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General Introduction

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1.1 Biological invasions

1.1.1 Overview

The impact of invasive species has been recognised for many decades (Elton 1958; Drake et al. 1989; Sakai et al. 2001). However, biological invasions have become increasingly topical, and there is now a large body of scientific literature that provides evidence and case studies which repeatedly document the spread and negative impacts of biological invaders (Mooney & Drake 1986; Drake et al. 1989; Williams 1994; Sandland et al. 1999; Pimentel 2002; Lockwood et al. 2007). The issue of biological invasions is also increasingly reaching the public arena because of serious economic and social consequences (Mack et al. 2000). For example, Pimentel et al. (2002) estimated over 120 000 exotic species were present in six countries (USA, UK, Australia, South Africa, India, Brazil), of which 20-30% were considered economic and environmental pests. The economic damage associated with invasive species in these countries was greater than US$336 billon per year from productivity losses and the direct cost of combating the pest species (Pimentel et al. 2002).

However, the impacts of biological invasions in natural ecosystems are also a major threat to global biodiversity; a threat considered second only to direct habitat destruction (Mack et al. 2000). Ecological changes resulting from invasive species are considered to rival the changes induced by continental glaciation cycles – but over a considerably shorter time frame (Mack et al. 2000). Numerous studies have summarised the impacts of invasive species on species and communities in natural ecosystems and ecosystem-level impacts are increasingly being studied (Sakai et al. 2001; Lockwood et al. 2007). The impacts of biological invasions can range from replacing or changing the roles of native species in communities, to causing radical changes in the abundance and extinction of species, and disrupting evolutionary processes (Mack et al. 2000). Large scale ecosystem functioning and properties may also be altered, such as; soil erosion, biogeochemical and hydrological cycles, fire regimes and the recruitment of native species (Mooney & Drake 1986).

Explaining and predicting biological invasions have been major aims of ecological research, and are of immense scientific and practical importance (Mack et al. 2000; Kolar & Lodge 2001; Heger & Trepl 2003). In practical terms, obtaining accurate explanations of the factors behind the invasion of a particular species may not only serve to assist in its management and control, but could be useful in the future to prevent other invasions. Successful predictions could reveal the most effective means to prevent future invasion and would be valuable in the prioritisation of resources toward surveillance, detection and control (Ricciardi & Rasmussen 1998; Mack et al. 2000). The focus of this thesis is on explanations and predictions associated with invasive ant species (Hymenoptera: Formicidae).

1.1.2 Definitions

Biological invasions have often been defined as "the geographical expansion of a species into an area not previously occupied by that species" Vermeij (1996, p4). However, this definition fails to recognise two important points. Firstly, 'invasion' is not just about geographical expansion, but is the result of a series of stages and processes (Richardson et al. 2000; Heger & Trepl 2003). To become invasive, individuals of a species must overcome barriers to dispersal, survival and reproduction, which allow the species to establish and spread throughout a new area (Richardson et al. 2000). The majority of species introduced to a new area are considered to perish by way of both abiotic and biotic factors (Mack et al. 2000). Of the few that establish and survive, even fewer go on to spread, and fewer still to have negative impacts (Mack et al. 2000; Richardson et al. 2000). Furthermore, geographical expansion is not necessarily correlated with impact. Therefore, the definition of a biological invader must encompass that fact that invasion is a process of steps and stages (Richardson et al. 2000; Heger & Trepl 2003), where few species make it through until the final stage, but many either fail to establish, or establish (naturalise, *sensu* Richardson et al. 2000) but do not go on to have negative impacts.

Secondly, it is also important to separate the effects of biological invasions which can be a natural phenomenon, occurring as the result of natural range expansion of a species (Huston 1994), versus the result of biological invasions mediated by humans. Although biological invasions can be a natural phenomenon, is it widely recognised that the current rate of invasion is almost entirely a human phenomenon (Huston 1994). Humans have transported species from a large array of taxonomic groups and geographic origins, both accidentally and deliberately (Mack et al. 2000). Human-mediated transport of species has increased greatly over the past 200-500 years as a direct result of human population growth, increasing utilisation of agro-forestry and animal husbandry practises, and associated long-distance transport and commerce networks (Huston 1994; Mack et al. 2000). It is human-mediated biological invasions that are the subject of this thesis.

In this thesis, the term exotic is used to define a species that is introduced to a new region having been transported there by humans, either accidentally or deliberately. Exotic species may overcome barriers to survival and reproduction to become naturalised (i.e. established). An invasive species is further defined as a species which subsequently disperses throughout the new (recipient) region, and impacts negatively on the recipient community. This definition encompasses a combination of terminology from the biological literature, but primarily from Richardson et al. (2000), although the definition given here is considered independent of taxonomic group, as opposed to Richardson et al. (2000) which are considerably plant focused. In this thesis, the terms 'exotic', 'alien', 'non-native', 'tramp' and 'introduced' are interchangeable (Clout 1999).

1.2 Invasive ants

Invasive ant species (Hymenoptera: Formicidae) have over the last decade received considerable attention from around the globe, with increasing evidence of economic and agricultural impacts, health effects on humans, and disruption to natural ecosystems (Williams 1994; Christian 2001; Holway et al. 2002; Lard et al. 2002; O'Dowd et al. 2003; Sanders et al. 2003). The attention directed towards invasive ants is also reflected by an increasing number of scientific publications (Figure 1.1). However, despite a considerable number of invasive ant publications, there have been two major limitations associated with the study of invasive ants. Firstly, the vast majority of the literature is primarily limited to just two species; the Argentine ant *Linepithema humile* Mayr and the red-imported fire ant, *Solenopsis invicta* Buren (Holway et al. 2002). Furthermore, the study of invasive ant species has also been predominantly directed at local and regional efforts to manage invasive species. It has previously been noted that intensive study on a few well known invasive species may have obscured broader patterns associated with biological invasions (Vermeij 1996; Davis et al. 2001). Consequently, there has been a lack of an overall framework for invasive ant species, and reviews of invasive ants have appeared only relatively recently compared with other taxa (Williams 1994; Moller 1996; Holway et al. 2002). Having a wider perspective is important in order to determine generalised patterns for invasive ants, and to develop explanations and predictions for their invasion. Historically, explanations and predictions of biological invasions have fallen into two major approaches (Mooney & Drake 1986; Lodge 1993); 1) identifying certain attributes (life history, morphological, behavioural) that predispose a species to becoming invasive, and 2) identifying particular habitats or communities that are highly vulnerable to invasion.

1.2.1 Attributes of invasive ants

There have been numerous attempts to make predictions of the potential "invasiveness" of a given species based on species-specific attributes or traits (Lodge 1993). Such an approach has its origins from early, or classical biological invasion literature where invaders were thought to possess some 'special' attributes conferring their invasive ability (Levine & D'Antonio 1999; Heger & Trepl 2003). Most attempts have resulted in lists of attributes of species that are predicted to confer increased invasive potential. Identifying such attributes and the species that possess them, could lead to preventative measures that preclude, or at least reduce the probability, of certain species arriving and establishing (Mack et al. 2000). A number of widely cited invasive species attributes, include: r-selected, high dispersal, single parent reproduction (including vegetative reproduction), a preference for pioneer habitats, high growth rate, high genetic variability, phenotypic plasticity, large native range, and human commensalism. Such attributes are thought to predispose a species to rapid population expansion through genetic and phenotypic plasticity (Lodge 1993; Sakai et al. 2001).

For ants, several authors have suggested that there are certain attributes that confer an invasive ability (Hölldobler & Wilson 1990; Passera 1994; Holway et al. 2002). McGlynn (1999a) found that invasive ants were significantly smaller than native species from the same genus. Invasive ants had workers typically in the size range of 1-2mm, but less than 5mm. Many invasive ants are described as "opportunistic" species and include a wide range of food sources in their diets, for example, scavenging on dead animals, preying on small invertebrates and harvesting the carbohydrates from both plants and sap-sucking insects (Homoptera) (Holway et al. 2002). McGlynn (1999b) also found that a large proportion (70%) of exotic ant species being transported around the globe were functionally categorised as; opportunists (28%), cryptic species (22%), or generalised myrmicines (20%). A considerable proportion of ant species transported into new environments by humans remain confined to human-modified habitats. These ant species are referred to as 'tramp species' because of their close association with humans and opportunistic habits (McGlynn 1999b).

The utilisation of carbohydrates from sap-sucking insects has been suggested as a significant factor in the success of invasive ant species. For example, Helms & Vinson (2003) showed that a mealybug (Homoptera: Pseudococcidae) provided 16-48% of the energy requirements of the invasive red imported fire ant. Associations between the yellow crazy ant, *Anoplolepis gracilipes* (Smith) and host-generalist scale insects have produced dramatic ecological change on Christmas Island in the Indian Ocean, with forest canopy die-back and the displacement of a ground-dwelling keystone species (O'Dowd et al. 2003). However, the utilisation of carbohydrates by invasive species does not mean this is necessarily an attribute of invasiveness; the utilisation of carbohydrates is well known among many ant taxa (Way 1963; Carroll & Janzen 1973).

The formation of supercolonies, or unicolonality, is also advocated as a strong characteristic of invasive ants (Holway et al. 2002). Ant species typically encounter aggression through intra-competition from nearby colonies in their native ranges. However, in their introduced range several invasive species are known to form expansive supercolonies where inter-specific aggression is almost absent (O'Dowd et al. 2003; Suarez et al. 1999, 2002; Tsutsui et al. 2000, 2003). The lack of intra-specific aggression may provide a numerical advantage to an invading species (through a large co-operating supercolony) that result in native ant species being overwhelmed by the invader. It is thought the mechanism for reduced intra-specific aggression is the result of a genetic bottleneck and lower genetic diversity at recognition loci following the introduction of a species (Suarez et al. 2002; Abbott et al. 2007). However, different genetic strains of a species may have different impacts when introduced to a new environment. For example, two different haplotypes of the yellow crazy ant, *A. gracilipes*, appear to have had a significant influence in determining its abundance and aggression on the Pacific islands of Tokelau (Abbott et al. 2007).

1.2.2 Susceptibility of communities to invasive ants

It is well recognised that few communities are impenetrable to invasion, but also that communities differ in their susceptibility to invasion (Mooney & Drake 1986; Drake et al. 1989; Williams 1994; Sandland et al. 1999; Sakai et al. 2001; Pimentel 2002). One approach to predicting biological invasions has been to determine whether there are certain combinations of environmental conditions that make some communities particularly susceptible to invasion (Huston 1994). Attempts to predict the relative community vulnerability to invasion have prompted three major generalisations about how invasibility is enhanced: 1) disturbance of an area before or upon arrival of an invasive species, 2) invaders escaping from biotic constraints and not acquiring new competitors and predators, and 3) communities with low species richness and vacant niches (i.e. communities are unsaturated).

However, for invasive ants, there appears to be a distinct lack of information surrounding this approach. Disturbance is often regarded as the single most important factor affecting the success of an invasion (Huston 1994; Mack et al. 2000). Numerous authors have reported or inferred that disturbance has played a part in invasion – particularly where human actions may encourage invasions by causing disturbances (Mack et al. 2000). For invasive ant species, the physical environment, fragmentation and the history of anthropogenic disturbance could all influence the susceptibility to invasion (Holway et al. 2002). For example, the effect of chemical eradication programs for *S. invicta* is thought to have unintentionally promoted its invasion by adversely affecting the recovery of native ants (Tschinkel 1993).

There is strong evidence that many invasive species essentially arrive in a new region without many of their biotic constraints present in their native range. Although this idea appears to have been poorly studied for invasive ants, Porter et al. (1997) provide strong evidence that the high density of *S. invicta* in the USA is the result of a lack of enemies (parasitic phorid flies, microorganisms, nematodes, and viruses) in the introduced range. Similarly, *Pseudacteon* (Phoridae) parasitoids are known to affect the foraging of Argentine ants in their native habitat, but are absent in the introduced range (Orr & Seike 1998).

The concepts of biotic richness and vacant niches are among the most discussed generalisations about community invasibility. Resistance to invasion may be enhanced in species-rich communities or in communities with diverse functional groups (Sakai et al. 2001). Conversely, communities with fewer species are more prone to invasion and are less likely to be adapted to resist novel invaders. However, several authors have suggested that rather than species richness, it is the absence, or near absence, of a taxonomic group or ecological guild that will result in minimum resistance to invaders (Simberloff 1986, 1995; Loope & Mueller-Dombois 1989). For example, Simberloff (1986, 1995) argues that the disharmonic nature of the Hawaiian entomological fauna is a better explanation of why there are so many invading insect species in Hawaii, than an explanation based on the low species diversity of the islands.

The vacant niche hypothesis has not been well studied for invasive ants, possibly because ant species are typically ubiquitous and diverse in the majority of environments. However, Le Breton *et al*. (2005) recently showed that food and nest site resources were not fully exploited by native ant communities in New Caledonia, creating a resource opportunity that has enabled the little fire ant, *Wasmannia auropunctata* (Roger), to invade and subsequently monopolise resources. Biotic resistance has been examined to a larger extent, particularly in terms of inter-specific competition between native and invasive ant species. In general, it appears that biotic resistance is not a strong effect, and does not prevent invasion, at least for *L. humile* (Rowles & O'Dowd 2007). However, the strength of biotic resistance may be contingent on several factors, including colony size (Walters & Mackay 2006), and species-specific microclimate and habitat tolerances (Thomas & Holway 2005).

1.2.3 Biological invasions: making the link

Although the concepts behind species attributes and susceptible communities are intuitively appealing, there are many exceptions and too much generalisation (Lodge 1993; Mack et al. 2000). It appears that there are several factors that potentially enhance invasion: species attributes, taxonomic or functional disharmony, low species richness, escape from natural enemies, and disturbance. However, it is not fundamentally clear what the prime factor is for invasibility, and how numerous factors interact to either enhance or resist invasion. Problems become apparent when attempts are made to derive specific predictions from lists of either attributes or susceptible communities. For example, Heger & Trepl (2003) give the example of several invasive plant species and a list of attributes they possess. No attributes were held by all of the species, and no species have all the attributes. Therefore, none of attributes was by itself suited to discriminate between invasive and non-invasive species (Heger & Trepl 2003). There is also the problem of testing hypotheses because of the enormous difficulties in separating the confounding effects of communities being invaded (Lodge 1993; Mack et al. 2000). That is, a reductionist approach to biological invasion, where a single variable can be manipulated and studied, while other variables are constant (e.g. disturbance, attributes of the invading organism, invasion opportunity, diversity of the recipient community), is often impossible to take.

Despite the many problems associated with explaining and predicting biological invasions, the principal problem with these approaches is that they investigate only one aspect of invasion; either the invader or the invaded community. Thus, a major feature of biological invasions, that is, the link between the attributes of invasive species and the invaded community, has been neglected. Sakai et al. (2001) have suggested that this could be a major reason why generalisations fail. It has become increasingly evident that both the characteristics of the recipient community and the attributes of the invader are important to the fate of invasions (Simberloff 1989; Lodge 1993; Simberloff 1995; Levine & D' Antonio 1999; Sakai et al. 2001; Shea & Cheeson 2002). Adoption of this new paradigm will lead to an increased understanding of biological invasions. This shift in focus has come about for a number of reasons.

Firstly, generalisations and traditional approaches have not been adequate to either explain or predict invasions. Heger and Trepl (2003) provide an analogy of the two traditional approaches with keys and locks. An invasive species is successful when it possesses the right keys (attributes) to invade a community. Conversely, a recipient community can possess certain characteristics that act as a lock, which prevents invasion (Heger & Trepl 2003). These approaches are non-relational. However, greater explanations for specific invasions can be provided if both approaches are used in combination, and in the context of viewing invasion as a process (Heger & Trepl 2003).

There has also been a realisation that biological invasions can help answer many longstanding questions in community ecology (e.g. community assembly rules, the importance of competition, the interaction between complexity and stability of ecosystems, the role of keystone species, and ecological niches) (Lodge 1993; Davis et al. 2001). The ability to accurately identify potential biological invaders would also be extremely informative for understanding the ecological and evolutionary processes of life history traits and how biotic communities interact and are assembled (Mack et al. 2000).

Lastly, a number of studies have found the success of invaders is strongly related to the environmental factors that are also responsible for the dynamics and diversity of native communities. Thus, understanding the environmental controls over native species (e.g. competition, disturbance, habitat, resources) may be an important approach to understanding invasions (Levine & D' Antonio 1999; Sakai et al. 2001). Shea and Cheeson (2002) state that the link between community ecology and invasion biology is natural, because, they argue, the criteria for a native species to survive, reproduce, and disperse in a community, are also the same criteria for an invasive species to be able to invade a community.

The combination of these reasons has significantly changed the way biological invasions should be studied, explained and predicted. Future progress in understanding biological invasions must 1) encompass community interactions between invaders and the recipient environment, 2) place invasion in the context of a process, and 3) model the spatial and temporal distribution of invading species (Lodge 1993; Levine & D' Antonio 1999; Sakai et al. 2001; Heger & Trepl 2003; Peterson 2003).

Distribution is a key part of community ecology (Begon et al. 1990). Interactions between abiotic and biotic factors determine the distribution of species and shape the characteristics of a community. An important step to managing invasive ant species is determining the factors responsible for their current and potential distribution.

1.2.4 The distribution of invasive ant species

For ant species, including invasive ant species, distribution is determined by a number of complex, and interacting factors. For invasive ants, the initial dispersal to a new region is a fundamental factor - providing the opportunity for invasion. Thus, trade routes associated with specific geographic regions represent an important filter for the transfer and arrival of specific invasive ant species.

Subsequently, there are several factors that primarily determine the distribution of ants. Climatic variables, especially temperature, rainfall and humidity, play a large role in determining the distribution of ant species. On large spatial scales ant abundance is strongly correlated with net primary productivity but climate also plays an important role by restricting foraging activity and regulating seasonal productivity (Kaspari et al. 2000). At the level of the colony, the location and construction of nests play an important role in regulating temperature and humidity. For example, nests can provide a thermal refuge in hot environments, allowing workers to retreat to a cool nest in the hottest part of the day (Hölldobler & Wilson 1990). Some ant species are known to move brood vertically within the nest to keep them at the optimum temperature for development (Hölldobler & Wilson 1990). Extremes of temperature are known to severely limit, or stop, the production of workers and reproductive castes of *S. invicta*, which can ultimately kill the colony (Korzukhin et al. 2001).

Habitat and microclimate structure are also important in determining the distribution and ecology of ants. For example, two-dimensional foraging surfaces (i.e. inter-connecting branches, bare ground) allows faster location and more rapid recruitment for effective defence and monopolisation of resources (Majer et al. 2004). Conversely, litter environments which are more complex three-dimensional microclimates, and the nature of inhabiting a decomposing habitat may affect colony and territory size (Kaspari 1996). The physical environment of different habitats is also fundamentally important. For example, Yanoviak and Kaspari (2000) discovered that differences in resource quality, physical complexity and microclimate between canopy and litter habitats strongly shape the distribution and composition of ant communities. Cole (1983) found that the physical exposure to wind and wave action affected small mangrove islands in the Florida Keys, and thus affected the establishment and distribution of several ant species.

Inter-specific competition is considered to be the major structuring force of ant communities (Wilson 1971; Andersen 1992; Morrison 1996; Davidson 1998; Holway 1999; Gotelli & Ellison 2002). Inter-specific competition results in dominance hierarchies being formed through inter-specific aggression, competitive exclusion at food resources and distinctive foraging strategies for either accessing resources or avoiding dominant species (Wilson 1971; Fellers 1987; Savolainen & Vepsäläinen 1989; Andersen 1992; Davidson 1998; Holway 1999). In particular, dominant species can control the spatial occurrence of other species, potentially structuring the ant community and creating mosaic-like patterns of species co-occurrence (Room 1975; Savolainen & Vepsäläinen 1989).

Thus, dispersal to a new region, climate variables, habitat requirements, and competition for resources are the primary factors involved in determining the distribution patterns of invasive ant species (Vepsäläinen & Pisarski 1982; Cole 1983; Hölldobler & Wilson 990; Andersen 2000; Kasapri et al. 2000; Majer et al. 2004; Ribas & Schoereder 2002).

1.3 Aims and layout of thesis

The focus of this thesis is the spatial distribution of invasive ant species. In particular, three questions emerge: 1) how the distribution of ant species is influenced by interactions between the invader(s) and the abiotic and biotic components of the recipient community, 2) can the distribution of invasive ant species be predicted using modeling techniques and 3) what are the geographic origins and diversity of invasive ant species arriving at the New Zealand border.

Emphasis is on the Pacific region which has a relatively high proportion of invasive species and where information on the native ant fauna is very limited. The research was conducted in Fiji and New Zealand, however, the research at these locations is used to address wider issues in biological invasions.

The thesis is presented as a series of self-contained chapters, but the chapters are grouped under the three questions of community interactions (chapters 2-5); distribution modeling (chapters 6-7); and the opportunity to invade (chapter 8).

Chapter Two highlights the number of invasive ant species established across the Pacific region, and specifically presents a checklist of Fijian ant fauna - an island region with little previous information in terms of invasive ants. Chapter Three examines the distribution of ant species on the Yasawa Islands, a remote island archipelago in Fiji, with emphasis on the coexistence of ant species and the influence that dominance, competition and habitat has on species composition and distribution. Chapter Four examines the ecological partitioning of ant species in canopy and litter habitats at Colo-i-Suva Park, in Fiji; studying the niche opportunities for invasive ant species. Chapter Five investigates the composition and structure of ant communities in different habitats in New Zealand. Emphasis is on the interactions between ant species and how species are spatially and temporally partitioned in the environment. Chapter Six models the potential global distribution of two invasive ant species, specifically examining the geographical transferability of models. Chapter Seven models the potential distribution of six common invasive ant species in New Zealand, with particular emphasis on analysing the utility of different methods and options for modeling. Chapter Eight examines the extent and diversity of exotic ant species arriving at the New Zealand border, with a summary of their pathways and origins. The general discussion (Chapter Nine) provides a synthesis of the above chapters.

The references, tables, figures and appendices are presented at the end of each chapter for the reader’s convenience. Modified versions of four chapters have been published, and a fifth paper has been submitted for publication.

