate of disappearance of Argentine ant populations. Two parsimonious models were suggested by a forward stepwise model selection algorithm, one of which is presented here. Model 1 had two main effects: total rainfall and mean maximum daily temperature. For presentation, the survival data were organized into four groups based on the medians for rainfall and mean maximum temperature. A Kaplan–Meier Survival Curve and Logrank statistic were used to estimate survival and compare groups. For further details on model selection and climate groupings (S2), see the electronic supplementary material.

To create our climate change model, we applied the Cox's PH survival model fitted to current and future climate data to estimate probabilities of colony persistence under local conditions of rainfall and mean maximum daily temperature. Data regarding the climate across all of New Zealand were obtained from www.worldclim.org. Current climate was described by the 1950–2000 monthly averages at 2.5 min resolution, while for future climate we used predictions for 2050 generated by the CSIRO A2 model. See the electronic supplementary material for details on the CSIRO A2 model.

All Auckland sites were selected to examine the effects of Argentine ants on communities, owing to the high diversity of its ant communities and the considerable length of time Argentine ants had been present. Three types of Auckland communities were assessed and compared for differences in species richness and community composition: (i) communities currently with Argentine ants; (ii) communities where Argentine ant populations were no longer detected; and (iii) communities where Argentine ants had never been recorded as present. The species richness of the three types of Auckland ant communities was examined using an ANOVA. To examine differences in the species composition between these communities, we used multivariate data analysis in Plymouth Routines in Multivariate Ecological Research (PRIMER, v. 6.1.11, 2008; Plymouth Marine Laboratory, UK). An ordination analysis was conducted using non-metric multidimensional scaling (MDS) plots that score communities based on their similarity or dissimilarity. The resemblance matrix was derived using Jaccard similarity coefficients, which use presence/absence data. Stress values on MDS plots below 0.2 are an indication of a good fit. A distance-based test for homogeneity of multivariate

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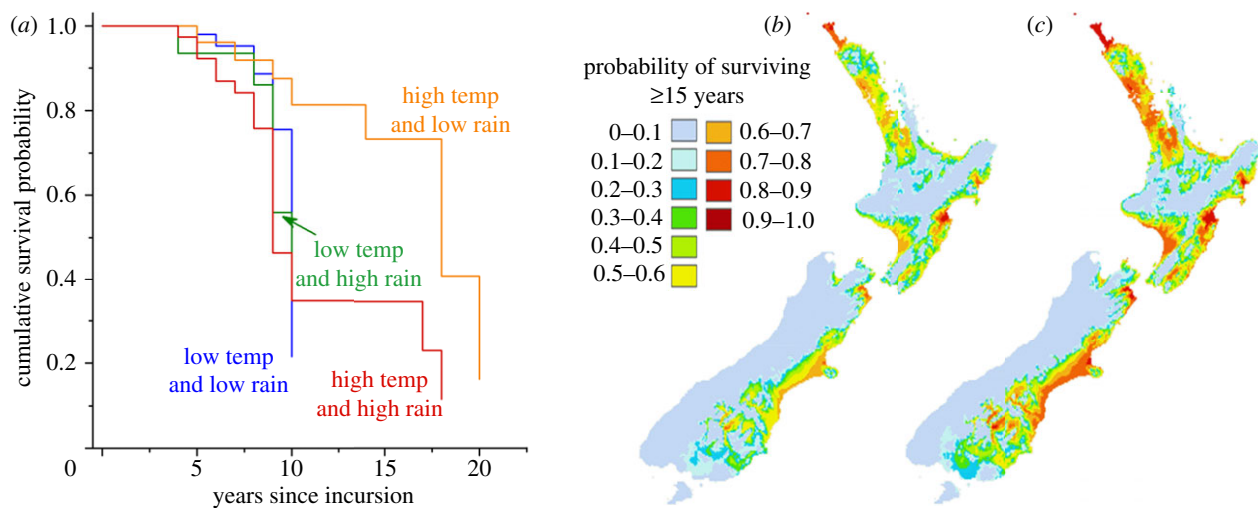


Figure 1. (a) Survivorship curves for Argentine ant populations, with data divided into subsets of high and low temperature and rainfall conditions. (b) Probability of Argentine ant incursions surviving for 15 years or more under current climate conditions, and (c) after the CSIRO A2 climate change predictions.