Chapter 2: Ward DF & Wetterer JK. (2006). Checklist of the ants of Fiji (Hymenoptera: Formicidae). In: Fiji Arthropod Series 3. Edited by NL Evenhuis & DJ Bickel. Occasional Papers of the Bishop Museum 85: 23-47.

Chapter 3: Ward DF & Beggs JR. (2007). Coexistence, habitat patterns and the assembly of ant communities in the Yasawa islands, Fiji. Acta Oecologica. In Press. DOI: 10.1016/j.acto.2007.05.002.

Chapter 4: Ward DF. Submitted. Niche opportunity, habitat and invasive species in a tropical rainforest ant community. Austral Ecology.

Chapter 7: Ward DF. (2007). Modelling the potential geographic distribution of invasive ant species in New Zealand. Biological Invasions. In Press. DOI: 10.1007/s10530-006-9072-y.

Chapter 8: Ward DF, Beggs JR, Clout MN, Harris R & O'Connor S. (2006). The diversity and origin of exotic ants arriving to New Zealand via human-mediated dispersal. Diversity & Distributions 12: 601-609.

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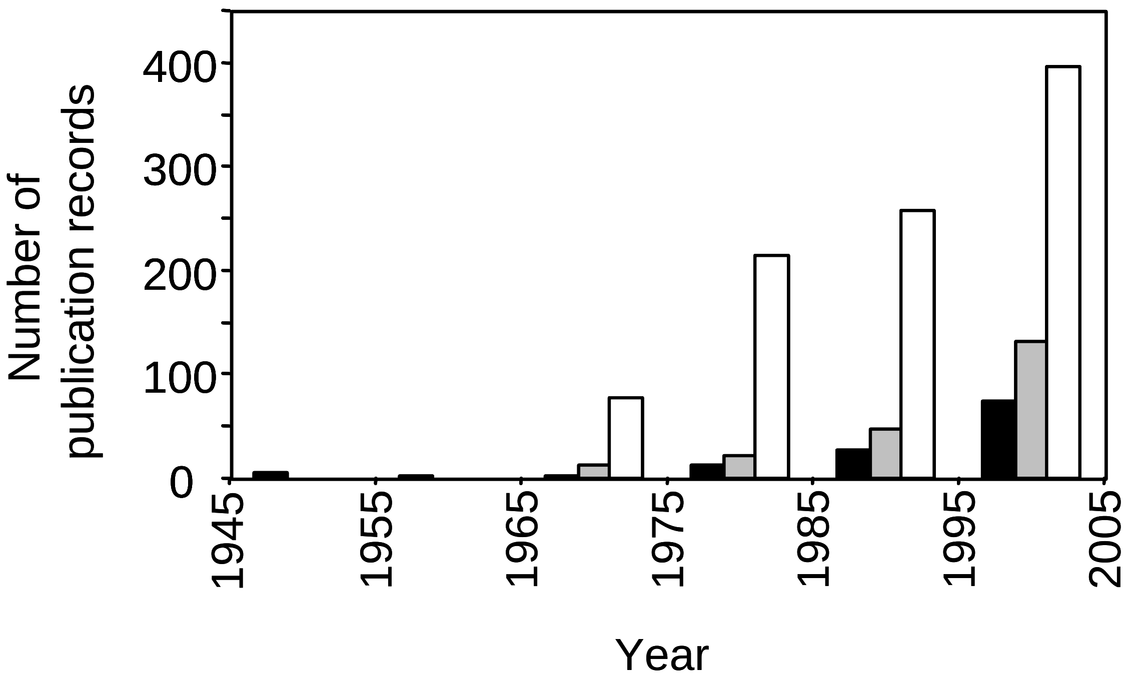

Figure 1.1 The number of publication records associated with ‘invasive’ ants per decade from 1945 to 2005. Sources of information: 1) Biological abstracts (online 1969-2005), search terms: ‘fire ant’ (n = 946, white bars) and ‘Argentine ant’ (n = 212, grey bars); 2) FORMIS (search term: ‘invasive’, n = 121, black bars). FORMIS is a composite of several ant literature databases, containing >30,000 references (http://www.ars.usda.gov/saa/cmave/ifahi/formis). Both databases accessed 18/5/2005.

Checklist of the Ants of Fiji (Hymenoptera: Formicidae) 2

Abstract

Given the relatively small size of the Pacific Island ant fauna, there has been a disproportionate amount of interest and study on the ant species of the region. Recent research has focused on the distribution and impact of invasive ant species. A total of 67 invasive ant species have become established in the Pacific region. Many of these species were present and widespread in the region as long ago as the mid-1800s and the early 1900s. There are a number of widespread invasive species; 15 species are recorded from ten or more island groups. However, the ant fauna of Fiji has received relatively little attention. An updated checklist of the ants of Fiji is presented which includes 146 currently valid species and subspecies: 99 Fijian endemics, 22 wide-ranging Pacific natives, and 25 invasive species. During a survey of Viti Levu in 2004, four invasive ant species were collected that had not previously been reported from Fiji; *Monomorium destructor, Monomorium sechellense, Platythyrea parallela* and *Tetramorium lanuginosum*. The endemic Fijian fauna appears to descend from migrants from the Papuan and Western Melanesian regions, with subsequent radiation in several genera, particularly *Camponotus, Cerapachys*, *Leptogenys*, *Lordomyrma, Pheidole*, and *Strumigenys*. The ever-increasing number of invasive ant species in Fiji, and across the broader Pacific region, has potential long-term impacts for the conservation of the region’s unique biota.

2.1 Introduction

Given the relatively small size of the Pacific Island ant fauna, there has been a disproportionate amount of interest and study in the ant species of the region. This interest appears to stem from two main sources; evolutionary study and natural history, and more recently invasive species. From the mid-1800s to the early 1900s, several authors (primarily Mayr, Emery, Forel, and Santschi) described much of the ant fauna of Oceania based on specimens accumulated from many sources. Towards the end of this period, Mann (1919, 1921) conducted major ant surveys in Fiji and the Solomon Islands. Wheeler (1935) summarized this knowledge in his checklist of the ants of Oceania.

In the 1950s and 1960s the ant fauna of the Pacific region was again the subject of attention. Wilson revised a number of tribes from the subfamily Ponerinae (Wilson 1958a, b, 1959a, b). Wilson and Taylor (1967) provided an identification guide and summary of the Polynesian fauna that remains today as the major reference and identification guide for Pacific Island ants. During this time, Pacific ants were used to study how island faunas were formed and also the dispersal, colonisation and extinction of faunas on small land masses. For example, Wilson (1959c) used the ant fauna of Melanesia to illustrate patterns of adaptive radiation, dispersal and taxon cycling. Wilson and Hunt (1967) used the ant fauna from islands in Polynesia to examine dispersal by ‘stepping-stones’ across island archipelagos.

Recently, there has been a new surge of interest in the ant fauna of the Pacific region; relating to the distribution and impact of invasive ant species (e.g. Morrison 1996a, 1996b, 1997; Wetterer 1997a, b, 1998, 2002; Collingwood & van Harten 2001; Wetterer & Vargo 2003; Lester & Tavite 2004). McGlynn (1999) has previously shown that the Pacific region has received many of the invasive ant species which have been transported around the globe by human trade activities. Much of the renewed interest has occurred primarily in Polynesia, which has a very limited native and endemic ant fauna. In Melanesia, which has a more diverse endemic ant fauna, most recent research has concerned the impact of the invasive little fire ant, *Wasmannia auropunctata*, in New Caledonia (e.g. Jourdan 1997; Jourdan et al. 2001, 2002; LeBreton et al*.* 2003, 2005).

However, the ant fauna of Fiji, a significant land mass in the Pacific region, has received relatively little attention. Fiji has been at the margins of much of the Pacific ant work, and there has not been a comprehensive overview of the Fijian ant fauna since Mann (1921). The lists of ant species from Fiji in Mann (1921) and Wheeler (1935) are now outdated as a result of numerous changes in nomenclature and descriptions of many additional species. This chapter aims to provide an overview of the invasive ant species in the Pacific region, but specifically aims to present an updated checklist to the ant species of Fiji, summarise the literature on the ant fauna of Fiji, and compile a species list of all known invasive ant species in Fiji.

2.2 Methods

2.2.1 Invasive ants in the Pacific

Species lists of invasive ants in the Pacific region were complied from published literature and personnel communications with ant researchers working in the Pacific. Key literature sources were: Wilson and Hunt (1967), Wilson and Taylor (1967), Morrison (1997), Wetterer (2002), Wetterer and Vargo (2003), Wetterer (2006), Abbott et al. (2006), and Landcare Research (2007).

2.2.2 The Islands of Fiji

Fiji lies in the central Pacific Ocean between 12-21° South and between 175° West and 177° East longitudes (Evenhuis & Bichel 2005; Figure 2.1). The Fijian archipelago consists of over 500 islands and islets, but the two main islands, Viti Levu and Vanua Levu, make up 87% of the total land area (Smith 1979; Figure 2.2). Viti Levu is also the main industrial and political area of Fiji. The islands of Fiji have been formed through volcanic activity and tectonic plate movements (Nunn 1998; Rapaport 1999). The main island of Fiji, Viti levu, is the oldest of the islands, and was once connected as part of a continuous island chain expanding to the Solomons and Papua New Guinea (Nunn 1998). The major part of Viti Levu was formed during uplifts approximately 10 million years ago, with subsequent erosion forming lowland and delta areas (Nunn 1998). In general, Fiji has a warm, humid tropical maritime climate, with mean monthly temperatures from 22°C in July to 26°C in January (Evenhuis & Bichel 2005). On the two major islands, a pronounced orographic effect of mountains produces a marked climate contrast - with diminished rainfall on the western or leeward sides and abundant rainfall on windward side (Evenhuis & Bichel 2005). Average annual rainfall on the lowland wet zone is between 3050-3450 mm while in the dry zone it is 1650-2290 mm (Evenhuis & Bichel 2005).

2.2.3 Species records from Fiji

Records of Fijian ant species were compiled from published literature, museum collections, personnel communications with invasive ant species specialists and field sampling in Fiji. The New Zealand Arthropod Collection (NZAC) was examined for Fijian ant specimens. Jim Wetterer (Atlantic University, Florida) provided records of Fijian ant species compiled from collections at the Natural History Museum in London, the Smithsonian Institute, the Museum of Comparative Zoology at Harvard University, and his own sampling from Fiji. Eli Sarnat (University of California, Davis) provided a list of new genera collected from Fiji during his current PhD research.

I collected ants in Fiji from 18 June - 30 July 2004 from throughout Viti Levu. The primary aim of this survey was to collect invasive species to confirm the species lists obtained from the literature. Hence a large proportion of the sampling was conducted in urban and industrial areas, and from around seaports, where it is likely that invasive ant species would first arrive and establish. Collections were made at 199 sites from urban and industrial areas (Suva, Tavua, Ba, Lautoka, Vuda Point, Nadi, Denerau Island, Sigatoka, Lami, and Pacific Harbour), rural areas (Navai village, Ellington wharf, Bukuya Rd-Inland Nadi, Rewa Delta, Korotogo beach, Lomolomo Guns, Momi Guns Rd., Nadarivatu, Koronivia Research Station, Rakiraki, Sigatoka Valley, Natadola beach, Vatia Point wharf, Vatukonia mine, Vaturu Dam Rd, Inland Rakiraki, Kula EcoPark), plantation forests (Galoa Mahogany forest, Lololo Pine forest, Nadarivatu forest, Colo-i-Suva Forest Park), and native forests (Mt. Korobaba, Mt. Victoria, Abaca Park, Koro'o Ridge, Vatia Point, Namosi Highland Rd. and the Sigatoka Sand Dunes).

At each site, 30 minutes was spent searching for ants, in an area of approximately 314 m^2 (10 m radius). Ants were collected with an aspirator by visually searching the ground, litter, on vegetation, tree trunks, and around buildings. Upon collection all specimens were stored in vials of 75% ethanol. At each site a GPS was used to obtain latitude/longitude and elevation readings. The online keys of Shattuck & Barnett (2001) were used for genus level identification. Species level identification was completed by examining reference specimens in the New Zealand Arthropod Collection (NZAC), and by using the following publications: Mann (1921), Wilson and Taylor (1967), *Cardiocondyla* (Seifert 2003), *Strumigenys* (Bolton 2000; Dlussky 1994a), *Hypoponera*: (Wilson 1958b). Taxonomic nomenclature follows Bolton (1995a). Specimens are held at the NZAC, with representatives of some species pinned and all other material kept in ethanol. Representatives of all invasive, and some native species, were sent for verification at the National Plant Pest Reference Laboratory (NPPRL) at the Ministry of Agriculture and Forestry (MAF), Auckland.

2.3 Results and Discussion

2.3.1 Invasive ants in the Pacific

A total of 67 invasive ant species have become established in the Pacific region (Appendix 2.1). Many of these species were present and widespread in the region as long ago as the mid-1800s (Mayr 1866, 1870), and the early 1900s (Mann 1921, Wheeler 1935). There are also a number of widespread species, for example, 15 species are recorded from ten or more island groups. It is likely that for some Pacific islands there is an absence of survey information. For example, there is less literature and information from islands in the western Pacific region, particularly islands from Micronesia, Vanuatu and the Solomons, than from Polynesia. Additional surveys in these areas would result in an increase in both the number of invasive species present and the distribution of known invasives.

Apart from the invasive species listed in Appendix 2.1, both Hawaii and New Zealand have additional invasive species. These species are native to the Pacific region. For example, Hawaii, has no endemic or native ant species, so all ant species recorded there are regarded as being invasive. The Hawaiian ant fauna consists of species that are invasive to the Pacific (listed in Appendix 2.1), but also a number of other species (n = 6) which are native to other parts of the Pacific region (see http://www.hawaiiantgroup.org). New Zealand has very few endemic ant species. The twenty-six invasive species listed in Appendix 2.1 for New Zealand are primarily from Australia (see Chapter Five). However, one additional ant species not recorded in Appendix 2.1, *Amblyopone australis*. This species is invasive in New Zealand but is native elsewhere in the Pacific (e.g. New Caledonia and the Solomon Islands).

2.3.2 The ant species of Fiji

Records were found for 146 species and subspecies from Fiji (Appendix 2.2). Overall, 99 taxa (68%) are Fijian endemics (restricted to Fiji only), 22 taxa (15%) are native, and 25 taxa (17%) are invasive. The endemic and native taxa are represented by 37 genera and eight subfamilies (Table 2.1).

From the literature, 21 invasive ant species had already been recorded from Fiji. During the 2004 survey, 14 of these species (67%) were collected. However, an additional four invasive ant species, which had not previously been reported from Fiji, were also collected during the survey: *Monomorium destructor, Monomorium sechellense, Platythyrea parallela* and *Tetramorium lanuginosum*. Thus, a total of 25 invasive species from 14 genera are now recorded from Fiji (Appendix 2.1, 2.2). Invasive species are predominantly from Myrmicinae (14 spp., 56%), with less representation from other subfamilies; Formicinae (5 spp., 20%), Ponerinae (5 spp., 20%) and Dolichoderinae (1 spp., 4%). Four invasive genera have no native or endemic relatives from Fiji. During the survey, the most frequently collected species were *Tapinoma melanocephalum* (at 43.2% of sites), *Paratrechina vaga* (31.7%), *Paratrechina longicornis* (22.6%), *Anoplolepis gracilipes* (19.1%), and *Solenopsis geminata* (18.6%). Many of the invasive species in Fiji are also widely distributed throughout the Pacific

(Appendix 2.1, 2.2). In particular, there is a high degree of overlap between the invasive ant species in Fiji and those in Samoa (88%), French Polynesia (84%) and Tonga (80%).

2.3.3 Biogeographical origins and diversification of Fijian endemic species

Wilson (1959c) extensively summarised the biogeographical origins and dispersal patterns of Ponerine ants throughout Melanesia. Based on Wilson's interpretations, Papua New Guinea is seen as the centre of origin for the native Fijian ant fauna. This is in concordance with other arthropod taxa (Evenhuis & Bickel 2005). Ancient stocks of ants dispersed into Papua New Guinea from the Oriental region and to a lesser extent from Australia, and then some stocks dispersed from Papua New Guinea outward into Melanesia in a unidirectional flow. Wilson (1959c) describes this as a classic 'filter-effect' with islands closest to Papua New Guinea receiving a higher proportion of dispersing stocks, with a diminishing effect outward across Melanesia and ultimately to Fiji.

Bolton (1995b) provides a taxonomic and zoogeographical census of the ant taxa, from which this filter-effect can be illustrated. Of the approximately 126 genera in the Indo-Australian region, only 33 (26%) have naturally reached Fiji. Of particular note is the absence of army ants from Fiji, including Aenictinae, Dorylinae and Leptanillinae. Wheeler (1935) comments on the lack of army ants in Oceania and suggests that their absence is because army ants have large-bodied queens, and they need workers to assist the queen in establishing a new colony. Such characteristics are not favourable for long distance dispersal across oceans. However, Fiji is also missing several genera (*Crematogaster*, *Pseudolasius*, *Myopias*, and *Myrmoteras*) found in the Indo-Australian region that are very species-rich (Bolton 1995b). Interestingly, *Polyrhachis rotumana*, the only representative of this very diverse genus in the Indo-Australian region, is found on the island of Rotuma, to the far north of the main Fijian islands, but appears not to be present on the main Fijian islands.

Although few stocks dispersed outwards from Papua New Guinea, there has been subsequent radiation in Fiji, particularly within several genera: *Camponotus* (Formicinae); *Cerapachys* (Cerapachyinae); *Leptogenys* (Ponerinae); and *Pheidole*, *Strumigenys* and *Lordomyrma* (Myrmicinae) (Mann 1921; Wheeler 1935). The Myrmicinae fauna contributes >40% of the native and endemic fauna, with *Strumigenys* (14 species) and *Pheidole* (10 species) the most diverse. These two genera also make a significant contribution to the diversity in the Indo-Australian region. For example, Fiji has 29% of all described species of *Strumigenys*, and 10% of all described species of *Pheidole* in the Indo-Australian region (data in Bolton 1995b). Additionally there are ten endemic species of *Lordomyrma* in Fiji, of only 20 described species in the genus worldwide (Bolton 1995b).

Wilson (1958a) considered the extensive radiation within the genus *Leptogenys* as remarkable for such a small land mass. He suggests that this radiation is possibly due to less competitive pressure from the relatively depauperate endemic ponerine-myrmicine fauna in Fiji. There are five genera, and only 15 native or endemic species of Ponerinae in Fiji - although the number of species is likely to increase with further intensive sampling of forest litter. Fiji also has a particularly diverse fauna of

Cerapachyinae, represented by seven species in the genus *Cerapachys* (Wilson 1959b). The diversity of both *Leptogenys* and *Cerapachys* may perhaps be attributed to the lack of army ants in Fiji. Both *Leptogenys* and *Cerapachys* show the army ant behaviour of group raiding and are predators of other ants, albeit less sophisticated than true army ants (Hölldobler & Wilson 1990; Fisher 1997). Fisher (1997) has recently suggested the absence of army ants in Madagascar has spurred the diversification of Cerapachyinae.

Another reason for the success of *Cerapachys* in Fiji could be related to their ability to nest in plant cavities, this has been suggested to greatly assist in the ‘rafting’ of colonies across ocean currents (Wheeler 1935; Fisher 1997). The inclination to nest in plant cavities may have also contributed to the diversity of *Camponotus* in Fiji. *Camponotus* is the most species rich genus in Fiji and contributes 25 of 29 (86%) species of the native and endemic Formicinae. Fiji also has 16% of all described species of *Camponotus* in the Indo-Australian region (data in Bolton 1995b).

2.3.4 Published records

Mayr (1866, 1870) produced the first publications that recorded ant species from Fiji, all from the island of Ovalau, at that time the capital and a major trading port. Mann (1921) was the first major publication of ant species for Fiji. Mann collected ants in Fiji for ten months in 1915–1916, and in several publications (Mann 1920, 1921, 1925) reported 96 ant taxa including subspecies and varieties, most of them new descriptions (Table 2.1). Mann (1921) also described the only endemic genus, *Poecilomyrma*.

Since Mann, a number of authors have recorded additional species from Fiji. Stitz (1925) described *Odontomachus politus* Stitz (= *O. angulatus*) from Fiji. Santschi (1928) reported on ants collected in Fiji's Lau group by EH Bryan in 1924, describing two new taxa, *Tetramorium scrobiferum liogaster* (= *Romblonella scrobifera liogaster*) and *Camponotus bryani*, and listing in 22 other forms, many of which have been subsequently synonymised.

Wheeler (1934) described three new *Camponotus, Camponotus dentatus humeralis* Wheeler, *C. manni* Wheeler and *C. manni umbratilis* Wheeler, based on material originally collected, but overlooked, by Mann in 1915-1916. Wheeler's (1935) checklist of Oceania included all previously reported ant taxa from Fiji except *C. polynesicus* and *L. tortuosa stoneri*, omitted apparently by mistake. Wheeler (1935) also listed *Pheidole oceanica nigriscapa* Santschi (= *Pheidole fervens* F. Smith) from Viti Levu. Smith (1953) described a new endemic species, *Romblonella vitiensis* M. Smith from Wakaya Island, in the Ovalau group based on specimens collected by Bryan in 1924.

In his revisions of the ant fauna from Melanesia, Wilson (1958) raised *Ponera biroi rugosa* Mann to full species status as *Ponera eutrepta* (= *Hypoponera eutrepta*), and also listed *P. colaensis*, *H. monticola*, *H. turaga*, and *H. vitiensis* in Fiji. Wilson (1959b) described *Cerapachys lindrothi* and

Cerapachys zimmermani from Fiji, and also listed *C. crypta* (= *C. cryptus*), *C. fuscior*, *C. majuscula*, *C. sculpturata*, and *C. vitiensis*.

Wilson and Taylor (1967) described three new species from Fiji: *Camponotus rotumanus*, *Polyrhachis rotumana*, and *Strumigenys mailei*. Wilson and Taylor (1967) also published the first records from Fiji of *Oligomyrmex atomus* (collected by Taylor in 1962) and *Tapinoma minutum*. Wilson and Taylor (1967) wrote that they had seen the first records of *Iridomyrmex anceps* (Roger) from Fiji, collected in 1956, though Mann (1921) reported *I. anceps ignobilis.* Wilson and Taylor (1967) synonymized *T. guineense* (= *T. bicarinatum*) with *T. guineense macra* (= *T. insolens*), though they are now considered separate species. Finally, Wilson and Taylor (1967) mentioned in passing a number of ant species in Fiji: *A. longipes* (= *A. gracilipes*), *C. bryani, C. chloroticus, C. dentatus*, *P. vaga, P. fervens*, *P. oceanica, P. umbonata*, *P. aluaudi, Trichoscapa membranifera* (= *P. membranifera*), *R. sublevinodis*, and *S. papuana*. *T. pacificum*, and *P. megacephala*.

Wilson and Hunt (1967), in the first checklist since Mann (1921), listed 88 ant species from Fiji, including the earliest published record of *Hypoponera punctatissima*. Wilson and Hunt (1967) omitted all subspecific designations used by earlier authors, truncating the subspecific designation of *R. scrobifera liogastefor* to *Romblonella scrobifera* and *Ponera biroi rugosa* (= *H*. *eutrepta*) to *Ponera rugosa* (= *Diacamma rugosum*). Wilson and Hunt (1967) listed *L. tortuosa stoneri* as *L. stoneri* (as did Dlussky 1994b, but not Bolton 1995a). Wilson and Hunt (1967) did not include *C. rotumanus* and *P. rotumana* in their checklist, presumably considering Rotuma as separate from Fiji. Finally, Wilson and Hunt (1967) omitted *C. lauënsis*, *T. insolens*, and *C. fuscior*, taxa which Wilson and Taylor (1967) had raised to full species.

Taylor (1967) described *Ponera manni* from Fiji based on specimens he collected in 1962, and also listed *P. colaensis*. Bolton (1977) listed Fijian records for *T. insolens*, *T. bicarinatum*, *T. simillimum*, *T. pacificum*, *Tetramorium tenuicrinis,* and *T. tonganum*. Bolton (1987) listed Fijian records for *M. floricole* and *M. pharoanis*. Taylor (1980a) described *Eurhopalothrix insidiatrix* from Fiji based on Mann specimens and also listed *E. emeryi*. Taylor (1980b) briefly reports on collections of *Myrmecina cacabau* from forest litter at Nadarivatu.

Dlussky (1994a) listed several dacetine ant species from Fiji: *T. membranifera* (= *P. membranifera*), *S. godeffroyi*, *S. mailei*, *S. jepsoni*, *S. nidifex*, *S. scelestus (= S. scelesta), S. wheeleri (= S. tumida*), and described *Strumigenys chernovi*. Dlussky (1994b) listed 93 ant species from Fiji based published records as well as specimens of 20 species collected by YI Chernov in 1977 and 12 species collected by G. M. Dlussky in 1980. The Chernov specimens included the first Fijian records of six species: *Cardiocondyla emeryi*, *Hypoponera opaciceps*, *Paratrechina chernovi*, *Paratrechina minutula*, *Strumigenys ursulus*, and *Vollenhovia denticulata*. Like Wilson and Hunt (1967), Dlussky (1994b) omitted all subspecific designations, thus listing *R. scrobifera* instead of *R. scrobifera liogaster* and omitting *T. insolens.* Dlussky (1994b) also omitted *Ca. bryani, Ca. dentatus, Ce. fuscior,* and *E. emeryi*, apparently by mistake.

Recently, Waterhouse (1997) noted the presence of the invasive tropical fire ant, *Solenopsis geminata*. Bolton (2000) included 16 dacetine species from Fiji: *Strumigenys basiliska*, *S. chernovi*, *Strumigenys daithma*, *Strumigenys ekasura*, *Strumigenys frivola*, *S. jepsoni*, *S. nidifex*, *Strumigenys panaulax*, *Strumigenys praefecta*, *S. scelesta*, *Strumigenys sulcata*, *S. tumida*, *S. godeffroyi*, *S. mailei*, *Strumigenys rogeri*, *Pyramica membranifera* and *P. trauma*. Finally, Baroni Urbani & de Andrade (2003) described *Proceratium oceanicum* from Viti Levu.

Surveys in the mid-1990s by Wetterer (*pers. comm.*) discovered a previously unrecorded invasive species, *Cardiocondyla obscurior*. Sarnat (2006) has recently revised the genus *Lordomyrma*, describing four new endemic species. Furthermore, with extensive litter sampling across the major islands of Fiji, he has also collected specimens of four genera previously unrecorded from Fiji (*Acropyga*, *Carebara*, *Discothyrea*, *Prionopelta*) (Sarnat *pers. comm.*). All of these new additions are very small, cryptic species which are typically collected in forest leaf litter.

There are several additional ant species with erroneous records from Fiji. Nishida and Evenhuis (2000) noted the presence of the highly invasive *Wasmannia auropunctata* from Fiji, but this was an error, and should have referred to its presence in Vanuatu. *Tetramorium guineense*, of African origin, has often been recorded from the Pacific (Wilson & Taylor 1967) but these records consist of a mix of the invasive *T. bicarinatum* and the Pacific native *T. insolens* (Wetterer & Vargo 2003). Mann (1921) listed *Prenolepis* (=*Paratrechina*) *vividula*, but Wilson and Taylor (1967) found these specimens were *Paratrechina vaga*. Wilson and Hunt (1967) list *Romblonella scrobiferum* from Fiji, but this was most likely meant to represent the subspecies *R. scrobifera liogaster* described by Santschi (1928) as *Tetramorium scrobifera liogaster*. Wetterer and Vargo (2003) list *Rogeria stigmatica* from Fiji on the basis of notes from Wilson and Taylor (1967). However, Wilson and Taylor (1967) actually refer to *R. stigmatica sublevinodis* (= *R. sublevinodis*), and state it is widespread in Fiji. There is one record of the Argentine ant, *Linepithema humile*, being intercepted at the New Zealand border in a shipment from Fiji (Ward, *unpub. data*), but there is no additional evidence that it has become established.

Two species (*Paratrechina chernovi*, *Strumigenys ursulus*) from Dlussky (1994b) are omitted because there are no published descriptions, and appear to be ‘manuscript names’. Dlussky (1994b) synonymized five Fijian endemic species with other taxa with broader distributions: *H. eutrepta* = *Hypoponera opaciceps*, *H. vitiensis* = *Hypoponera confinis*, *M. vitiense* = *Monomorium talpa, P. oceanica* = *Paratrechina minutula*, and *P. vitiensis* = *P. vaga*. Although all these synonymies are plausible, they are tentative because it appears that no specimens were actually examined by Dlussky.

2.3.5 Conclusions

Although collections have been made on several major islands over a >100 year period, knowledge of the Fijian ant diversity, distribution and ecology is still largely rudimentary. Of particular interest for native biodiversity studies in Fiji are the numerous unsurveyed islands, and also the highland forests of Viti Levu, Vanua Levu, and Taveuni, as they represent some of the last remaining near-pristine forests of Fiji. Intensive sampling of litter habitats in these forests has recently revealed many new taxa, including four genera not previously recorded from Fiji (Sarnat, *pers. comm*.).

Surveys across more islands in Fiji (and the Pacific) will also serve to highlight the extent of the distribution of invasive ants. Fortunately, several highly invasive species still have a limited distribution, or are not established in the Pacific. The Argentine ant, *Linepithema humile*, appears unsuited to the tropical environment and is only present in the cooler temperate regions of New Zealand, Easter Island and at high elevations in Hawaii (Wetterer 1998). The little fire ant, *Wasmannia auropunctata*, has a relatively limited distribution in the Pacific, but has recently been recorded in several new island archipelagos (Vanuatu, Jourdan et al. 2002; Hawaii and French Polynesia, O'Connor, *pers. comm*.). Fortunately, the red imported fire ant, *Solenopsis invicta*, appears not to have established in the Pacific.

However, a number of invasive ant species are already present and widespread in the Pacific region. Invasive ant species are likely to have long-term detrimental impacts for the conservation of biodiversity in this region (Jourdan 1997; Wetterer 1997b; Nishida & Evenhuis 2000; Lester & Tavite 2004). A greater understanding of invasive ant species is required, including their ability to spread from island to island, their potential distribution, coexistence and interactions with native ant species, and their impacts on native biodiversity in the Pacific.

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Table 2.1 The taxonomic composition of endemic and native species in Fiji.

Subfamily	**Genera**	**Species/subspecies**	**% of species total**
Myrmicinae	18	56	46.3
Formicinae	4	30	24.8
Ponerinae	5	15	12.4
Dolichoderinae	5	8	6.6
Cerapachyinae	1	7	5.8
Proceratiinae	2	3	2.5
Ectatomminae	1	1	0.8
Amblyoponinae	1	1	0.8
Total	37	121	

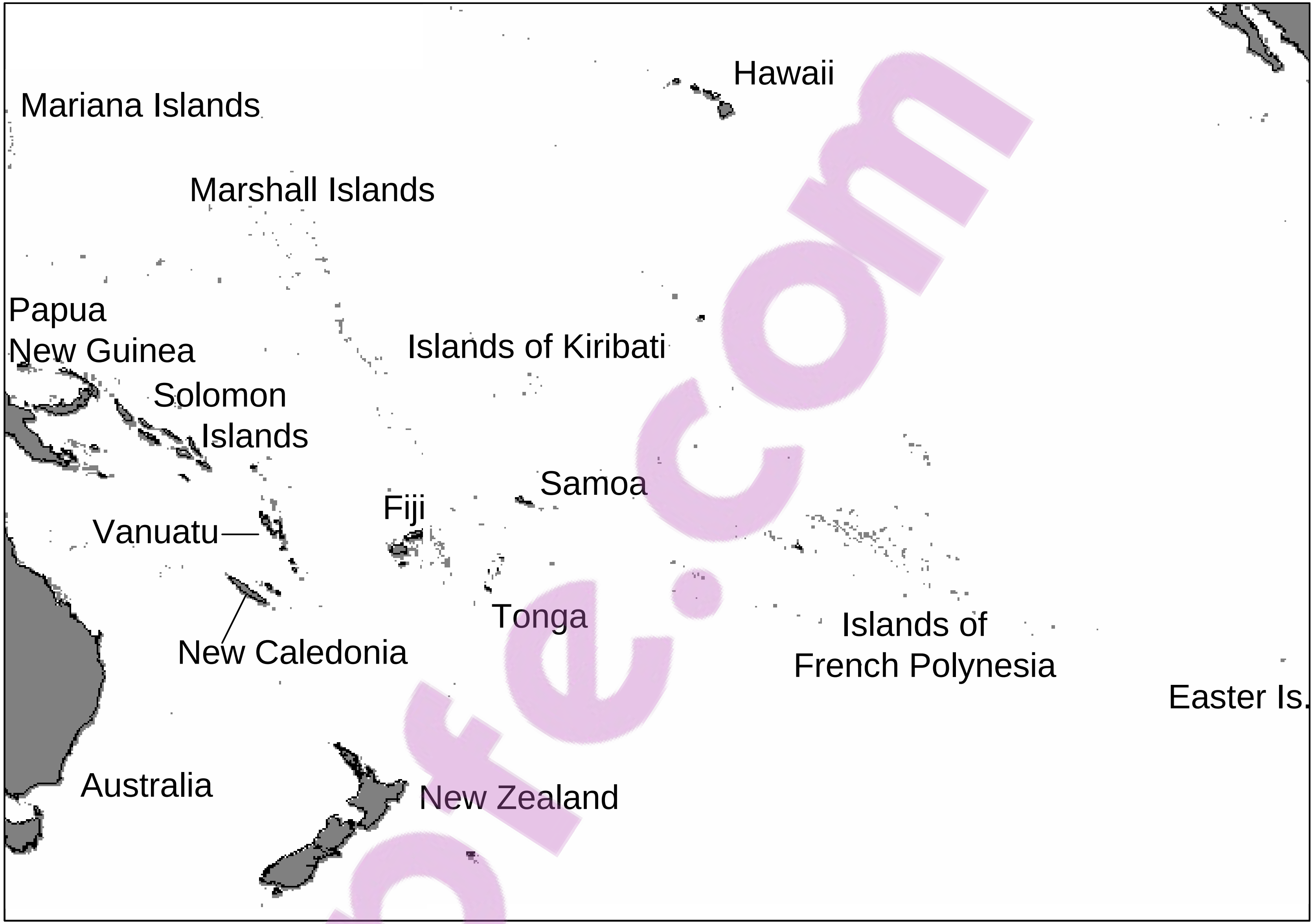

Figure 2.1 Major land masses and island chains in the Pacific region.

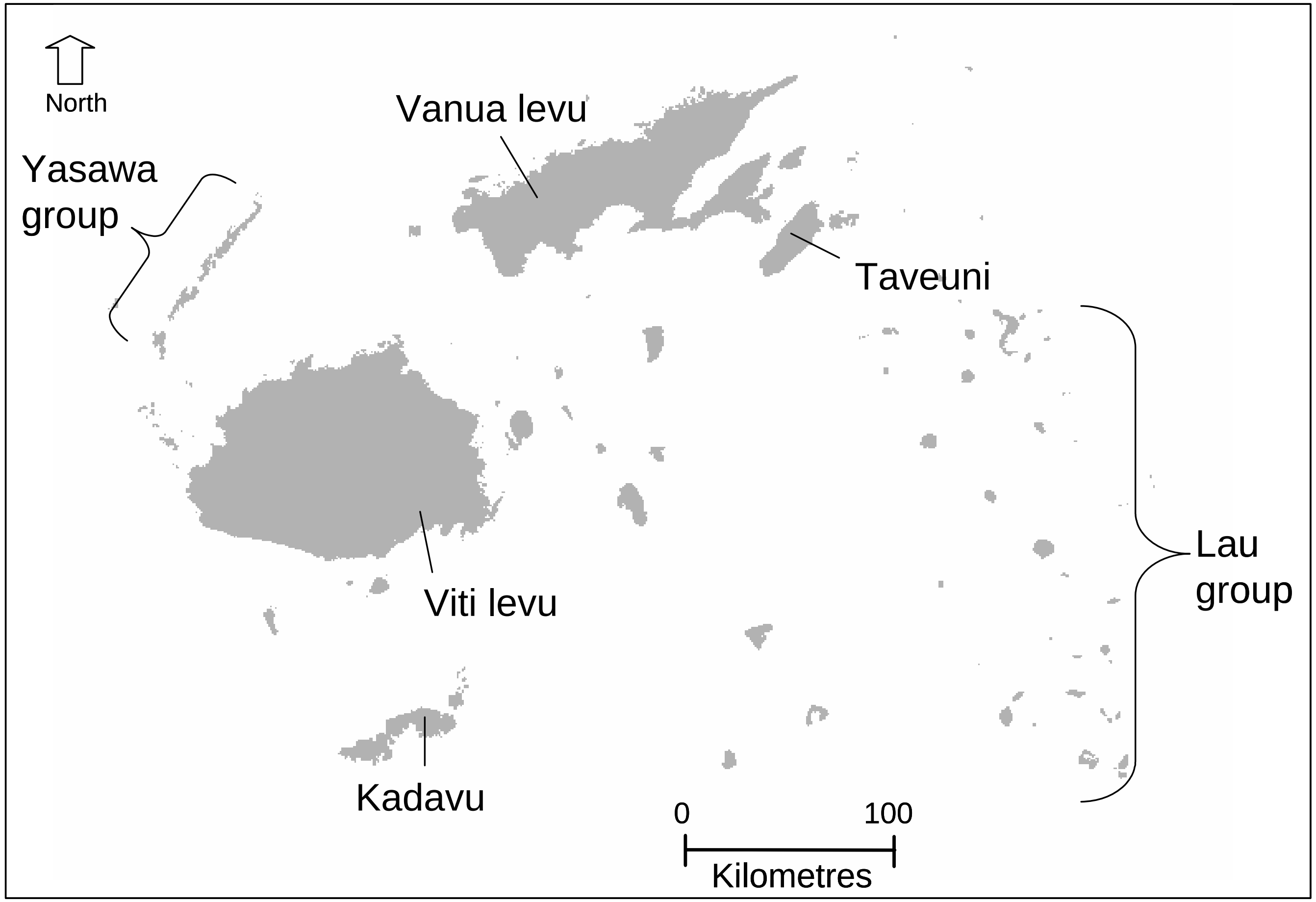

Figure 2.2 The major islands of Fiji.

Appendix 2.1 Checklist of invasive ant species recorded from the Pacific region (1 = presence). The table is sorted from left to right in decreasing order of the number of species. Only species which are invasive to the Pacific region are listed. Therefore, some islands have additional ant species, such as New Zealand and Hawaii where species native or endemic to the Pacific region are also established.

Invasive Species	**Hawaii**	**New Zealand**	**French Polynesia**	**Samoa's**	**Fiji**	**Mariana**	**Tonga**	**Cook**	**Solomon**	**FSM**	**New Caledonia**	**Niue**	**Wallis & Futuna**	**Kiribati**	**Vanuatu**	**Tokelau**	**Marshall**	**Pitcairn**	**Tuvalu**	**Easter**	**Palau**	**Number**
Amblyopone zwaluwenburgi	1																					**1**
Anoplolepis gracilipes	1		1	1	1	1	1	1	1	1	1	1	1	1	1	1	1		1		1	**18**
Brachymyrmex obscurior	1			1																		**2**
Camponotus variegatus	1																					**1**
Cardiocondyla emeryi	1		1	1	1	1	1	1				1	1					1				**10**
Cardiocondyla minutior		1																				**1**
Cardiocondyla obscurior				1	1	1																**3**
Cardiocondyla venustula	1																					**1**
Cardiocondyla wroughtonii	1		1			1		1										1				**5**
Cerapachys biroi	1			1		1																**3**
Doleromyrma darwiniana		1																				**1**
Hypoponera gleadowi					1						1				1							**3**
Hypoponera opaciceps	1		1	1	1		1	1			1											**7**
Hypoponera punctatissima	1	1	1	1	1	1	1		1	1	1	1	1		1					1		**14**
Hypoponera zwaluwenburgi	1																					**1**
Hypoponera eduardi		1						1														**2**
Hypoponera elliptica											1											**1**
Iridomyrmex spA		1																				**1**

Appendix 2.1 continued.

Invasive Species	**Hawaii**	**New Zealand**	**French Polynesia**	**Samoa's**	**Fiji**	**Mariana**	**Tonga**	**Cook**	**Solomon**	**FSM**	**New Caledonia**	**Niue**	**Wallis & Futuna**	**Kiribati**	**Vanuatu**	**Tokelau**	**Marshall**	**Pitcairn**	**Tuvalu**	**Easter**	**Palau**	**Number**
Lepisiota sp.	1																					**1**
Leptogenys falcigera	1							1						1								**3**
Linepithema humile	1	1																		1		**3**
Mayriella abstinens		1																				**1**
Monomorium antipodum (fieldi)		1																				**1**
Monomorium destructor	1		1	1	1	1		1	1			1		1			1					**10**
Monomorium floricole	1		1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1			1	**18**
Monomorium pharaonis	1	1	1	1	1	1	1		1	1				1	1	1	1				1	**14**
Monomorium sechellense	1			1	1	1	1	1		1												**7**
Monomorium sydneyense		1																				**1**
Monomorium chinense						1																**1**
Monomorium monomorium	1		1	1																		**3**
Ochetellus glaber	1	1																				**2**
Orectognathus antennatus		1																				**1**
Pachycondyla stigma				1	1				1	1												**4**
Paratrechina bourbonica	1		1	1	1	1	1	1	1	1	1	1	1	1		1	1	1	1	1		**18**
Paratrechina longicornis	1		1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1		**19**
Paratrechina spA		1																				**1**
Paratrechina spB		1																				**1**
Paratrechina vaga	1		1	1	1	1	1	1	1	1	1	1	1	1		1		1	1			**16**
Paratrechina vividula									1													**1**
Pheidole fervens	1		1	1	1	1	1	1		1	1					1		1				**11**
Pheidole megacephala	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1				1	**18**
Pheidole proxima		1																				**1**
Pheidole rugosula		1																				**1**

Appendix 2.1 continued.

Invasive Species	**Hawaii**	**New Zealand**	**French Polynesia**	**Samoa's**	**Fiji**	**Mariana**	**Tonga**	**Cook**	**Solomon**	**FSM**	**New Caledonia**	**Niue**	**Wallis & Futuna**	**Kiribati**	**Vanuatu**	**Tokelau**	**Marshall**	**Pitcairn**	**Tuvalu**	**Easter**	**Palau**	**Number**
Pheidole vigilans		1																				**1**
Plagiolepis alluaudi	1		1		1		1	1			1	1								1		**8**
Platythyrea parallela			1		1																	**2**
Ponera leae		1																				**1**
Ponera swezeyi	1																					**1**
Pseudomyrmex gracilis	1																					**1**
Pyramica membranifera	1		1	1	1	1	1		1	1			1						1			**10**
Rhytidoponera chalybaea		1																				**1**
Rhytidoponera chalybaea		1																				**1**
Solenopsis geminata	1		1	1	1	1	1	1	1	1	1			1	1		1		1			**14**
Solenopsis sp.		1																				**1**
Strumigenys xenos		1																				**1**
Strumigenys emmae	1		1	1		1	1		1						1							**7**
Strumigenys lewisi	1											1										**2**
Strumigenys perplexa		1																				**1**
Strumigenys rogeri	1		1	1	1	1	1		1	1	1	1	1		1							**12**
Tapinoma melanocephalum	1		1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1			1	**18**
Tetramorium bicarinatum	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	**21**
Tetramorium caldarium			1																			**1**
Tetramorium grassii		1																				**1**
Tetramorium lanuginosum			1	1	1	1	1	1	1	1			1	1		1					1	**12**
Tetramorium simillimum	1		1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1		**19**
Tetramorium smithi												1										**1**
Wasmannia auropunctata	1		1								1		1		1							**5**
Number of Species (n = 67)	37	26	26	26	25	24	21	20	19	18	18	16	15	14	14	12	11	10	8	7	7	

Appendix 2.2 Checklist of ant taxa recorded from Fiji. Biostatus: E = Endemic, N = Native, I = Invasive. Frequency refers to the incidence that invasive species were collected during the 2004 survey (199 sites), NC = not collected.