Table 1. Kaplan–Meier estimates of survival time of Argentine ant populations under four different climate regimes.

climate regime	<i>n</i>	time (years)	95% CI
low rainfall–low temperature	50	10.5	10.1–10.9
high rainfall–low temperature	34	12.4	11.0–13.7
low rainfall–high temperature	22	17.8	15.6–20.0
high rainfall–high temperature	44	13.0	11.0–15.0
overall	150	14.1	12.9–15.3

dispersions (PERMDISP) was used to assess the differences in species composition between the groups on the MDS plot using 9999 permutations.

3. RESULTS

Argentine ant populations had collapsed in 60 of the 150 locations. Of the Argentine ant populations that did remain, many had shrunk from numerous nests covering multiple hectares with extremely high abundances to just one or two nests covering a very small area with low worker densities. A Kaplan–Meier estimator found the time to collapse was negatively influenced by mean maximum daily temperature and positively influenced by total annual rainfall ($p \leq 0.001$). Mean time to population collapse of these ants ranged from 10.48 years (10.10–10.86 years; 95% CI) in conditions of low rainfall and low temperature, to 17.80 years (15.59–20.01 years) under conditions of low rainfall and high temperature (figure 1a and table 1).

Climate change was predicted to increase the probability of Argentine ant survival in many regions (figure 1b,c). Under the CSIRO A2 model, the area of New Zealand in which populations have a greater than 80 per cent chance of surviving for 15 years or more increases from 0.26 to 1.29 per cent. Nowhere did survival probability decrease with climate change.

Ant species richness was significantly affected by the presence of Argentine ants ($F_{2,58} = 6.041$, $p = 0.004$; figure 2a). Post hoc Tukey tests showed that the ant communities with Argentine ants had significantly

fewer ant species than communities without Argentine ants. The species richness of ant communities after Argentine ant collapse was intermediate, likely indicating that the communities were at various stages of recovery post Argentine ant collapse. Communities with Argentine ants had significantly different community composition from those without Argentine ants present (PERMDISP; $t = 5.359$, $p < 0.001$) and from communities where populations had collapsed (PERMDISP, $t = 3.119$, $p < 0.001$; figure 2b). In contrast, communities where Argentine ants had collapsed were indistinguishable from those which had never been invaded (PERMDISP, $t = 0.615$, $p = 0.596$).

4. DISCUSSION

Argentine ants had disappeared from 40 per cent of our sampling sites. In many other sites, Argentine ant populations had been reduced from occupying multiple nests encompassing large areas to one or two small nests in a few square metres. These results are consistent with our observations of the slow shrinkage and disappearance of large Argentine ant infestations in areas, such as Wellington. They do not appear to move and to our knowledge are not managed by humans in any way that might reduce their abundance.

The shrinking and eventual disappearance of invasive species populations, including invasive ant populations, has historically been observed elsewhere [3]. For example, yellow crazy ant (*Anoplolepis gracilipes*) populations in the Seychelles declined dramatically over time and in some areas disappeared [10]. The reasons