Subfamily – Genus – Species	Authority	Biostatus	Frequency
Amblyoponinae			
Prionopelta sp.	Eli Sarnat *pers. comm.*	E	
Cerapachyinae			
Cerapachys cryptus	Mann 1921: 408	E	
Cerapachys fuscior	Mann 1921: 410	E	
Cerapachys lindrothi	Wilson 1959b: 52	E	
Cerapachys majusculus	Mann 1921: 408	E	
Cerapachys sculpturatus	Mann 1921: 407	E	
Cerapachys vitiensis	Mann 1921: 406	E	
Cerapachys zimmermani	Wilson 1959b: 54	E	
Dolichoderinae			
Iridomyrmex anceps	(Roger) 1863: 164	N	
Iridomyrmex anceps ignobilis	Mann 1921: 472	E	
Ochetellus sororis	(Mann) 1921: 469	E	
Philidris nagasau	(Mann) 1921: 470	E	
Philidris nagasau agnata	(Mann) 1921: 472	E	
Philidris nagasau alticola	(Mann) 1921: 472	E	
Tapinoma melanocephalum	(Fabricius) 1793: 353	I	0.432
Tapinoma minutum	Mayr 1862: 703	N	
Technomyrmex albipes	(F. Smith) 1861: 38	N	
Ectatomminae			
Gnamptogenys aterrima	(Mann) 1921: 411	E	
Formicinae			
Acropyga sp.	Eli Sarnat *pers. comm.*	E	
Anoplolepis gracilipes	(F. Smith) 1857: 55	I	0.191
Camponotus bryani	Santschi 1928: 72	E	
Camponotus chloroticus	Emery 1897: 574	N	
Camponotus cristatus	Mayr 1866: 489	E	
Camponotus cristatus nagasau	Mann 1921: 482	E	
Camponotus cristatus sadinus	Mann 1921: 482	E	
Camponotus dentatus	(Mayr) 1866: 492	E	
Camponotus dentatus humeralis	Wheeler 1934: 416	E	
Camponotus janussus	Bolton 1995a: 106	E	
Camponotus laminatus	Mayr 1866: 489	E	
Camponotus laminatus levuanus	Mann 1921: 479	E	
Camponotus lauensis	Mann 1921: 488	E	
Camponotus maafui	Mann 1921: 482	E	
Camponotus manni	Wheeler 1934: 418	E	
Camponotus manni umbratilis	Wheeler 1934: 420	E	
Camponotus maudella	Mann 1921: 496	E	
Camponotus maudella seemanni	Mann 1921: 498	E	
Camponotus oceanicus	(Mayr) 1870: 943	E	
Camponotus polynesicus	Emery 1896: 374	E	
Camponotus rotumanus	Wilson & Taylor 1967: 98	E	
Camponotus rufifrons	(F. Smith) 1860: 95	N	
Camponotus schmeltzi	Mayr 1866: 490	E	
Camponotus schmeltzi kadi	Mann 1921: 485	E	
Camponotus schmeltzi loloma	Mann 1921: 486	E	
Camponotus schmeltzi trotteri	Mann 1921: 486	E	

Appendix 2.2 continued.

Subfamily – Genus – Species	**Authority**	**Biostatus**	**Frequency**
Camponotus vitiensis	Mann 1921: 490	E	
Paratrechina bourbonica	(Forel) 1886: 210	I	0.025
Paratrechina longicornis	(Latreille) 1802: 11	I	0.226
Paratrechina minutula	(Forel) 1901: 25	N	
Paratrechina oceanica	(Mann) 1921: 476	E	
Paratrechina vaga	(Forel) 1901: 26	I	0.317
Paratrechina vitiensis	(Mann) 1921: 474	E	
Plagiolepis alluaudi	Emery 1894: 71	I	NC
Polyrhachis rotumana	Wilson & Taylor 1967: 99	E	
Myrmicinae			
Adelomyrmex hirsutus	Mann 1921: 458	N	
Cardiocondyla emeryi	Forel 1881: 5	I	0.106
Cardiocondyla nuda	(Mayr) 1866: 508	N	
Cardiocondyla obscurior	Wheeler 1929: 44	I	NC
Carebara sp.	Eli Sarnat *pers. comm.*	E	
Eurhopalothrix emeryi	(Forel) 1912: 58	E	
Eurhopalothrix insidiatrix	Taylor 1980a: 238	E	
Lordomyrma curvata	Sarnat 2006: 15	E	
Lordomyrma desupra	Sarnat 2006: 17	E	
Lordomyrma levifrons	(Mann) 1921: 453	E	
Lordomyrma polita	(Mann) 1921: 453	E	
Lordomyrma rugosa	(Mann) 1921: 455	E	
Lordomyrma stoneri	(Mann) 1925: 5	E	
Lordomyrma striatella	(Mann) 1921: 454	E	
Lordomyrma sukuna	Sarnat 2006: 29	E	
Lordomyrma tortuosa	(Mann) 1921: 452	E	
Lordomyrma vuda	Sarnat 2006: 34	E	
Monomorium destructor	(Jerdon) 1851: 105	I	0.015
Monomorium floricole	(Jerdon) 1851: 107	I	0.010
Monomorium pharaonis	(Linnaeus) 1758: 580	I	0.015
Monomorium sechellense	Emery 1894: 69	I	0.010
Monomorium vitiense	Mann 1921: 444	E	
Myrmecina cacabau	(Mann) 1921: 449	E	
Oligomyrmex atomus	Emery 1900: 328	N	
Pheidole caldwelli	Mann 1921: 434	E	
Pheidole colaensis	Mann 1921: 441	E	
Pheidole fervens	Smith 1858: 176	I	0.146
Pheidole knowlesi	Mann 1921: 436	E	
Pheidole knowlesi extensa	Mann 1921: 438	E	
Pheidole megacephala	(Fabricius) 1793: 361	I	0.131
Pheidole oceanica	Mayr 1866: 510	N	
Pheidole onifera	Mann 1921: 427	E	
Pheidole roosevelti	Mann 1921: 438	E	
Pheidole umbonata	Mayr 1870: 978	N	
Pheidole vatu	Mann 1921: 431	E	
Pheidole wilsoni	Mann 1921: 433	E	
Poecilomyrma s. myrmecodiae	Mann 1921: 448	E	
Poecilomyrma senirewae	Mann 1921: 446	E	
Pristomyrmex mandibularis	Mann 1921: 444	E	
Pyramica membranifera	(Emery) 1869: 24	I	NC
Pyramica trauma	Bolton 2000: 408	E	
Rogeria sublevinodis	Emery 1914: 415	N	
Romblonella scrobifera liogaster	(Santschi) 1928: 69	E	
Romblonella vitiensis	Smith 1953: 79	E	

Appendix 2.2 continued.

Subfamily – Genus – Species	Authority	Biostatus	Frequency
Solenopsis geminata	(Fabricius) 1804: 423	I	0.186
Solenopsis papuana	Emery 1900: 330	N	
Strumigenys basiliska	Bolton 2000: 750	E	
Strumigenys chernovi	Dlussky 1994a: 57	E	
Strumigenys daithma	Bolton 2000: 756	E	
Strumigenys ekasura	Bolton 2000: 807	E	
Strumigenys frivola	Bolton 2000: 817	E	
Strumigenys godeffroyi	Mayr 1866: 516	N	
Strumigenys jepsoni	Mann 1921: 462	E	
Strumigenys mailei	Wilson & Taylor 1967: 38	N	
Strumigenys nidifex	Mann 1921: 464	E	
Strumigenys panaulax	Bolton 2000: 811	E	
Strumigenys praefecta	Bolton 2000: 826	E	
Strumigenys rogeri	Emery 1890: 68	I	0.010
Strumigenys scelesta	Mann 1921: 463	E	
Strumigenys sulcata	Bolton 2000: 828	E	
Strumigenys tumida	(Bolton) 2000: 830	E	
Tetramorium bicarinatum	(Nylander) 1846: 1061	I	0.166
Tetramorium insolens	(F. Smith) 1861: 47	N	
Tetramorium lanuginosum	Mayr 1870: 976	I	0.015
Tetramorium manni	Bolton 1985: 247	E	
Tetramorium pacificum	Mayr 1870: 976	N	
Tetramorium simillimum	(F. Smith) 1851: 118	I	0.116
Tetramorium tenuicrine	(Emery) 1914: 416	N	
Tetramorium tonganum	Mayr 1870: 976	N	
Vollenhovia denticulata	Emery 1914: 405	N	
Ponerinae			
Anochetus graeffei	Mayr 1870: 961	N	
Hypoponera eutrepta	(Wilson) 1958: 344	E	
Hypoponera gleadowi	Emery 1895: 60	I	NC
Hypoponera monticola	(Mann) 1921: 418	E	
Hypoponera opaciceps	(Mayr) 1887: 536	I	NC
Hypoponera punctatissima	(Roger) 1859: 246	I	NC
Hypoponera turaga	(Mann) 1921: 416	E	
Hypoponera vitiensis	(Mann) 1921: 414	E	
Leptogenys foveopunctata	Mann 1921: 421	E	
Leptogenys fugax	Mann 1921: 422	E	
Leptogenys humiliata	Mann 1921: 421	E	
Leptogenys letilae	Mann 1921: 419	E	
Leptogenys navua	Mann 1921: 423	E	
Leptogenys vitiensis	Mann 1921: 424	E	
Odontomachus angulatus	Mayr 1866: 500	E	
Odontomachus simillimus	Smith 1858: 80	N	
Pachycondyla stigma	(Fabricius) 1804: 400	I	NC
Platythyrea parallela	(F. Smith) 1859: 143	I	0.015
Ponera colaensis	Mann 1921: 417	E	
Ponera manni	Taylor 1967: 86	E	
Proceratiinae			
Discothyrea	Eli Sarnat *pers. comm.*	E	
Proceratium oceanicum	de Andrade 2003: 310	E	
Proceratium relictum	Mann 1921: 413	E	

Coexistence, Habitat Patterns and the Assembly of Ant Communities in the Yasawa islands, Fiji

3

Abstract

Community assembly rules are important to help understand the dynamics of biological invasions. The coexistence of native and invasive ant species were examined by litter sampling on six remote islands within the Yasawa archipelago, Fiji, in the Pacific Ocean. The composition of ant assemblages on the islands and also of three different habitats across islands was very similar to each other. Estimates of species richness indicated that the sampling effort had generally captured a large proportion of ant species (60-97%). Analysis at two different spatial scales (regional [islands within an archipelago], and local [plots within an islandl]) and on two null model data sets (co-occurrence and body size), showed the majority (10 of 12) of assemblages were not different from randomly assembled communities. Habitat type played an important role in the co-occurrence patterns. Scrub and coconut habitats, which are non-native habitats and frequently disturbed, strongly influenced the assembly of the ant community. However, two invasive species, *Pheidole megacephala* and *Anoplolepis gracilipes* may have also shaped the ant communities through inter-specific competition. These two species excel at both the discovery and domination of resources, and could have 'disassembled' the native ant fauna. Recent surveys and ecological studies from other Pacific islands show that the set of invasive species in the Yasawa islands is ubiquitous throughout the region. Thus, the patterns of competition, co-occurrence and community organisation that exist in the Yasawa islands could be manifested throughout the Pacific region.

3.1 Introduction

One of the fundamental questions in community ecology is whether assembly rules determine the order of species establishment and the structure of natural communities (Diamond 1975; Gotelli & McCabe 2002). Assembly rules assume that inter-specific competition is greatest between species that are most similar in morphology and function (and thus resource use), and as a consequence, patterns of species co-occurrence are manifested (MacArthur & Levins 1967; Diamond 1975; Gotelli & Ellison 2002). Gotelli and Ellison (2002) state that competing species should co-occur less often than expected by chance between a set of communities, and within a community species that do co-occur should differ substantially in body size or morphology – so that overlap in resource utilisation is reduced. Thus, there is a limit to the similarity of species that can coexist in a community (MacArthur & Levins 1967; Szabó & Meszéna 2006).

Assembly rules are also important to the study of biological invasions, in particular, whether certain rules govern the ability of invasive species to establish and spread within a native community. Inter-specific competition and limited similarity between species may influence the ability of new species to invade a native community. Resident species are expected to strongly compete with and resist the establishment of invading species that have similar resource requirements (Fargione et al. 2003). However, the strong link between community ecology theory and invasion biology has only recently become apparent (Lodge 1993; Shea & Chesson 2002; Fargione et al. 2003). Studies on invasive species in native communities have the potential to examine fundamental questions of community ecology through the interactions of species (Lodge 1993).

Inter-specific competition is considered to be the major structuring force of ant (Hymenoptera: Formicidae) communities (Wilson 1971; Andersen 1992; Morrison 1996; Davidson 1998; Holway 1999; Gotelli & Ellison 2002). Although abiotic factors, habitat requirements, and dispersal abilities are among several factors that can interact to shape ant communities (Cole 1983; Savolainen & Vepsäläinen 1989; Morrison, 1996), inter-specific competition is thought to play the major role at local spatial scales. Inter-specific competition results in dominance hierarchies being formed through inter-specific aggression, competitive exclusion at food resources and distinctive foraging strategies for either accessing resources or avoiding dominant species (Wilson 1971; Fellers 1987; Savolainen & Vepsäläinen 1989; Andersen 1992; Davidson 1998; Holway 1999). In particular, dominant species can control the spatial occurrence of other species, thus structuring the ant community and creating mosaic-like patterns of species co-occurrence (Room 1975; Savolainen & Vepsäläinen 1989). Body size could also facilitate coexistence in tropical ant communities via differential use of habitats and can also influence competitive interactions.

The factors shaping ant communities are numerous, and many have been well studied, but there have been relatively few studies examining the role of invasive ant species on community structure (Holway et al. 2002). To date, these studies have focused on the invasion of a native community by a single invasive ant species, principally the Argentine ant *Linepithema humile*, or the red-imported fire ant *Solenopsis invicta* (Holway et al. 2002). The interactions and coexistence between multiple invasive ant species within the context of a native ant community have seldom been examined. Morrison (1996) examined the competitive interactions among numerous invasive ant species on several remote Pacific islands, but these islands had no native ant species. More recently, von Aesch and Cherix (2005) have examined the native and invasive ant fauna on Floreana Island (Galápagos) and the competitive mechanisms leading to the establishment of invasive species. However, they did not specifically examine, or test patterns of coexistence within and between ant assemblages.

In this chapter the distribution of ant species on an island archipelago from Fiji, in the Pacific region is investigated. I examine how dominance and competition affect the coexistence of ant species at both local and regional scales. In particular, I examine the influence of habitat and the presence of invasive species on the structure of the native ant community.

3.2 Methods

3.2.1 The Yasawa Islands

Fiji lies in the central Pacific Ocean between 12-21° South and between 175° West and 177° East longitudes (Evenhuis & Bichel 2005; Figure 3.1). The Fijian archipelago consists of over 500 islands and islets, with the two main islands, Viti Levu and Vanua Levu, making up 87% of the total land area (Smith 1979). The Yasawa island group is approximately 40 km northwest of Viti Levu (Figure 3.1). The island group is a 90 km long chain of ancient volcanic islands and consists of 11 main islands. The Yasawa Islands (and Fiji in general) has a warm, humid tropical maritime climate, with mean monthly temperatures from 22° C in July to 26° C in January (Evenhuis & Bichel 2005). The average annual rainfall in the Yasawa islands is approximately 1650-2290 mm, with most of that falling in the wet season from November to April (Evenhuis & Bichel 2005). Overall the islands are sparsely populated, (estimated <5000 total), with permanent human settlements on most of the larger islands. There are no roads or motorised vehicles on the islands, and the largest-scale infrastructure is restricted to backpacker resorts. Almost all movement of people and goods to and from the Yasawa islands is via sea transportation from the city of Nadi on the main island of Viti Levu. Movement between islands is via small outboard boats (<20 people).

3.2.2 Sampling

Sampling took place on six islands in the Yasawa group (Kuata, Waya, Naviti, Matacawalevu, Tavewa, and Nanuya lailai) from the 5th-16th September 2005. Islands were chosen because they represented differing degrees of size (area) and isolation from the mainland. Two days were spent on each island, moving south-north using a tourist catamaran that serviced the Yasawa group daily. Local walking tracks and topographical maps (scale 1:50000, Fiji map series 31, edition 1 and 2, produced by the Lands and Survey Department, Suva) were used to navigate around each island.

Three major habitats were sampled on the Yasawa islands; deciduous coastal dry forest, scrub and coconut groves. Deciduous coastal dry forest is the natural forest cover on the Yasawa islands (Watling 2005). Canopy species include *Gyrocarpus americanus* Jacq. (Hernandiaceae), *Pongamia pinnata* (L.) Pierre (Fabaceae), *Pleiogynium timoriense* (DC.) Leenh (Anacardiaceae), and a common understorey species was *Mallotus tiliifolius* (Blume) (Euphorbiaceae) (Smith 1981, 1985; Watling 2005). The second habitat (scrub) was largely a monoculture of *Leucaena leucocephala* (Lam.) (Fabaceae). This is an invasive species in Fiji, and is considered invasive on many Pacific islands as it replaces indigenous vegetation. The third habitat sampled was coconut groves, *Cocos nucifera* L. (Arecaceae). Coconuts were once a major economic crop of Fiji for the copra industry (Smith 1979). However, coconuts are no longer widely cultivated and many plantations have been abandoned, including those on the Yasawa islands.

To sample ants a 0.5 x 0.5 m quadrat was placed on the ground and litter within the quadrat was scooped into a white tray (30 x 40 x 10 cm). Litter was sifted through a 1 x 1 cm wire mesh to exclude larger debris. Sticks and rotten wood within the quadrat were broken apart into the tray. Not all the litter from the quadrat could be placed into the tray at once; 1-4 trays were needed. However, a standardised time of 15 minutes was spent searching through the litter of each quadrat. An aspirator was used to collect ants and transfer them to a single vial of 75% ethanol. Ants were collected from 30 quadrats on each island. Quadrats were placed haphazardly on the ground and spaced at least 15 m apart, and at least 50 m off walking trails. While on each island, ant species were collected opportunistically by visually searching the ground, litter, foliage, tree trunks, and inside hostels. However, these opportunistically collected species were not included in statistical analyses. It was not possible to use other sampling techniques such as pitfall traps or Winkler bags due to time and luggage constraints on each island.

Not all islands had the same habitat types, but habitats were deliberately sampled in an approximate proportion to their occurrence on each island. The islands and the number of litter quadrats sampled from each habitat (F = forest, S = scrub, C = coconut) were: Kuata (F = 20 , S = 10, C = 0), Waya (F = 23, S = 7, C = 0), Naviti (F = 17, S = 13, C = 0), Matacawalevu (F = 0, S = 10, C = 19), Tavewa (F = 10, S = 0, C = 20), and Nanuya lailai (F = 10, S = 0, C = 20).

3.2.3 Food baiting experiment

To determine which ant species were numerically and behaviourally dominant, tuna baits were used to attract ants. A grid was setup that consisted of 24 bait stations placed 5 m apart in a 6 x 4 rectangular array. At each station approximately 2 g of tuna (Sealord™ chunky style tuna in spring water) was directly placed on a white plastic index card (7 cm x 7 cm), on top of the leaf litter. The index card was used to assist in the identification and counting of ants. Stations were examined in a fixed routine, at 12, 24, 36, 48, and 60 minutes after the bait was placed out. Each station was examined for 20 seconds. The number of ants present on the index card of each species was recorded, along with any behavioural interactions, defined as aggression, avoidance and coexistence as described by Human and Gordon (1999). Abundance at baits was scored as: 1 = < 5 ants, 2 = 5 - 9, 3 = 10 - 19, 4 = 20 - 50, 5 = > 50. Sampling took place between 10 am and 4 pm. The identification of most ant species could not be determined in the field. Several specimens were collected from baits with an aspirator for later identification, with care taken not to displace other ants from the bait. Baiting grids were setup in four habitats; forest (2 grids: Waya x2), scrub (3 grids: Kuata x2, Matacawalevu), coconut (2 grids: Matacawalevu, Tavewa), and grassland (grass < 0.5 m tall, used for stock grazing, 5 grids: Kuata, Waya, Naviti, Tavewa x2).

3.2.4 Specimen curation

Knowledge of the ant fauna of Fiji is rudimentary, and many islands remain unexplored for ants, including the Yasawa island group (Ward & Wetterer 2006). There is no single publication to identify the ant species of Fiji. Shattuck and Barnett (2001) was used for generic identifications, and species-level identification was completed by examining reference specimens in the New Zealand Arthropod Collection (NZAC), and by using the following publications: Mann (1921), Wilson and Taylor (1967), for *Cardiocondyla* (Seifert 2003), *Tetramorium* (Bolton 1977, 1979), *Strumigenys* (Bolton 2000; Dlussky 1994), *Hypoponera* (Wilson 1958), and *Monomorium* (Heterick, 2001). Ward and Wetterer (2006) was used to categorise species as invasive, native or endemic. Taxonomic nomenclature and subfamily classification follows Bolton (2003) and generic classification from Bolton (1995). All specimens are held at the NZAC.

3.2.5 Statistical analyses

Faunal composition

The number and frequency of each ant species collected was determined for each island and habitat from litter quadrats. Estimates of species richness and accumulation for each island and habitat were made using ESTIMATES v7.0 software (Colwell 2005). Rarefaction curves were plotted using observed species richness and the estimated number of ant species was calculated using the Chao 2 estimator of species richness (Colwell 2005). The default parameters in ESTIMATES were used, with 50 runs. The efficiency of litter sampling was evaluated using the number of observed species divided by the Chao 2 estimate of species richness. The Shannon Diversity index (H`) and Simpson’s index of evenness (1/D) were also calculated using ESTIMATES. The composition of ant species from different habitats and islands was examined using non-metric multidimensional scaling in PRIMER v5.0 software, using a Bray-Curtis similarity matrix on presence-absence data from 50 runs (Clarke & Warwick 2005). Pairwise tests of islands and habitats were examined using Analysis of Similarities (ANOSIM) with 999 permutations.

Coexistence in litter communities

Co-occurrence of species was examined using EcoSim software (Gotelli & Entsminger 2005). At the regional scale, a presence-absence matrix was constructed with each row representing a different species, and each column representing an island. Regional analyses consisted of three separate matrices, one for each habitat type (forest, scrub, and coconut), in order to separate the effect of habitat.

At the local scale, a presence-absence matrix was constructed for each habitat type on each island. Each row of the data matrix represents a different species, and each column represents a different quadrat. Thus, 12 presence-absence matrices were constructed for analysis at the local scale, 5 matrices from forest, 4 matrices from scrub and 3 matrices from coconut. The C-score was used as a metric to quantify the pattern of co-occurrence. The observed C-score was compared to a histogram of simulated indices from 5000 randomly constructed communities. A fixed-fixed model setting (default) was used, where the row and column sums of the original matrix are preserved. Thus each random community generated by EcoSim contains the same number of species, and the same frequency of each species as the original community (Gotelli & Entsminger 2005). For an assemblage that is competitively structured, species will co-occur less than expected (i.e. segregation), and the observed C-score should be significantly larger than expected by chance.

At the local scale, a meta-analysis of effect sizes for co-occurrence patterns was used to determine the overall co-occurrence pattern for each habitat. The meta-analysis followed Gotelli and Ellison (2002), where the standardised effect size (SES) for the set of assemblages does not differ from zero. SES is generated in EcoSim, where SES = $(I_{obs} - I_{sim})/s_{sim}$ where I_{sim} is the mean index of the simulated communities, s_{sim} is the standard deviation, and I_{obs} is the observed index. Communities with little co-occurrence should frequently reject the null hypothesis in the upper tail, and the meta-analysis pattern would show an average effect size significantly greater than zero.

Head width was used as an index of body size, a widely used measure of size in ants (see Hölldobler & Wilson 1990). Measurements were made on ten specimens of each species where possible. Only the minor caste of polymorphic taxa were used (e.g. *Pheidole*). Measurements were made of mounted specimens, using an ocular micrometer calibrated with a stage micrometer to an accuracy of 0.1 mm. Body size overlap of coexisting species within a community was examined using EcoSim (size overlap module) at the two spatial scales as described above in the co-occurrence section. At the local scale, a meta-analysis of effect sizes for variance in body size was used to determine the overall pattern for each local site as described in the co-occurrence section.

At both regional and local scales the EcoSim module orders head width from the smallest to the largest measurement, calculates the difference in size between two consecutive species (segments), and from these segments a variance in segment length (σ^2) is used as an index of constancy in body size ratio. We used the uniform body distribution option in EcoSim, where the endpoints of the body size distribution are fixed by the largest and smallest species in the assemblage. The remaining species are randomly chosen from a log uniform distribution. Observed values are compared to a null model generated from 1000 randomly constructed communities. The hypothesis was that a competitively structured community should contain species that have a constant variance in body size ratios between species compared to a randomly assembled community. If coexisting species differ from one another by a constant size ratio, then the segments would be identical in length and $\sigma^2 = 0$. More heterogeneity in the size ratios of adjacent species means that the σ^2 will be larger. A competitively structured community should contain species that generate significantly smaller σ^2 compared to a randomly assembled community.

The numerical and behavioural dominance of different species were assessed using criteria from Andersen (1992) and Davidson (1998). Numerical dominance was measured as those species that; 1) occur at a high proportion of baits; 2) dominated baits (defined as the proportion of abundance score of $\geq$4); and 3) that have a high average abundance score (average of abundance scores at only those baits at which they occurred). Interference competition was measured by 1) aggressive behaviour (defined as the number of times a species "attacked" or "was avoided" as a proportion of the total interactions), and 2) the ability to monopolise baits (i.e. being the only species present on baits at the end of the 60 minute baiting period). The time taken by a species to discover bait (proportion of occurrence at baits at 12 minutes) was also examined as a measure of exploitative competition.

3.3 Results

3.3.1 Faunal composition

Litter quadrats yielded 27 species, 17 species were native (including six endemic to Fiji), and ten were invasive (Table 3.1). Three additional species were opportunistically collected that were not present in the litter quadrats; two invasive species, *Tetramorium bicarinatum* (Nylander) (Waya, Matacawalevu), and *Paratrechina longicornis* (Latreille) (Waya, Tavewa) and the native *Iridomyrmex anceps* (Roger) (Naviti, Tavewa, Nanuya lailai).

Three of the four species found on all six islands were invasive (Table 3.1). A further ten species (a mix of invasive and native) were found on four or more islands. Six species were only detected on one island (Table 3.1). In general, Chao 2 estimates of species richness showed that sampling was highly successful in capturing ant species in the litter (Table 3.2). Species diversity was the lowest on the three islands that were numerically dominated by a single species (low 1/D ratio) (Table 3.2): Tavewa, which was dominated by *Pheidole megacephala*; and Naviti and Kuata, which were dominated by *Anoplolepis gracilipes*.

Pairwise comparisons from ANOSIM showed that overall the ant composition of islands were very similar (Table 3.3). The differences (defined as $R > 0.5$, Clarke & Warwick 2005) that existed between islands in the composition of ant species are largely attributable to the frequency of two species, *P. megacephala* and *A. gracilipes*. For example, *P. megacephala* was widespread and abundant in the coconut plantations of Tavewa, but were absent from this habitat on Matacawalevu and Nanuya lailai. *Anoplolepis gracilipes* was very common in forest on Naviti and Kuata, but was recorded only once in forest on Tavewa.

Although forest habitat had more species than other habitats, sampling efficiency for forest habitat was lower than other habitats (Table 3.2), indicating that other species are present in the litter, but were not detected using the litter quadrats. The coconut habitat had the lowest species diversity, and was numerically dominated either by *Tapinoma minutum* or *Pheidole megacephala*. Pairwise comparisons also showed that the ant composition in different habitats (across all islands) was barely separable (defined as $R < 0.25$, Clarke & Warwick 2005); forest-scrub, $R = 0.135$; forest-coconut, $R = 0.252$; and scrub-coconut, $R = 0.217$.

3.3.2 Coexistence in litter communities

At the regional scale, observed C-scores were not significantly different from expected C-scores generated by null models for forest, scrub or coconut ant assemblages (forest, observed index [I_{obs}] =

0.775, mean of simulated indices [I_{sim}] = 0.789, p = 0.71; scrub, I_{obs} = 0.583, I_{sim} = 0.565, p = 0.23; coconut, I_{obs} = 0.373, I_{sim} = 0.374, p = 0.51). These results indicate that at the regional level assemblages were not different from random expectation. At the local scale, ant communities were also randomly assembled (Table 3.4). However, there was some evidence (but not statistical significance) of segregation for forest ant communities (as the average effect size was greater than zero), and aggregation in scrub ant communities (the average effect size was less than zero).

Body size measurements, at the regional scale, were not significantly different from random communities generated by null models for scrub or coconut ant assemblages (scrub, I_{obs} = 0.00111, I_{sim} = 0.00131, p = 0.46; coconut, I_{obs} = 0.00564, I_{sim} = 0.00327, p = 0.91). These results indicate that there was no constant ratio of body size between adjacent species. However, for forest ant assemblages, there was a greater heterogeneity in size ratios than expected by null models, and thus body size in forest ant assemblages was significantly aggregated (forest, observed index [I_{obs}] = 0.00445, mean of simulated indices [I_{sim}] = 0.00198, p = 0.03). At the local scale, body size analysis mirrored the regional pattern, with forest ant communities significantly aggregated, as the average effect size (SES) was greater than zero (p = 0.004, Table 3.5). Body sizes in ant communities from scrub and coconut were randomly assembled (Table 3.5).

Eleven species were recorded during the baiting experiment (Table 3.6). Overall there was significantly more avoidance behaviour at baits than attack or coexistence behaviour (Chi-square = 21.71, d.f. = 2, p < 0.001). Species that showed high proportions of aggressive behaviour were *A. gracilipes, I. anceps* and *T. melanocephalum*. No behavioural interactions were observed for *P. megacephala* because it seldom occurred at baits with other species. The four species above also showed a high level of ability to monopolise baits (Table 3.6). There was a positive correlation (ρ = 0.165) between species ranked by discovery and dominance (interference) abilities (Figure 3.2).

3.4 Discussion

This is the first survey of ants from the Yasawa islands of Fiji, where a total of 27 species were collected from six islands. Estimates of species richness indicated that the sampling effort had captured a large proportion (60-97%) of the ant species present in leaf litter. Compared to scrub and coconut habitats, sampling was less effective in forest habitats, indicating that further species remain to be detected. There were no differences in the composition of ant assemblages between the three different habitats sampled. This was surprising, given that habitat often plays a significant role in shaping ant communities (Morrison 1996; Hoffmann et al. 1999).

Despite two different types of null model analyses (co-occurrence and body size) and analysis at two different spatial scales, there is little evidence to support the hypothesis that ant assemblages in the

Yasawa islands are competitively structured. Both local and regional models generally showed that ant communities in different habitats were randomly assembled.

However, there is evidence to show habitat plays an important role in the assembly of these ant communities. At the local scale co-occurrence patterns were considerably different between habitats. Local forest communities were the only assemblages to show a segregation pattern – consistent with assumptions regarding assembly rules and inter-specific competition. In scrub and coconut habitats, there were random or aggregated species co-occurrence patterns. Both scrub and coconut habitats consist of vegetation which is not native to these islands. Furthermore, both these habitats are also subject to frequent disturbance through human activities (e.g. stock grazing, fire wood collecting), much more than the forest habitat. Therefore, it is possible that disturbance has acted to influence the assembly of the ant fauna in scrub and coconut habitats. Gotelli and Ellison (2002) also found evidence that habitat type influenced the assembly of native ant assemblages of New England, USA. They suggested that harsh environments (habitats) were the primary filter for assembly rules, restricting potential colonists and thus altering co-occurrence patterns (Gotelli & Ellison 2002).

However, we also suggest an additional explanation for these patterns of species co-occurrence, based on two recent studies on invasive ants. Gotelli and Arnett (2000), and Sanders et al. (2003) have both recently shown that invasive ant species have the ability to ‘disassemble’ native ant faunas through inter-specific competition; causing random or aggregated patterns of species occurrence.

It is well known that invasive species often have a strong negative impact on native ant species by exploiting similar resources and by interference competition (Human & Gordon 1999; Holway et al. 2002). Thus, I suggest that in the Yasawa islands the native ant fauna could have been disassembled by invasive species, primarily *A. gracilipes* and *P. megacephala*. These two species were primarily responsible for differences in species composition between islands and both species also excel at exploiting and monopolising resources. Additionally, the baiting experiment provides evidence that both *A. gracilipes* and *P. megacephala* break a fundamental trade-off pattern. This trade-off represents an evolutionary balance between exploitative and interference competition that promotes coexistence in ant communities (Davidson 1998). In the Yasawa islands there was a positive correlation with the trade-off between dominance and discovery. This positive correlation indicates *A. gracilipes* and *P. megacephala* excel at both the discovery and the dominance of resources, and thus, strongly influence the ant community by monopolising resources through inter-specific competition. However, in native ant communities a negative correlation should be evident (Davidson 1998; Holway 1999).

3.4.1 Conclusions

Habitat appears to act as a strong filter for the assembly of ant communities in the Yasawa islands. Habitat type strongly influenced patterns of species coexistence. Although we have not fully teased apart the effects of invasive ant species and habitat, given the results of Gotelli and Arnett (2000), and

Sanders et al. (2003), it seems possible that invasive ant species in the Yasawa islands could have also disassembled the native ant community. Recent surveys and ecological studies from other Pacific islands show that a very similar set of invasive species are ubiquitous throughout the region (Morrison 1996; Wetterer 2002; Abbott et al. 2006; Ward & Wetterer 2006). Thus, patterns of competition, co-occurrence and community organisation that exist in the Yasawa islands could be manifested throughout the Pacific region.

3.5 References

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Table 3.1 The frequency of species collected from the Yasawa Islands; from each habitat type and from all litter quadrats. Numbers in parentheses are the number of litter quadrats. # Islands refers to the number of islands where a species was found.

Species	**Forest (80)**	**Scrub (40)**	**Coconut (59)**	**All (179)**	**# Islands**
Endemic					
Hypoponera eutrepta (Wilson)	0.038			0.017	2
Hypoponera monticola (Mann)		0.050		0.011	1
Ochetellus sororis (Mann)		0.050		0.011	1
Pheidole cf *wilsoni* Mann	0.050		0.017	0.028	3
Strumigenys chernovi Dlussky	0.013			0.006	1
Tetramorium manni Bolton	0.050	0.025	0.017	0.034	3
Native					
Anochetus graeffi Mayr	0.300	0.225	0.136	0.229	5
Cardiocondyla nuda (Mayr)	0.063	0.175	0.153	0.117	5
Odontomachus simillimus Smith	0.213		0.220	0.168	5
Oligomyrmex atomus Emery	0.050	0.050	0.017	0.039	4
Paratrechina minutula (Forel)	0.438	0.025	0.085	0.229	4
Pheidole oceanica Mayr	0.013	0.100		0.028	2
Pheidole umbonata Mayr	0.150		0.068	0.089	5
Rogeria sublevinodis Emery	0.013		0.017	0.011	2
Tapinoma minutum Mayr	0.288	0.600	0.390	0.391	6
Technomyrmex albipes (F. Smith)	0.013			0.006	1
Tetramorium tonganum Mayr	0.275	0.075		0.140	5
Invasive					
Anoplolepis gracilipes (F. Smith)	0.538	0.775	0.068	0.436	6
Cardiocondyla emeryi Forel	0.013			0.006	1
Monomorium fieldi Forel	0.063	0.025	0.034	0.045	4
Monomorium sechellense Emery	0.213	0.100	0.153	0.168	6
Paratrechina vaga (Forel)	0.363		0.186	0.223	5
Pheidole megacephala (Fabricius)			0.356	0.117	2
Strumigenys rogeri Emery		0.025		0.006	1
Tapinoma melanocephalum (Fabricius)	0.175		0.085	0.106	4
Tetramorium lanuginosum Mayr	0.038	0.050		0.028	3
Tetramorium simillimum (Smith)	0.250	0.275	0.169	0.229	6
Number of species	23	16	17	27	

Table 3.2 Estimates of species richness and sampling efficacy for different islands and habitats from litter quadrats. A higher Shannon Diversity (H`) and Simpson (1/D) index means the community is more diverse.

	Number of Species						
Island/habitat	**Observed**	**Chao 2 estimate**	**Sampling efficacy %**	**Singletons**	**Doubletons**	**H`**	**1/D**
Kuata	16	18.9	84.6	4	1	2.32	8.09
Waya	19	22.2	85.5	5	2	2.58	11.49
Naviti	14	15.5	90.6	3	1	2.16	6.90
Matacawalevu	19	31.2	60.8	7	2	2.48	9.75
Tavewa	11	11.3	97.2	2	2	2.02	5.96
Nanuya lailai	13	15.9	81.8	3	0	2.37	11.43
All	27	27.9	96.7	4	2	2.75	12.77
Forest	23	32.9	70.0	5	0	2.26	12.28
Scrub	16	17.2	93.2	4	4	2.55	11.37
Coconut	17	20.9	81.3	4	1	2.18	6.53

Table 3.3 Pairwise comparisons between islands (R test statistic) of faunal composition for all habitats and within each habitat. Stress (two-dimensional) is a measure of goodness-of-fit (Clarke and Warwick 2005). R values give an absolute measure of the separation of pairwise comparisons on a scale from -1 to 1; well separated > 0.75, clearly different > 0.5, and barely separable < 0.25 (Clarke and Warwick 2005). R values of > 0.5 are highlighted in bold.

Pairwise comparison	**All**	**Forest**	**Scrub**	**Coconut**
Stress	0.13	0.20	0.14	0.08
Kuata, Waya	.434	.446	**.696**	
Kuata, Naviti	.378	.435	.397	
Kuata, Matacawalevu	.292		.030	
Kuata, Tavewa	**.626**	**.614**		
Kuata, Nanuya lailai	.245	.237		
Waya, Naviti	.292	.372	.044	
Waya, Matacawalevu	.219		.383	
Waya, Tavewa	.438	.381		
Waya, Nanuya lailai	.060	.450		
Naviti, Matacawalevu	.064		.141	
Naviti, Tavewa	**.607**	**.794**		
Naviti, Nanuya lailai	.228	.455		
Matacawalevu, Tavewa	**.504**			**.845**
Matacawalevu, Nanuya lailai	.150			.299
Tavewa, Nanuya lailai	.253	.342		**.661**

Table 3.4 Meta-analysis of effect sizes for co-occurrence patterns at the local scale for each habitat. Numbers in the lower and upper tails indicate the number of assemblages for which the C-score was respectively less than or greater than predicted by the null model. The number in parentheses indicates the number of assemblages with significant patterns ($p<0.05$, one-tailed test). A one-sample t-test was used to test the hypothesis that the standardized effect size (SES) for the set of assemblages does not differ from zero. See methods for description of meta-analysis. Communities with little co-occurrence should frequently reject the null hypothesis in the upper tail, and the meta-analysis pattern would be an effect size significantly greater than zero (^{NS} non significant, significance is at $p = 0.05/3 = 0.016$).

Habitat	**Lower tail**	**Upper tail**	**Average effect size**	**SD effect size**	**t**	**p**
Forest	1 (0)	4 (2)	1.22	1.36	2.00	0.058 ^{NS}
Scrub	4 (0)	0 (0)	-0.78	0.52	3.01	0.028 ^{NS}
Coconut	1 (0)	2 (0)	0.43	1.03	0.73	0.271 ^{NS}

Table 3.5 Meta-analysis of effect sizes for body size overlap patterns at the local scale. Data organised as in Table 3.4. Communities with constant body size ratios should frequently reject the null hypothesis in the lower tail, and the meta-analysis pattern would be an effect size significantly less than zero (^{NS} non significant, * significance at $p = 0.05/3 = 0.016$).

Habitat	**Lower tail**	**Upper tail**	**Average effect size**	**SD effect size**	**t**	**p**
Forest	0 (0)	5 (0)	0.685	0.318	4.82	0.004*
Scrub	3 (0)	1 (0)	-0.080	0.404	0.39	0.360 ^{NS}
Coconut	1 (0)	2 (1)	0.884	1.331	1.15	0.185 ^{NS}

Table 3.6 Dominance measures of species for the food baiting experiment. See methods for definitions of each dominance measure. Species are sorted in decreasing order of monopoly. No behavioural interactions were observed for *Pheidole megacephala*.

	Numerical Dominance			**Interference competition**		**Exploitative competition**
Species (+ species code)	**Mean occurrence**	**Baits dominated**	**Mean abundance score**	**Behavioural Dominance**	**Monopoly**	**Discovery**
Anoplolepis gracilipes (Ag)	0.84	0.20	2.29	0.59	0.94	0.81
Pheidole megacephala (Pm)	0.96	0.95	4.82	NA	0.90	0.87
Tapinoma melanocephalum (Tme)	0.27	0.31	2.54	0.80	0.75	0.23
Iridomyrmex anceps (Ia)	0.52	0.62	3.32	0.70	0.68	0.60
Paratrechina minutula (Pmi)	0.63	0.20	2.20	0.22	0.33	0.33
Monomorium fieldi (Mf)	0.23	0.30	2.73	0.35	0.18	0.46
Tetramorium simillimum (Ts)	0.07	0.00	1.00	0.00	0.00	0.60
Paratrechina vaga (Pv)	0.28	0.11	1.96	0.26	0.00	0.56
Cardiocondyla nuda (Cn)	0.26	0.00	1.06	0.15	0.00	0.55
Tetramorium lanuginosum (Tl)	0.10	0.00	1.00	0.00	0.00	0.25
Tapinoma minutum (Tmi)	0.24	0.00	1.25	0.00	0.00	0.24

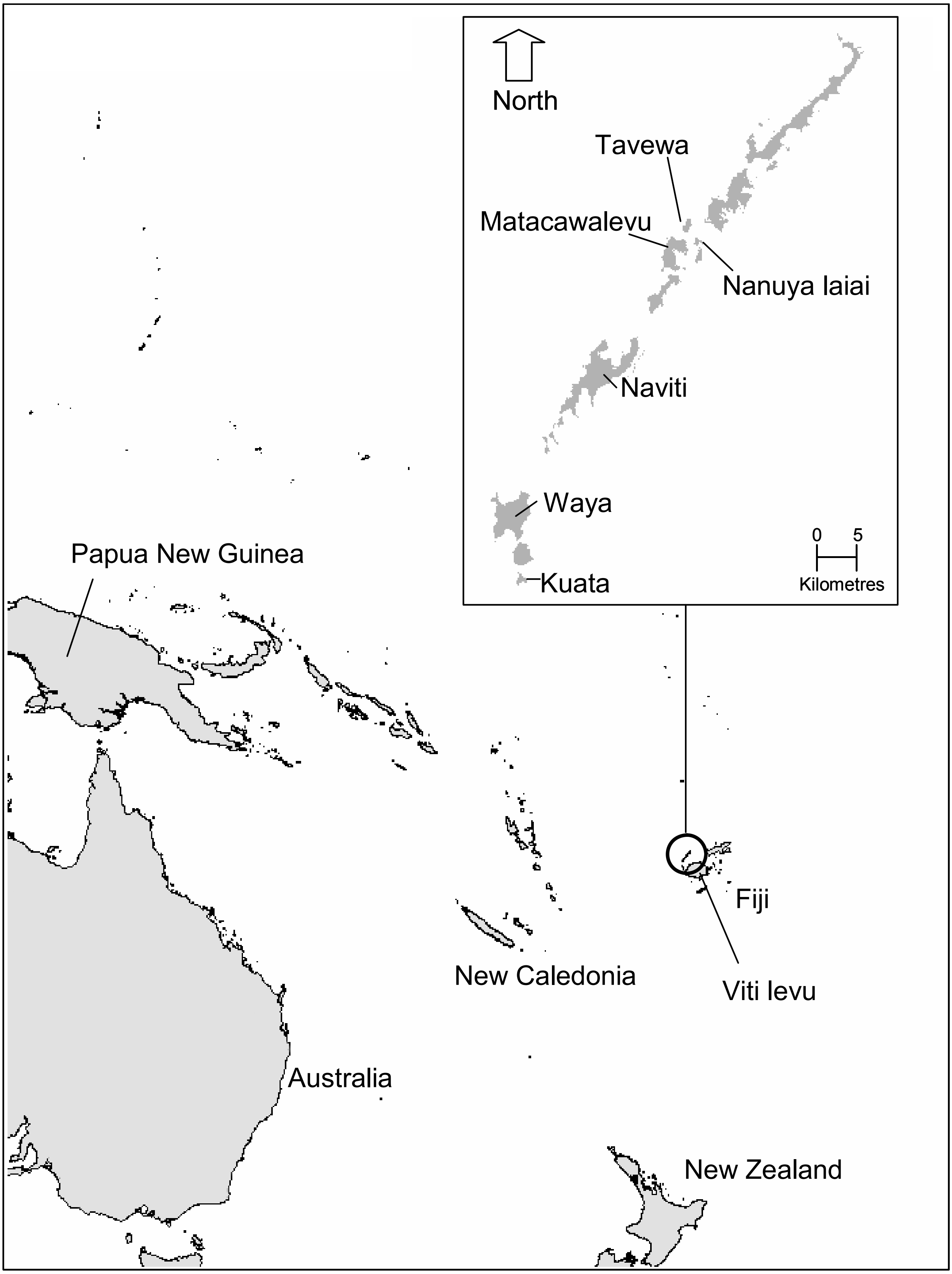

Figure 3.1 Fiji in relation to the western Pacific Ocean, the Yasawa Island archipelago of Fiji and the six islands sampled (inset).