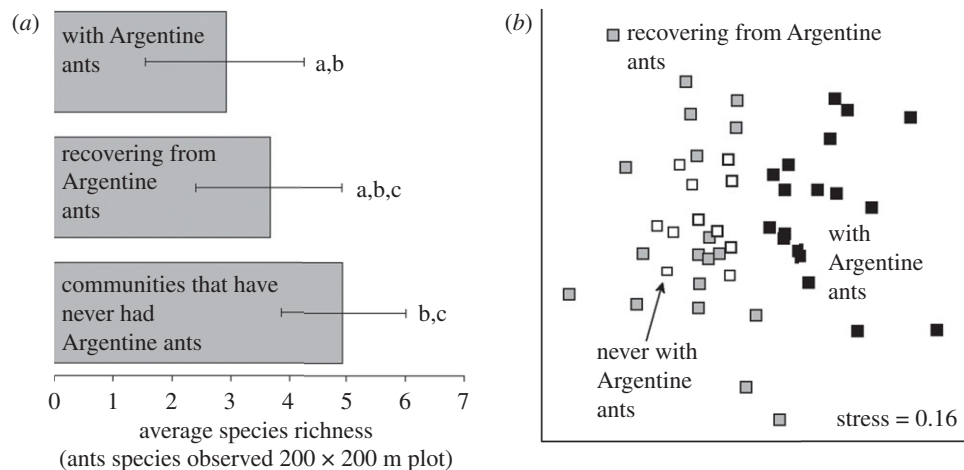


Figure 2. (a) The influence of Argentine ants on mean species richness of ant communities in Auckland (\pm s.e.). Letters represent results from post hoc Tukey test groupings. (b) A multi-dimensional scaling analysis of Auckland ant communities currently with Argentine ants ($n = 23$), without ever having Argentine ants ($n = 11$), or communities recovering from incursions ($n = 27$).

for the population collapse of Argentine or yellow crazy ant populations are not yet known. However, population genetics predicts that invasive species might collapse owing to inbreeding depression or an inability to adapt to their new environment [12]. Previous genetic studies have revealed that the New Zealand population of Argentine ants has among the lowest recorded genetic diversity of any introduced Argentine ant population worldwide, indicative of the entire supercolony having arisen from an incursion of just one nest [7,12]. Low genetic diversity, perhaps in combination with pathogens [13] or a depletion of local resources [10], is a candidate mechanism for these collapses.

Our results indicate that the survival of Argentine ant infestations is negatively influenced by increasing rainfall and positively influenced by increasing temperature, which is in agreement with previous work [5,9]. Consequently, our survival model, when applied to future climate data, indicates increased survival times in all parts of the country. The total New Zealand area with a higher than 80 per cent chance of having populations survive 15 years or more substantially increases from 0.26 (69 685 km²) to 1.29 per cent (345 747 km²). However, we note that, even under current conditions of high temperatures and low rainfall, the probability of Argentine ants persisting more than 20 years was less than 20 per cent (figure 1a). While climate change may increase persistence, this increase in persistence is not dramatic.

Argentine ants are well known to competitively displace other ant species [6], but we found 61 per cent of sites where Argentine ants were still present to have other ant species living side by side. Many of these populations had shrunk to tiny remnant populations with multiple ant species present at the same site. In places where Argentine ants were at very high abundances there were very few or no co-occurring ant species, but at sites where Argentine ant densities were low there were many other ant species. When present in low abundance, Argentine ants are less competitive and prone to local extinction [14]. Thus, any process that reduces Argentine ant densities (such as pathogens) is likely to have compounding effects on the ability of these invasive

ants to persist. Impacts may also lessen over time and interact with climate [8]. Other ant species re-colonized all areas where Argentine ant populations had collapsed. Our community analysis suggests ant communities that were formerly invaded by Argentine ants are recovering and regaining their pre-invasion structure.

Given the local presence of this invasive species for short durations of 10–20 years, and the apparent recovery of the resident communities after their collapse, it seems that the long-term ecological or evolutionary effects of Argentine ants in New Zealand may not be as dire as first feared. The control of Argentine ants was predicted to cost New Zealand up to \$68 million per year [15]. Such economic and environmental costs will be considerably smaller here and in other countries, however, if populations collapse on their own accord. Other invasive species and climate change clearly contribute to the current global biodiversity crisis [1], and their costs may be substantial. Determining which species are susceptible and the mechanisms for these collapses should be a high priority for invasion biologists.

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