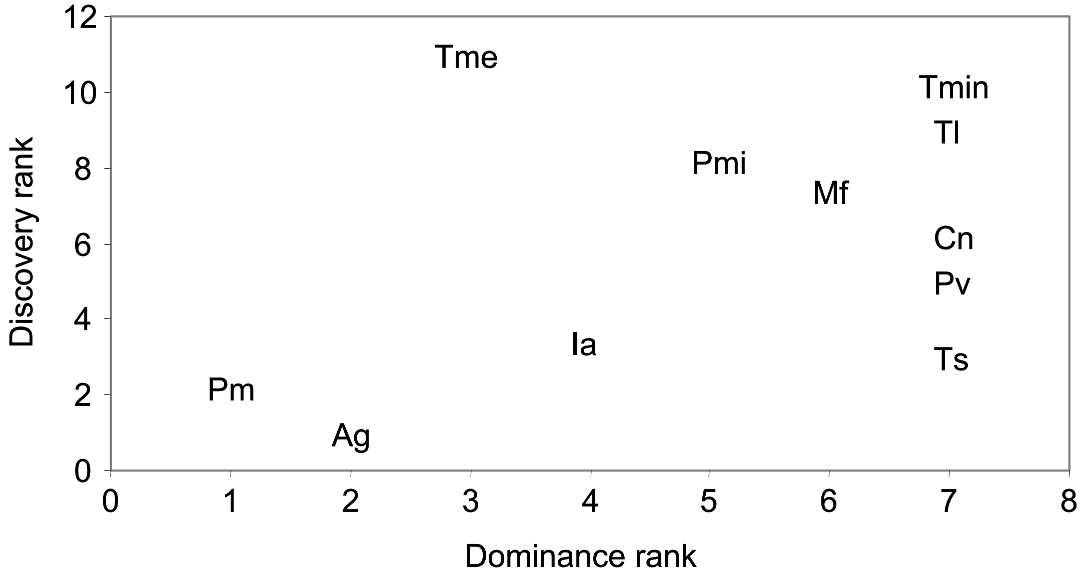

Figure 3.2 The relationship between exploitative and interference competition. Species are ranked by dominance - the ability to exclude species from resources (proportion of baits monopolised after 60 minutes) and discovery - a measure of the ability to find and exploit resources quickly (proportion of occurrence at baits at 12 minutes). Spearman rank correlation = 0.165. Species codes are given in Table 3.6.

Ecological Partitioning and Invasive Species in a Tropical Rainforest Community

4

Abstract

Niche partitioning is a key factor in shaping ant communities and in the coexistence of ant species. Determining the composition and structure of ant communities may help understand how niche opportunities become available for invasive ant species and ultimately how communities are invaded. The present study describes the composition and structure of an ant community from a tropical rainforest in Fiji, specifically looking at spatial partitioning and the presence of invasive ant species. A total of 27 species were collected, including five invasive species. Spatial partitioning between the canopy and litter was evident with a relatively low species overlap and a different composition of ant genera. Within the canopy there was no evidence that ant assemblages were partitioned on the basis of floral associations. At baits, the abundance of ants from litter microhabitats (under litter, on top of litter) was significantly higher compared to the shrub microhabitat (2m above ground). The composition of ants was also significantly different between litter and shrub microhabitats. However, there was no difference between bait types (oil, sugar, and tuna) in the abundance or composition of ants. In terms of invasive ant species, there was no difference in the number of invasive species between the canopy and litter. However, the most common species, *Paratrechina vaga*, was significantly less abundant and less frequently collected in the canopy. Also in the canopy, invasive species were significantly smaller than native species, but not in the litter. The average niche overlap between invasive and native species was significantly smaller in the canopy than the overlap from the litter. Thus, a combination of taxonomic disharmony, habitat characteristics and body size appear to be important in shaping niche opportunities for invasive ant species in this study.

4.1 Introduction

The composition and structure of ant communities are affected by multiple factors, which interact on different spatial and temporal scales. Inter-specific competition is considered to be a major structuring force of ant communities (Andersen 1992; Davidson 1998; Holway 1999; Albrecht & Gotelli 2001). Inter-specific competition results in dominance hierarchies being formed through behavioural aggression, competitive exclusion at food resources, and distinctive foraging strategies for either accessing resources or avoiding dominant species (Fellers 1987; Savolainen & Vepsäläinen 1989; Andersen 1992; Davidson 1998; Holway 1999). The partitioning of resources, especially via space, diet and time also plays a large role in the coexistence of competing ant species (Schoener 1974; Albrecht & Gotelli 2001).

However, abiotic factors, habitat requirements, and dispersal abilities also strongly interact to shape ant communities (Cole, 1983; Andersen 1986; Savolainen & Vepsäläinen, 1989; Majer et al. 2004).

Andersen (1986) showed that patterns of ant community organisation varied with habitat, and the strength of inter-specific competition was also dependent on habitat type. Several recent studies have illustrated how habitat shapes ant communities (Yanoviak & Kaspari 2000; Gotelli & Ellison 2002; Ratchford et al. 2005). For example, there has been a major contrast between the canopy and the ground litter, and how these two habitat templets form distinct ant communities (Yanoviak & Kaspari 2000). Environmental harshness can also be important by limiting the number and type of species able to colonise a habitat, and hence shape community composition (Gotelli & Ellison 2002).

Invasive ant species can also play a considerable role in determining the composition and structure of native ant communities. Invasive ant species are currently receiving considerable attention from around the globe, with increasing evidence of disruption to natural ant communities via inter-specific competition (Holway 1999; Christian 2001; Holway et al*.* 2002; O'Dowd et al*.* 2003; Sanders et al*.* 2003).

Explaining and predicting the success of invasive species, the susceptibility of different habitats, and the role of the native community are major themes in biological invasions (Drake et al. 1989; Shea & Chesson 2002). Niche opportunity provides an excellent theoretical framework in which to study biological invasions, particularly as it encompasses both invasive species and the native community (Shea & Chesson 2002). A niche opportunity is the potential provided by a native community for an invasive species to have a positive rate of increase from low density (Shea & Chesson 2002). The main factors responsible for niche opportunities are increased resource availability and/or fewer enemies and competitors. However, native communities that have a disharmonious (unbalanced) biota are also thought to be more susceptible to invasion because there are missing 'elements' to the biota and consequently have under-utilised resources. Thus, these communities have increased niche opportunities for invading species (Mack et al. 2000; Shea & Chesson 2002). Low levels of niche opportunity lead to biotic resistance from the native community and should impede invasion (Shea & Chesson 2002).

Le Breton et al. (2005) have recently examined the opportunity for invasion by the little fire ant, *Wasmannia auropunctata* (Roger), in New Caledonia - a disharmonious island ant community. They showed that food and nest site resources were not fully exploited by native ant communities. *W. auropunctata* also exploited the carbohydrate resources from native scale insects (Margarodidae) more effectively than native ants. As a result, the density of ants from invaded sites (100% *W. auropunctata*) is now far greater than the natural densities of ants before invasion.

The present study describes the composition and structure of an ant community from a tropical rainforest in Fiji, specifically looking at the partitioning of canopy and litter habitats and food resources, the niche opportunities for invasive ant species, and the difference in susceptibility of canopy and litter habitats to invasive species.

4.2 Methods

4.2.1 Study site

Colo-i-suva Forest Park (18.05°S, 178.46°E, Fiji Map series O28:695867), is a 245 ha park located approximately 11 km north of Suva city on the main island of Viti Levu (Figure 4.1). The park is 100-200 m above sea level and has an annual rainfall of >4100 mm, of which the majority falls during the wet season of November to April (Evenhuis & Bickel 2005). The Colo-i-suva area has a humid tropical maritime climate, with mean daily temperatures from 19-23 °C in July, to 23-29 °C in January (Ash 1987). The park's flora is a mixture of native plant species, inter-planted with South American mahogany (*Swietenia macrophylla*), an introduced tree used for timber production. The park was last logged in the 1950s.

4.2.2 Canopy sampling

The foliage of epiphytes, ferns, palms and trees (hereafter referred to as 'trees') were sampled by beating. Foliage was brushed/tapped with a 2 m long wooden stick five times to dislodge ants onto a white calico collecting sheet (110 x 75 cm). Sampled foliage was approximately 2 – 4 m off the ground, and is hereafter referred to as 'canopy sampling' (*sensu* Moffett 2000). Although, canopy sampling traditionally refers to the upper areas of trees, Moffett's (2000) review of canopy sampling terminology advocates that any sampling above the level of the ground should be classified as canopy.

There are no identification guides to the native plant species in Fiji or Colo-i-suva Forest Park. Specimens of foliage were taken to park staff to obtain identification, and the publications of Smith (1979) and Watling (2005) used for diagnostics and information. Canopy samples were classified into five broad categories: mahogany (*Swietenia macrophylla*), palms (*Metroxylon vitiense*, *Pinanga coronata*), tree ferns (*Cyathea hornei*), native tree species (mixture of *Calophyllum vitiense*, *Palaquium* spp., *Endiandra* spp., *Canarium vitiense* and *Garcinia* nr *vitiensis*), and epiphytes (unidentified species). Epiphytes were sampled because several ant species from Fiji are known to inhabit them (J. Wetterer *pers. comm.*).

In order to avoid repeat sampling of the same colony, sampled trees were spaced at least 15 m apart and the foliage of sampled trees did not interconnect or touch. Trees were haphazardly picked for sampling. Sampling took place on three days (24th September, 4th and 5th October 2005) between 8 am and 4 pm. All ants were collected in fair to sunny weather, and were collected from the beating sheet with an aspirator and immediately placed into a vial of 75% ethanol. Sampled trees were collected along the Kalabu road area and the walking tracks beside Waisila creek at least 5 m off established tracks (Figure 4.1).

4.2.3 Litter sampling

To sample litter dwelling ants a 0.5 x 0.5 m quadrat was placed on the ground and litter within the quadrat was scooped into a white tray (30 x 40 x 10 cm). Litter was sifted through a 1 x 1 cm wire mesh to exclude larger debris. Sticks and rotten wood within the quadrat were broken apart into the tray. Not all the litter from the quadrat could be placed into the tray at once; 1-4 trays were needed. However, a standardised time of 15 minutes was spent searching through the litter of each quadrat. Quadrats were spaced at least 15 m apart, and were collected haphazardly along the Kalabu road area and the walking tracks beside Waisila creek (Figure 4.1). Sampling took place over two days (21st-22nd September 2005).

4.2.4 Baiting experiment

Within the park, five transects (150 m) were marked, starting 1m from the main edge (road, or walking track) and running into the forest interior, along a north-south axis. Ten stations were located along the 150 m transects, 15 m apart. At each station, three microhabitats were examined; under the litter, on top of litter, and on canopy vegetation approximately 2 m off the ground (see earlier comment on the definition of canopy, Moffett 2000). In order to distinguish the two types of canopy sampling used in this study (i.e. beating and baiting), I refer to canopy baiting as the ‘shrub layer’.

Within each microhabitat, three types of baits were used; cotton wool soaked in a saturated sucrose solution (sugar bait), cotton wool soaked in soy cooking oil (oil bait), and tuna (Sealord™ chunky style tuna in spring water, tuna bait). Each cotton wool ball was approximately 5 ml in volume, with an exposed surface area of 4 - 7cm^2. Approximately 2 g of tuna was used in each vial. Fresh baits were placed into a 25 ml plastic vial (25 mm diameter). For the shrub microhabitat, the vial was tied with wire to vegetation approximately 2 m off the ground. The baits within each microhabitat were placed in a triangular array, equidistant from each other with 30 cm spacing and between microhabitats (within a station) there was at least 1 m spacing. After one hour, vials were collected, capped and returned to the laboratory. Vials were frozen to kill ants, and then ants were removed from the bait and placed into 75% ethanol. Each transect was completed on a separate day (23rd, 30th September, 1st, 2nd, 3rd October 2005), between 10 am and 4 pm. Sampling was not undertaken when rain had fallen in the previous six hours. This gave 90 vials per transect and 450 vials overall.

4.2.5 Specimen identification

There is no single publication to identify the ant species of Fiji, and knowledge of the ant fauna of Fiji is limited (Ward & Wetterer 2006). Shattuck and Barnett (2001) was used for identification to genera, and species-level identification was completed by examining reference specimens in the New Zealand Arthropod Collection (NZAC), and by using the publications of Mann (1921), Wilson and Taylor (1967a), and for *Cardiocondyla* (Seifert 2003), *Tetramorium* (Bolton 1977, 1979), *Strumigenys* (Dlussky 1994; Bolton 2000), *Hypoponera* (Wilson 1958), and *Monomorium* (Heterick 2001). All specimens have been lodged in the NZAC.

4.2.5 Statistical analyses

Diversity

The percentage similarity between litter and canopy samples was calculated by the Sorensen's Quotient of Similarity (Q/S). Q/S = [2j/(a+b)]*100, where a is the total number of species in sample #1, b is the number of species in sample #2, and j is the number of species common to both samples. Rarefaction (Coleman) curves were plotted of observed species richness and the estimated number of ant species was calculated using the Chao 2 estimator of species richness using EstimateS v7.0 software (Colwell 2005). The default parameters in EstimateS were used, with 50 runs. The efficiency of litter sampling was evaluated using the number of observed species divided by the Chao 2 estimate of species richness. The Shannon Diversity index (H`) and Simpson’s index of evenness (D) were also calculated using EstimateS.

Differences in the ant species composition between the different tree categories from canopy sampling (epiphytes, tree ferns, native species, mahogany, and palm) were determined by non-metric multidimensional scaling in PRIMER v5.0 software, using a Bray-Curtis similarity matrix on presence-absence data from 10 runs (Clarke & Warwick 2005). Pairwise tests between the different tree categories were examined using Analysis of Similarities (ANOSIM) with 999 permutations. ANOSIM gives an R value, which is a measure of the separation of pairwise comparisons on a scale from -1 to 1; well separated > 0.75, clearly different > 0.5, and barely separable < 0.25 (Clarke & Warwick 2005).

Body size

Head width was used as an index of body size, a widely used measure of size in ants (Hölldobler & Wilson 1990). Measurements were made of mounted specimens, using an ocular micrometer calibrated with a stage micrometer to an accuracy of 0.01 mm. Specimens were obtained from the above mentioned sampling. Measurements were made on ten specimens of each species where possible. Only the minor caste of polymorphic taxa were used (e.g. *Pheidole*, *Camponotus*). Wilcoxon paired sign tests were used to compare the differences in average body size of invasive and native (including endemic) species from each sample.

Abundance, composition and niche overlap at baits

To examine the abundance of ants at different microhabitat and food resources, each resource state was summed across all stations within a transect. For example, the number of ants caught from the resource state of ‘oil-shrub’ was summed across all stations within a transect. A two-factor ANOVA was used to examine microhabitat and bait on abundance (log transformed data) using SPSS v12.0.2 software. Transects were used as a covariate with Bonferroni post-hoc tests. Differences in the composition of ant species from different microhabitat and food resources were determined by non-metric multidimensional scaling in PRIMER, using a Bray-Curtis similarity matrix on presence-absence data from 10 runs (Clarke & Warwick 2005). Pairwise tests between microhabitats and food types were examined using Analysis of Similarities (ANOSIM) with 999 permutations.

Niche overlap was examined in EcoSim v7.71 software, using Pianka's (1973) index of niche overlap (Gotelli & Entsminger 2005). The proportional abundance of each species was examined for nine resource states (three baits x three microhabitat combinations). The RA2 randomisation algorithm (niche breadth relaxed/zero states retained) was used and each resource state was assumed to be equally usable by all species, and was compared with simulated indices from 1000 randomly constructed communities (Gotelli & Entsminger 2005). From these analyses, species pairwise niche overlaps were calculated.

4.3 Results

4.3.1 Diversity

A total of 2421 ants were collected from Colo-i-suva park, representing 27 species. Nine species were endemic to Fiji, 13 were native, and five species were invasive (Table 4.1). Nineteen species were caught in the canopy, and 15 species from the litter. However, litter sampling caught six species not in the canopy, and canopy sampling caught ten species not found in the litter. Sorensen's Quotient of Similarity (Q/S) between litter-canopy was 52.9%, with nine species common to both the canopy and litter (Table 4.1). Canopy samples were dominated by species of *Tetramorium*, *Camponotus* and *Technomyrmex*, whereas litter samples were dominated by species of *Pheidole*, *Odontomachus*, *Hypoponera*, and *Solenopsis*. Only two species, *Paratrechina minutula* and *P*. *vaga* were frequently in both habitats. Ants were present in 93% (n = 57) of the litter quadrats, whereas in the canopy, ants were present in only 65% (n = 217) of samples. In the baiting experiment, ants were collected from only 51% of baited vials (n = 450).

Sampling was highly efficient, with the observed number of species being close to the Chao 2 estimated number of species for both the canopy (85.1%) and litter (77.8%). Shannon's (H`) and Simpson's (1/D) diversity indices indicated that the canopy had a higher diversity and eveness of species (H` = 2.19, D = 6.74) than litter quadrats (H` = 1.98, D = 5.26). Within the canopy habitat, the type of tree sampled did not affect the composition of ant species. Pairwise comparisons showed that the ant composition of host tree categories were very similar to each other (ANOSIM R < 0.25, 2D stress = 0.09).

There was no difference in the number of invasive species caught from the canopy or litter (Table 4.1) 2x2 contingency table, $X^2 = 0.147$, $p = 0.351$). *Paratrechina vaga*, an invasive species, was the most common species in the litter, and the third most common from canopy samples (Table 4.1). *P. vaga*, was caught twice as frequently in the litter compared to the canopy. This trend was repeated in the baiting experiment, where *P. vaga*, was also caught twice as frequently in the litter (both top and under) compared to the shrub microhabitat. All other invasive species were seldom collected (Table 4.1).

4.3.2 Body size

Although the canopy ant fauna had a larger head width (mean ± SE = 0.74 ± 0.09mm), it was not significantly different (Wilcoxon two sample test, W = 193.5, $p = 0.159$) than in the litter (0.59 ± 0.11mm). The distribution of body sizes was not significantly different between canopy and litter (two sample Kolmogorov-Smirnov Z = 0.735, $p = 0.653$). In the canopy, the head width of invasive species were significantly smaller (0.50 ± 0.008mm) than native species (0.76 ± 0.07mm) (Wilcoxon paired test, N = 26, $p < 0.001$). However, in the litter, there was no significant difference in head width between invasive (0.50 ± 0.005mm) and native species (0.54 ± 0.065mm) (Wilcoxon paired test, N = 26, $p = 0.112$).

4.3.3 Abundance, composition and niche overlap at baits

Abundance data were skewed, but log transformed data were normally distributed (one sample Kolmogorov-Smirnov Z = 0.921, $p = 0.365$). There was a significant difference in the abundance of ants between microhabitats (two factor ANOVA, F = 26.53, d.f. = 2, $p < 0.001$, Figure 4.2), but abundance was not significantly different between bait types (F = 1.16, d.f. = 2, $p < 0.323$). Bonferroni post-hoc tests showed that both litter microhabitats had significantly more ants than shrub ($p < 0.05$). There was no effect of transect as a covariate (F = 0.005, $p < 0.942$). However, there was some evidence for an interaction between microhabitat and bait (F = 2.45, d.f. = 4, $p < 0.065$), with a higher abundance of ants collected from tuna on shrub, than from other baits (oil and sugar) on shrub. The abundance of the most common invasive species, *P. vaga*, was significantly lower in the shrub microhabitat than either on the top or under the litter (F = 10.76, d.f. = 2, $p < 0.001$).

The composition of ant species was significantly different between the shrub and both litter layers (Shrub – top of litter, ANOSIM R = 0.46, $p < 0.001$; Shrub – under litter, R = 0.53, $p < 0.001$; 2D stress = 0.08). However, the composition of ant species from the top of the litter was very similar to under the litter (under litter – top of litter, R = 0.11, $p < 0.083$). The composition of ant species at the three bait types was indistinguishable from one another (all combinations, ANOSIM R < 0.10, $p > 0.30$).

There was significantly less niche overlap than expected from communities generated by null models ($I_{obs} = 0.246$, $I_{sim} = 0.288$, $p = 0.022$). Furthermore, the average niche overlap between invasive-native pairs of species for the canopy (mean niche overlap 0.09 ± SE = 0.06) was significantly smaller (two sample t-test, t = 6.91, d.f. = 22, $p < 0.001$) than the overlap from the litter (mean niche overlap 0.76 ± SE = 0.27).

4.4 Discussion

Canopy and litter habitats are expected to have distinct ant communities - the result of differences in resources and physical complexity (Yanoviak & Kaspari 2000). This was confirmed at Colo-i-suva

Forest Park, where there was a relatively low species overlap between canopy and litter habitats. Compared to the litter, the canopy had a different composition of ant genera and also a higher diversity of species. However, in the canopy there was no evidence that ant assemblages were partitioned on the basis of floral associations. Each tree category (e.g. mahogany, palms, tree ferns, native tree species, and epiphytes) had a very similar ant species composition.

The importance of spatial partitioning was further supported with the baiting experiment, which showed a strong difference in the composition of ant species between the shrub and litter layers. However, bait type was not partitioned by species, despite food being advocated as a major resource axis (Schoener 1974). Ant abundance was also significantly higher in litter microhabitats than from the shrub layer, in line with the results of Kaspari and Weiser (2000). Overall, there were no significant differences in the abundance of ants between the bait types, although there was a higher abundance ($p = 0.065$) of ants on tuna baits from the shrub layer. Yanoviak and Kaspari (2000) have previously shown that the abundance of canopy ant species was higher on protein (tuna) baits compared to carbohydrate (sugar) baits, and suggested this was the result of greater nitrogen limitation in the canopy.

Susceptibility to invasion is related to the niche opportunities provided by different environments (Shea & Chesson 2002). There are already a disproportionate number of invasive species in the Pacific region (McGlynn 1999a). One of the reasons for the success of invasive ant species in this region may be that the native ant fauna is taxonomically unbalanced, creating opportunities for invasive ant species (Le Breton et al. 2005). In general, there is a trend of increasing disharmony from Papua New Guinea eastwards across the Pacific region. The most isolated islands of Polynesia are considered to contain no endemic ant species (Wilson & Taylor 1967b; Morrison 1997), and Hawaii, no ant species at all (Wilson 1996). This disharmony extends to both the canopy and the litter. For example, in the canopy, many ant genera are absent from the Pacific region (including Fiji) which are common and diverse in the canopy elsewhere (e.g. *Crematogaster*; *Pseudomyrmex*; *Dolichoderus*, *Oecophylla*, *Polyrachis*) (Ward & Wetterer 2006). Ants are also less abundant in the canopy compared to elsewhere, for example, in New Caledonia native ants represent less than 5% of all canopy arthropods (Le Breton et al. 2005), and this is probably typical of other Pacific islands.

However, at Colo-i-suva Forest Park, three of the five invasive species had native/endemic congeners. Therefore, taxonomic disharmony is not a complete explanation for the success of all invasive species. I suggest that for Colo-i-suva Forest Park a combination of resource utilisation, habitat characteristics, and the body size of the native fauna are important components shaping niche opportunities for invasive species. Le Breton et al. (2005) recently showed that food and nest site resources were not fully exploited by native ant communities in New Caledonia, creating a resource opportunity that has enabled the little fire ant, *W. auropunctata*, to invade and subsequently monopolise resources.

The canopy is predicted to have a greater diversity of ant species, which have a higher degree of specialisation, and where resource utilisation, monopolisation and behavioural aggression is higher (Yanoviak & Kaspari 2000). As a consequence, the canopy environment should provide more biotic resistance, and thus be a more difficult environment to exploit for invasive ant species. At Colo-i-suva Forest Park, there was conflicting support for a difference in the susceptibility between the two habitats. The most common invasive species, *P. vaga*, was significantly less abundant, and less frequently collected, in the canopy compared to the litter. This suggests that *P. vaga* was less able to exploit the canopy. However, there was no difference in the total number of invasive ant species present between the canopy or the litter, suggesting there was no difference in the susceptibility of the two habitats to invasion.

In the canopy, but not the litter, invasive species were significantly smaller than native species. The body size of invasive species did not change between the canopy and litter, but rather the native ant fauna in the canopy was larger. Therefore, a larger-bodied ant fauna in the canopy may have created a niche opportunity where small invasive ant species can reduce/avoid inter-specific competition with native species. Previous work on the body size of invasive ant species has shown they are on average significantly smaller than related native congeners (McGlynn 1999b). A reason for being smaller could relate to success at inter-specific competition - smaller species are often able to produce more workers and thus have larger colonies, which are more capable of defending/exploiting resources (McGlynn 1999b). However, being significantly different in size compared to the native fauna may also reduce inter-specific competition with native species. At Colo-i-suva Forest Park, there was a significantly lower average niche overlap between invasive and native species in the canopy. A reduction in resource overlap, and hence inter-specific competition, with native species would provide a niche opportunity for invasive species.

Taxonomic disharmony is a strong explanation for the success of invasive species in areas without similar native species. However, other factors such as habitat characteristics and body size also appear to be important in shaping niche opportunities for invasive ant species at Colo-i-suva Forest Park, and possibly across the Pacific region.

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Table 4.1 The frequency of occurrence of species collected from Colo-i-suva Forest Park for canopy (beating), litter (quadrats) and the three microhabitat layers from the baiting experiment (shrub, top of the litter, and under the litter). Species are listed in alphabetical order within the categories of endemic, native and invasive.

Species	**Canopy**	**Litter**	**Shrub**	**Litter-top**	**Litter-under**
Endemic					
Camponotus dentatus (Mayr)	0.029				
Camponotus laminatus Mayr	0.057		0.188		
Camponotus maudella Mann	0.021				
Camponotus manni umbratilis Mann	0.043				
Camponotus schmeltzi Mayr	0.050		0.031		
Cerapachys cryptus Mann		0.019			
Hypoponera eutrepta (Wilson)		0.151			
Pheidole caldwelli Mann	0.014	0.491	0.094	0.217	0.248
Pheidole wilsoni Mann	0.007				
Native					
Odontomachus simillimus Smith	0.007	0.226		0.022	
Oligomyrmex atomus Emery				0.011	0.019
Paratrechina minutula (Forel)	0.286	0.264	0.031		0.010
Pheidole oceanica Mayr	0.007		0.031	0.011	0.038
Pheidole umbonata Mayr		0.038	0.031	0.033	0.010
Rogeria sublevinodis Emery					0.010
Solenopsis papuana Emery		0.075	0.063	0.043	0.171
Strumigenys godeffroyi Emery		0.019			
Tapinoma minutum Emery	0.093				
Technomyrmex albipes (F. Smith)	0.143	0.038			
Tetramorium insolens (F. Smith)	0.064	0.019	0.063	0.011	
Tetramorium pacificum Mayr	0.486	0.057	0.375		
Vollenhovia denticulata Emery	0.007				
Invasive					
Anoplolepis gracilipes (F. Smith)	0.014	0.019			
Monomorium sechellense Emery		0.038			
Paratrechina vaga (Forel)	0.250	0.585	0.125	0.283	0.276
Pheidole fervens Smith	0.007		0.031	0.011	0.048
Tapinoma melanocephalum (Fab.)	0.043	0.019			
Total number of ants	519	188	124	649	941
Number of species	19	15	11	9	9
Number of samples	140	53	32	92	105

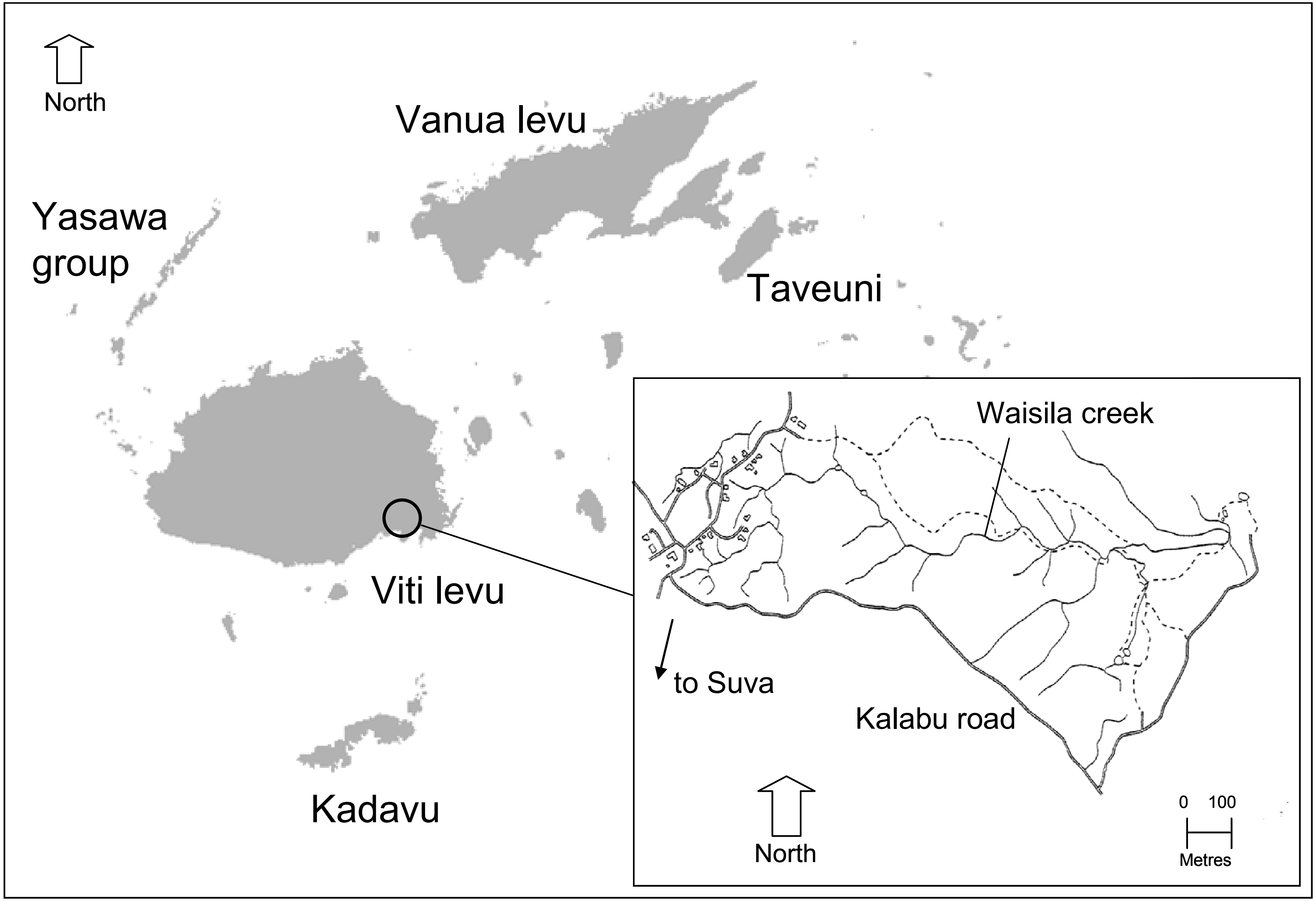

Figure 4.1 The main islands of Fiji and inset, Colo-i-suva Forest Park with walking tracks (dotted lines) and creeks (solid lines).

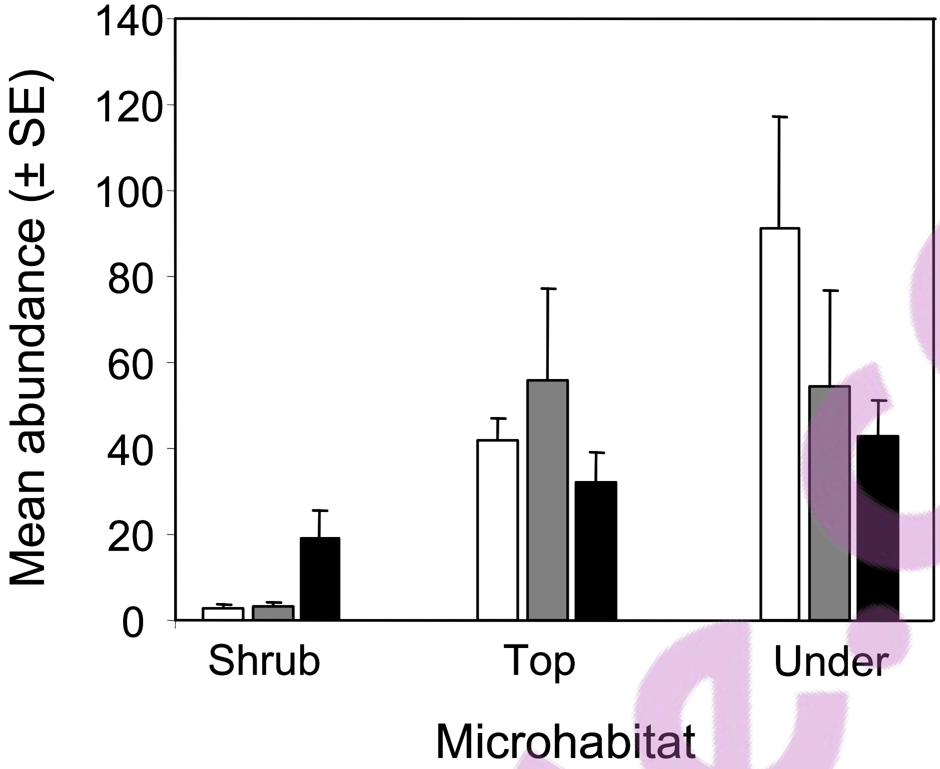

Figure 4.2 The mean abundance and standard error of ants from baited vials of oil (white), sugar (grey) and tuna (black), for the three microhabitat layers (shrub, under litter, on top of litter).

The Role of Habitat and Competition in Shaping Ant Communities in New Zealand

5

Abstract

Factors that shape the composition and structure of ant communities include climatic variables, habitat and inter-specific competition. New Zealand has only 11 species of endemic ants but 28 exotic species have established and become invasive. However, very little is known about either the endemic or the invasive ant fauna in New Zealand. This chapter investigates the composition and structure of ant communities in urban, scrub and forest habitats in New Zealand, with particular emphasis on interactions between ant species and how species are spatially and temporally partitioned in the environment. There was a significant difference between scrub and forest habitat in terms of species composition and the overall partitioning of species. As a consequence two distinct ant communities are formed, one of endemic ant species in forest habitats, and the other of invasive ant species in more disturbed habitats of scrub and urban sites. In both habitats three species contributed 90% of total abundance. Although both the abundance and species richness of ants declined in winter months, species composition was consistent throughout the year. Consequently, patterns of niche overlap were aggregated, confirming the same species co-occurred throughout the year and were not temporally partitioned on an annual scale via species-specific activity cycles. Some scrub sites (but not forest sites) could be individually distinguished by their ant composition throughout the year. This suggests that site history and/or colonisation abilities can play a role in structuring the ant communities in this type of habitat.

In a baiting study in urbanised sites, there was no evidence that inter-specific competition structured the community at either regional or local scales. Unexpectedly, the ability to discover, and also to numerically and behaviourally dominate baits, was similar for many of the species detected. Furthermore, New Zealand environments are not fully saturated with ants. On average only 56% of baits were occupied, and at half of the sites there were three or fewer ant species (25 baits per site, 20 sites). Of interest to the study of invasive ants in New Zealand is why environments remain largely unsaturated in terms of ants (both their abundance and species richness), despite being effectively unoccupied by endemic ant species – and thus presumably with little biotic resistance. Population and colony level studies would be useful to examine this issue further.

5.1 Introduction

Understanding how assemblages of species are structured and organised is the principal aim of community ecology. There are several well known factors that shape communities of ants (Hymenoptera: Formicidae).

Climatic variables, especially temperature, rainfall and humidity, play a large role in determining the distribution, and coexistence, of ant species (Hölldobler & Wilson 1990). On large spatial scales ant abundance is strongly correlated with net primary productivity (a function of solar radiation and rainfall) (Kaspari et al. 2000). Temperature also plays an important role in the abundance of ants by restricting foraging activity and regulating seasonal productivity (Kaspari et al. 2000). Environments with high rainfall reduce the time able to be spent on foraging activities (Vega & Rust 2001). Conversely, in xeric habitats, the lack of water and soil moisture can also limit the distribution of some species (Holway & Suarez 2006). Temperature and humidity also play an important role at the level of the colony. Temperature primarily controls the development of the eggs, larvae and pupae (Hartley & Lester 2003). Nests can also provide a thermal refuge in hot environments, allowing workers to retreat to a cool nest in the hottest part of the day (Hölldobler & Wilson 1990). Thermal stresses produced by fluctuations in daily and seasonal temperatures create conditional changes in the foraging activity and dominance of different species (Cros et al. 1997; Thomas & Holway 2005). This can lead to the ecological partitioning and coexistence of species.

Habitat requirements also strongly shape ant communities (Andersen 1986a; Yanoviak & Kaspari 2000; Majer et al. 2004; Ratchford et al. 2005; Sarty et al. 2006). For example, the contrasting physical conditions of canopy and ground litter habitats can structure distinct ant communities (Yanoviak & Kaspari 2000). Environmental harshness can also be important by limiting the number and type of species able to colonise a habitat, and hence shape community composition (Gotelli & Ellison 2002). The physical conditions of habitats also interact with climatic variables to influence the diversity and composition an ant community (Cros et al. 1997; Ratchford et al. 2005). For example, Cros et al. (1997) showed that the canopy in forest habitats produced a mosaic of sunny and shade microclimates, allowing heat-intolerant species to thrive. Conversely, in more open canopy habitats where there was a lack of shade from trees and thus increased ground temperature, heat-tolerant species dominated (Cros et al. 1997).

Inter-specific competition is often considered to be the major structuring force of ant communities but particularly at local spatial scales (Andersen 1992; Morrison 1996; Davidson 1998; Holway 1999; Gotelli & Ellison 2002). Inter-specific competition results in dominance hierarchies being formed through inter-specific aggression, competitive exclusion at food resources and distinctive foraging strategies for either accessing resources or avoiding dominant species (Fellers 1987; Savolainen & Vepsäläinen 1988; Andersen 1992; Davidson 1998; Holway 1999). Dominant species can control the spatial occurrence of other species, thus structuring the ant community and creating mosaic-like patterns of species co-occurrence (Savolainen & Vepsäläinen 1988; Morrison 1996; Gotelli & Ellison 2002), although this is not universally accepted (Floren & Linsenmair 2000; Ribas & Schoereder 2002; Blüthgen & Stork 2007).

In general terms, climatic variables are considered to be the major influence on the ant community at large spatial scales, whereas habitat and then inter-specific competition become more apparent at local levels (Hölldobler & Wilson 1990; Andersen 1986a; Majer et al. 2004). However, these factors all interact and produce species-specific responses to environmental conditions, that is, the activity, abundance and dominance of a species is conditional on certain circumstances (Andersen 1986a; Cros et al. 1997, Thomas & Holway 2005). For example, inter-specific competition is of major importance in arid regions in Australia, whereas habitat appears to have a much greater influence on community organisation in mesic regions (Andersen 1986a). Additionally, in mesic regions, weak interactions between species suggest the communities are not tightly structured (Andersen 1986a).

Understanding these conditional circumstances is important to understanding how ant communities are structured and organised. New Zealand is one of the few large land areas in the world to have an almost complete lack of social insects. There are no native social bees, wasps, only three endemic species of termites and eleven species of endemic ants (Valentine & Walker 1991; Ward 2005). However, there are a considerable number of invasive social insects established in New Zealand (Valentine & Walker 1991; Moller 1996; Beggs 2001; Ward 2005). One major generalisation of invasion biology is that invading species which occupy vacant or unsaturated niches will have the greatest impacts (Lodge 1993; Parker et al. 1999; Mack et al. 2000; Shea & Chesson 2002). Thus, in New Zealand invasive social insects may cause considerable adverse impacts because of the lack of native social insects. Although a considerable amount of research has been completed on the negative ecological impacts of *Vespula* wasps (Beggs 2001), very little is known about either the endemic or the invasive ant fauna in New Zealand. This chapter investigates the composition and structure of ant communities in native scrub, forest and urban environments in New Zealand. Emphasis is on the interactions between ant species and how species are spatially and temporally partitioned in the environment.

5.2 Methods

5.2.1 Habitat partitioning

Study sites

The eight study sites (four scrub, four forest) are situated in the western range of the wider Auckland city region, at approximately 36° 52.23S, 174° 35.41E (Table 5.1, Figure 5.1). The region is a sub-tropical climate zone, with warm humid summers and mild winters (NIWA 2006). Maximum summer temperatures range from 22 °C to 26 °C, and winter from 12 °C to 17 °C. Annual sunshine average 2000 hours, and average rainfall is approximately 100 mm per month (NIWA 2006). All sites are heavily influenced by surrounding human activities, in a matrix of (at least one of) residential houses, parkland, or farm pasture. The rationale behind comparing such distinct habitats, is that previous studies have shown large differences in community structure and organisation between relatively open canopy habitats (scrub/heath) compared to closed canopy habitats (forest) (Andersen 1986a).

The vegetation at four of these sites (Sherwood, Chilcott, Corbans, and Shona) consists of regenerating scrub, planted in 1999 to assess the survival and growth of native plant species in a restoration study context. The area of these sites is approximately 70 x 45 m. Vegetation is predominantly of native species; cabbage tree (*Cordyline australis*), karamu (*Coprosma robusta*), kohuhu (*Pittosporum tenuifolium*), lemonwood (*Pittosporum eugenioides*), mahoe (*Melicytus ramiflorus*), mapou (*Myrsine australis*), manuka (*Leptospermum scoparium*), koromiko (*Hebe stricta*) and houhere (*Hoheria populnea*). However, a number of invasive weeds have established in the sites, principally tree privet (*Ligustrum lucidum*), Chinese privet (*L. sinense*), and *Acacia* species. Vegetation height is between 3-10 m, and canopy cover is generally low (<30%), but can reach >75% in areas under manuka.

The ant fauna of these scrub sites was compared to four sites of native forest (Shona Reserve, Oratia, Swanson, and Huapai). Prior to human settlement, the Auckland area consisted of temperate forest dominated either by kauri (*Agathis australis*) or a mixture of podocarp and broad-leaved hardwood forest (Thomas & Odgen 1983). Huapai is a 15 ha University of Auckland reserve, with several very large kauri trees at >30m tall, nikau palms (*Rhopalostylis sapida*), and silver tree ferns (*Cyathea dealbata*) (Thomas & Odgen 1983). The Oratia and Swanson sites are also kauri forest (and University of Auckland reserves), but are younger sites (regenerating after milling) and are dominated by kauri rickers and silver tree ferns. At Swanson there are also mahoe, kanuka (*Kunzea ericoides*) and invasive pine (*Pinus radiata*). Shona Reserve is a podocarp and broad-leaved forest with stands of rimu (*Dacrydium cupressinum*), kahikatea (*Dacrycarpus dacrydioides*), pigeonwood (*Hedycarya arborea*), mahoe, and several species of tree ferns.

Sampling

At each site, the foliage of ten plants was brushed/tapped with a wooden stick five times to dislodge ants onto a white calico collecting sheet (110 x 75 cm). Ants were collected with an aspirator and placed into 75% ethanol. Plants were haphazardly chosen for beating each month. At each site 12 pitfall traps were set in a 6x2 grid with 5 m spacing. Each trap consisted of a 100 mm deep plastic cup with a diameter of 105 mm containing 100 ml of a 75% ethanol to mono-propylene glycol mix (70/30), sunk vertically in the ground. A lid was secured a few centimetres above the trap to minimise debris entering the trap. Traps were left open for 7 days per month and pooled into a ‘site sample’. Sampling was undertaken once a month for twelve months; 23 February 2005 - 2 March, 18 - 25 March, 7 - 14 April, 12 - 19 May, 16 - 23 June, 14 - 21 July, 18 - 25 August, 15 - 22 September, 20 - 27 October, 17 - 24 November, 13 - 20 December, 17 - 24 January 2006.

Statistical analyses

The abundance and species richness of ants were calculated for each month at each site and analysed using a two-way ANOVA. Abundance was log transformed to normalise data. Estimates of species richness and accumulation for each site were made using ESTIMATES v7.0 software (Colwell, 2005). Rarefaction curves were plotted of observed species richness and the estimated number of ant species was calculated using the Chao 2 estimator of species richness (Colwell, 2005). The default parameters in ESTIMATES were used, with 50 runs. The efficiency of pitfall sampling was evaluated using the number of observed species divided by the Chao 2 estimate of species richness.

The composition of ant species from the 8 sites was examined using non-metric multidimensional scaling in PRIMER v5.0 software, using a Bray-Curtis similarity matrix (4th root transformation) from 50 runs (Clarke and Warwick, 2005). Sites were used as replicates. Analysis of similarities (ANOSIM) was used to analyse differences between the two habitat types (scrub and forest). ANOSIM creates an overall test statistic (R) that indicates if differences between habitat types exist. As R approaches 1, there is more dissimilarity between habitats. A SIMPER analysis was used to indicate which species were principally responsible for the differences between scrub and forest. Both the overall annual composition (months pooled) and the seasonal (monthly) composition of ant species were examined.

The BIOENV function (in PRIMER) was used to examine the influence of climate variables on the composition of the ant fauna at each site. BIOENV uses a Spearman rank correlation coefficient (ρ) as a measure of agreement between an environmental (Euclidean distance) and a faunal similarity matrix (Bray-Curtis), matching the elements (months) in the two matrices. Correlations were calculated for all possible combinations of environmental variables. Nine climate variables were examined; mean monthly air temperature (°C), mean daily maximum air temperature (°C), mean 10 cm earth temperature (ºC), mean monthly sunshine (hours), mean monthly rainfall (mm), mean daily global radiation (megajoules/square metre), mean relative humidity (%), mean number of days of ground frost, mean daily minimum air temperature (°C), representing climate information for the 1971-2000 period for Auckland (NIWA 2006). Draftsman's plots, principal component analysis (PCA), and Spearman correlations of pairwise comparisons for each variable were also examined for collinearity (Clarke and Warwick 2005).

To investigate whether there was temporal niche partitioning (over an annual time period), Pianka's (1973) index of niche overlap was examined using EcoSim v7.71 software (Gotelli & Entsminger 2005). A dataset consisted of 12 columns (months) and rows were species. Scrub and forest sites were separated into two datasets because of the different species composition. For each month, a species was scored on how many sites it occurred, from zero, to a maximum of four sites. The RA2 randomisation algorithm (niche breadth relaxed/zero states retained) and RA3 algorithm (niche breadth retained/zero states reshuffled) were used and each month was assumed to be equally usable by all species. Observed data was compared to simulated indices from 1000 randomly constructed communities.

5.2.2 Competitive interactions

Study sites

To investigate competitive interactions, 20 study sites were sampled which were situated in the greater Auckland region, at approximately 36° 52.23S, 174° 35.41E (Figure 5.1). The elevation, rainfall, and temperature are the same as the previous section ‘Habitat Partitioning’. The sites are generally classified as ‘urban parks’, and were typically recreation grounds that were regularly disturbed by frequent mowing and/or sports activities. Sampling was carried out on the edges of these parks underneath large amenity trees (pohutakawa - *Metrosideros excelsa*, kanuka, cabbage tree, gum trees - *Eucalyptus* spp., pine - *Pinus radiata*), where there was little or no understorey. Four sites (Sherwood, Chilcott, Corbans, Shona) described from the previous section (‘Habitat Partitioning’) were also used, which consisted of denser vegetation. However, most sites were of the former description.

Sampling

To determine the relative occurrence of ant species, and which species were numerically and behaviourally dominant, baits were used to attract ants. At each site a grid was set up that consisted of 25 bait stations placed 5 m apart in a 5 x 5 grid. At each station approximately 1 g of tuna (Sealord™ chunky style tuna in spring water, “tuna” bait) was placed on a white plastic index card (7 x 7cm), on top of the ground. The index card was used to assist with the identification and counting of ants. Stations were examined in a fixed routine, at 12, 24, 36, 48, and 60 minutes after the bait was placed out. Each station was examined for 20 seconds. Temperature and relative humidity were recorded at the end of each 12 minute interval. Abundance of ants at baits was scored as: 1 = <5 ants, 2 = 5 - 9, 3 = 10 - 19, 4 = 20 - 50, 5 = >50. Sampling took place between 10 am and 4 pm.

At each site a number of environmental variables were recorded, including: an estimate of the ground cover of the grid (% of bare ground, litter, stone/rock, plant, grass, other); and litter depth. Canopy cover (%) and plant height (m) were estimated at each corner of the baiting grid. Dominant plant taxa were noted.

Statistical analyses

Chi-square tests were used to examine the occupancy of bait stations and the time interval at which ants first arrived at a bait station.

The numerical and behavioural dominance of different species were assessed using criteria from Andersen (1992) and Davidson (1998). Numerical dominance was measured as those species that; 1) occur at a high proportion of baits, 2) dominated baits by having a high abundance at baits (defined as the proportion of baits with an abundance score of 4 or 5 at the 60 minute interval). Interference competition was measured by; 1) species turnover at baits, where a change of species at a bait from one time interval to another occurs (measured as the proportion of turnover ‘wins’ and ‘losses’ for each species), 2) the ability to monopolise baits (i.e. being the only species present on baits at the end of the 60 minute baiting period). The time taken by a species to discover bait was also examined as a measure of exploitative competition (proportion of occurrence at baits at 12 minutes).

Patterns of species co-occurrence were examined using EcoSim v7.71 software (Gotelli & Entsminger 2005). At the regional scale, a presence-absence matrix was constructed with each row representing a different species, and each column representing a site. At the local scale, a presence-absence matrix was constructed for each site. Each row of the local scale data matrix represents a different species, and each column represents a different bait station. Furthermore, local scale data was examined for the 12 minute and 60 minute observation periods, as patterns of species co-occurrence could change over time.

The C-score was used as a metric to quantify the pattern of co-occurrence and was compared to simulated indices from 5000 randomly constructed communities (Gotelli & Entsminger 2005). For an assemblage that is competitively structured, species will co-occur less than expected (i.e. segregation), and the observed C-score should be significantly larger than expected by chance. For regional and local analysis, an equiprobable (columns) and fixed (rows) model option was used, which randomises the occurrence of each species among the sites. This option corresponds to a model of community assembly in which species colonise sites independently of one another (Gotelli & Entsminger 2005).

Because there were multiple local scale analyses, a meta-analysis of effect sizes was used to determine the overall co-occurrence pattern. The meta-analysis follows Gotelli and Ellison (2002), where the null hypothesis of the standardised effect size (SES) does not differ from zero. SES is generated in EcoSim, where SES = $(I_{obs} – I_{sim})/s_{sim}$ where I_{sim} is the mean index of the simulated communities, s_{sim} is the standard deviation, and I_{obs} is the observed index. Communities with little co-occurrence (i.e. species are segregated) should frequently reject the null hypothesis in the upper tail, and the meta-analysis pattern would show an average effect size significantly greater than zero.

The BIOENV function (in PRIMER) was used to examine the influence of environmental variables on the composition of the ant fauna. BIOENV uses a Spearman rank correlation coefficient (ρ) as a measure of agreement between an environmental matrix (Euclidean distance) and a faunal similarity matrix (Bray-Curtis), matching the elements (sites) in the two matrices. Environmental variables were compared with two faunal matrices; the presence/absence of ant species at a site, and also to the frequency of species occurrence (a maximum score of 25 corresponding to the number of bait stations at a site). Correlations were calculated for all possible combinations of environmental variables. Four environmental variables were examined; % ground cover of the grid (% of bare ground, litter, stone/rock, plant, grass, other), litter depth (cm), canopy cover (%) and plant height (m). Draftsman’s plots and Spearman correlations of pairwise comparisons for each variable were also examined for collinearity (Clarke and Warwick 2005).

5.2.3 Identification and curation

Upon collection all specimens were stored in vials of 75% ethanol. Identification of ants followed Harris (2002), from the list of species in Table 5.2. All specimens are held at the NZAC in ethanol.

5.3 Results

5.3.1 Habitat partitioning

A total of 3657 specimens and 17 species were caught in pitfall traps over the twelve month period; 2787 (76%) from the scrub sites and 870 (24%) from forest sites. Only 74 ants and 6 species were collected from beating samples. Beating did not collect any species not caught in pitfall traps. The majority of ants collected from beating were from the scrub sites (93%), all of which were invasive species. The two most common species caught in beating samples were *Paratrechina* spp. (66%) and *Technomyrmex albipes* (22%). No further analyses of beating data were undertaken.

In pitfalls, the three most abundant species at scrub sites contributed 89.8% of all ants; *Pheidole rugosula* (34.7%), *Paratrechina* spp. (30.9%) and *Tetramorium grassii* (24.2%). The three most abundant species at forest sites contributed 91.3% of all ants; *Heteroponera brounii* (44.0%), *Pachycondyla* sp. (39.4%) and *Prolasius advenus* (7.9%). There was a strong correlation between abundance and incidence (presence per month) for scrub ($\rho = 0.850$) and forest sites ($\rho = 0.934$).

From pitfall samples, estimates of species richness (using the Chao 2 estimator) showed that sampling was highly successful (>90%) in capturing ant species in the litter at seven of the eight sites (Table 5.1). The low efficiency at Huapai (46%) was due to the fact that five of the eight species caught were singletons.

On average, only 40% of the total number of species were caught in first month (range = 30-65%, Figure 5.2). However, there was a very strong relationship between the accumulation of species over time (months), $y = 0.2342\mathrm{Ln}(x) + 0.4164$ ($R^2 = 0.99$). For example, after 4 months approximately 75% of species had been caught at a site (Figure 5.2).

The abundance of ants at scrub sites (mean 54.64 ± SD 55.87) was significantly greater ($F = 32.40$, d.f. = 1, $p < 0.001$) than at forest sites (mean 17.81 ± SD 17.01). The abundance of ants was considerably lower in the cooler months of the year (May - August), although this pattern was more evident at scrub sites (Figure 5.3). In both scrub and forest sites the seasonal trend was largely driven by the abundance of the most common three species (as mentioned above). At forest sites, abundance was low and variance high making an overall seasonal trend less obvious. However, the common species all declined over the winter period (May - August), and two common species, *Prolasius advenus* and *Monomorium antarcticum*, were completely absent. There was also a very strong difference between months of the year (F = 5.82, d.f. = 11, $p < 0.001$) and no interaction effect between habitat type and month (F = 1.29, d.f. = 11, $p < 0.24$).

The number of ant species at scrub sites (mean 4.56 ± SD 1.68) was significantly greater (F = 35.94, d.f. = 1, $p < 0.001$) than at forest sites (mean 2.83 ± SD 1.32). There was a decline in species richness over winter which was evident for both scrub and forest habitats (Figure 5.4). There was also a strong difference between months of the year (F = 2.91, d.f. = 11, $p < 0.01$) and no interaction effect between habitat type and month (F = 0.39, d.f. = 11, $p < 0.95$).

There was a very strong difference in the composition of ant species between scrub and forest sites (Global R = 1.0, p = 0.029), and this was consistent between months (Figure 5.5). The differences in composition were almost entirely based on whether species were endemic or invasive. For example, 97.2% of the abundance of ants at scrub sites were invasive species, but at forest sites, 97.0% of the abundance of ants were endemic species. SIMPER analysis showed the abundance of five species contributed >53% of the overall difference between scrub and forest sites. In particular, *Paratrechina* spp., *Tetramorium grassii* and *Pheidole rugosula* (all invasive species) were very abundant in the scrub sites, but almost completely absent from forest sites. Conversely, *Heteroponera brounii* and *Prolasius advenus* (both endemic species) were more abundant in the forest sites.

The composition of species at Corban's and Shona scrub sites could be distinguished each month (i.e. monthly data points for a site group closely, Figure 5.6A), but this was less true at Sherwood and Chilcott. However, at forest sites there was considerable overlap in composition of species between months; making it difficult to distinguish site differences (i.e. monthly data points for a site are intermixed with other sites, Figure 5.6B). The average pairwise similarity of species composition between forest sites was greater than 75%.

The composition of ants at three scrub sites (Sherwood, Chilcott, Shona) were correlated ($\rho > 0.66$) with monthly environmental variables (Table 5.1), representing seasonal climatic conditions. However, there was no single environmental variable that was in itself strongly correlated to the monthly composition of ant composition. A principal component analysis (PCA) also showed that 88.2% of the variation in the environmental data is on the 1st PCA component, with equal weighting of all environmental variables. Furthermore, all environmental variables were strongly correlated (average collinearity $\rho = 0.87$). The composition of ants at Corban's and all forest sites was not well correlated with environmental variables (range = 0.29 - 0.44).

For scrub sites there was significantly higher niche overlap than expected from communities generated by null models, using either the RA2 ($I_{obs} = 0.520$, $I_{sim} = 0.435$, $p < 0.001$) or RA3 algorithm ($I_{obs} = 0.520$, $I_{sim} = 0.507$, $p < 0.001$). Similarly, for forest sites there was significantly higher niche overlap than expected from communities generated by null models, using either the RA2 ($I_{obs} = 0.387$, $I_{sim} = 0.325$, $p < 0.002$) or RA3 algorithm ($I_{obs} = 0.520$, $I_{sim} = 0.333$, $p = 0.023$).

5.3.2 Competitive interactions

Eight species were observed on baits from twenty sites (Table 5.3). However, three sites had no ants, and 50% of sites had less than three species (Figure 5.7). Environmental variables were not correlated with the composition of ant species at sites, whether or not the frequency of species ($\rho = 0.246$) or presence/absence of species was used ($\rho = 0.197$).

The occupancy of bait stations at a site was overall relatively low, with on average only 40% of bait stations occupied by ants at the 12 minute interval, and 56% of bait stations occupied at the 60 minute interval. Of the baits that were eventually occupied, the majority of these were first occupied in the 12 and 24 minute intervals ($X^2 = 268.19$, d.f. = 4, $p < 0.001$). This was also relatively consistent for each species (Figure 5.8).

Tetramorium grassii was the most common species (found at 17 sites) but its mean occurrence on baits within a grid was low, that is, it was not frequently found at baits within a grid. Most of the baiting grids were numerically dominated by two species, *Paratrechina* spp., and *Pheidole rugosula* (Table 5.3). These two species had both a high mean occurrence on baits within a grid and also a high mean abundance score. *Pheidole rugosula* was the most behaviourally dominant species. However, several other species also had the ability to displace other species at baits, and (to a lesser degree) monopolise baits. *Tetramorium grassii* was the only species that had a lower than 50% score of turnover ability. There was no strong correlation between discovery and turnover ($r^2 = 0.13$), or discovery and monopoly ($r^2 = -0.19$).

At the regional scale, the observed C-score was significantly smaller than the expected C-scores generated by null models (observed index [$\mathbf{I}_{obs}$] = 3.464, mean of simulated indices [$\mathbf{I}_{sim}$] = 5.012, p = 0.055; Figure 5.9). This indicates that species co-occurred more often than expected. There was no evidence for segregation (p = 0.947) via inter-specific competition at the regional scale. This result is not surprising as the three most common species co-occur at almost all sites. At the local scale, there was also no evidence for segregation within bait grids. Rather, the meta-analyses indicated that ant communities were strongly aggregated as the average effect size (SES) was significantly smaller than zero (12 minute interval p = 0.009; 60 minute interval, $p < 0.001$; Table 5.4).

5.4 Discussion

This is the first study to examine the composition and structure of ant communities in New Zealand. There are three major findings in this study. First, habitat played a major role in the partitioning of species. There was a significant separation between scrub and forest habitats in terms of species composition. This separation corresponded very strongly with the presence of invasive ant species in scrub habitats and endemic ant species in forest habitats.

Second, climatic factors did play a major role in structuring the community in terms of abundance and richness, but did not have any affect on the partitioning of species. The abundance and species richness declined in winter months at both scrub and forest habitats, although the decline in abundance was more noticeable in scrub because of the high abundance in the summer months. In terms of species composition, the separation of scrub and forest habitats was consistent throughout the year. This consistency in composition was also evidenced by the lack of species turnover throughout the year for either scrub or forest communities. Significant aggregation patterns of niche overlap indicated the same species co-occurred throughout the year, rather than partitioning the environment on an annual time scale. Although there was no annual partitioning of species, some scrub sites had a species composition that could be consistently distinguished throughout the year. That is, there was a unique combination of species at some scrub sites. This did not occur in the forest habitat; all forest sites had all of the common species. This suggests that site history, possibly related to dispersal and colonisation, has an important role to play in determining the composition of species in scrub sites.

Third, in terms of spatial co-occurrence patterns, there was no evidence that inter-specific competition structured the community of invasive ant species at either regional or local scales. At the regional scale, null model analysis indicates that species co-occurred more often than expected (i.e. were aggregated). Inter-specific competition was expected to result in segregation patterns of species co-occurrence at the local scale. However, this did not occur, and again a strong aggregated pattern was evident from the meta-analysis of local sites.

The difference in species composition between scrub and forest habitats is unlikely to explained by limited dispersal ability - all of these sites have the potential to be colonised by all of the ant species (either endemic or invasive).

A combination of microhabitat and abiotic factors is most likely to explain the difference in species composition of scrub versus forest habitats. Microhabitat plays a key role in the movement and foraging of ants (Majer et al. 2004). Fast movement allows rapid discovery and recruitment for defence. However, movement becomes more difficult in complex, or three-dimensional environments such as forest leaf litter (Majer et al. 2004). Movement is more effective on foraging surfaces such as inter-connecting branches and the bare ground. The common species in the forest habitat are defined functionally as cold climate specialists, and solitary predators, which are generally cryptic with relatively small colonies (Brown 2000). They do not rely on mass recruitment and fast locomotion in order to exploit or dominate resources. Conversely, *Paratrechina* and *Pheidole* (in scrub habitats) are defined functionally as opportunistic or generalised foragers, respectively (Brown 2000). Their foraging strategy is essentially based on the fast discovery of resources (*Paratrechina)*, or on behavioural dominance (*Pheidole*). Thus, it may be difficult for *Paratrechina* and *Pheidole* species to maximise their respective foraging strategies in a forest environment.

Sarty et al. (2006) have recently shown that habitat complexity can play a role in species coexistence by determining which species are able to dominate resources. Differences in microhabitat are also likely to influence overall community composition. For example, large differences in ant communities were found between relatively open canopy habitats (scrub/heath) compared to closed canopy habitats (forest) in south-western Australia (Andersen 1986a).

Seasonal climates often produce a strong seasonal trend in ant abundance (Lynch 1981; Andersen 1986b; Albrecht & Gotelli 2001). In general, the foraging activity of many ant species increases in spring due to increased worker production after winter die-off (Hölldobler & Wilson 1990). In the current study, there was a seasonal trend in ant abundance in both scrub and forest habitats, with the common species all following this trend.

However, abiotic factors, especially seasonal temperature is also likely to affect the composition of species in different habitats. In New Zealand, Davis-Colley et al. (2000) found differences in air and soil temperature between closed canopy forest and open pasture habitats. Soil temperature was 2–5^{o}C higher in the pasture compared to forests in summer due to solar heating of the soil surface (Davis-Colley et al. 2000). If species have different tolerances and preferences for different abiotic conditions this could affect community composition through the temporal partitioning of species. For example, Andersen (1986b) found although total ant activity followed seasonal cycles, individual species followed distinct foraging cycles in south-eastern Australia. However, despite a strong seasonal trend in ant activity (lower activity in cooler months), Albrecht and Gotelli (2001) found no evidence of seasonal niche partitioning by ground-foraging ants (i.e. species-specific responses).

It is likely that endemic species in New Zealand are able to tolerate cooler forest environments. They are found throughout New Zealand, in environments considerably cooler than the Auckland region. Conversely, the invasive species originate from eastern Australia and South Africa, where temperatures are considerably warmer than New Zealand. Additionally, these invasive species are currently restricted to the warmer parts of New Zealand, although large-scale climatic modeling suggests they have potential to spread further in New Zealand (see Chapter Seven).

Differences in food and nest resources will also determine which species can persist in different habitats. For example, in a study of fens (open grass, wetland) versus closed forest, Ratchford et al. (2005) found ant species richness was higher in forests. This was explained by the forest habitat having more suitable nest sites (e.g. under rocks, in rotting logs) compared to the saturated wetland fen areas. It is possible that food and nest resources are not suitable for invasive species in the forest habitats in this study. This needs further research. Food resources were examined in heavily urbanised sites, with the aim of further examining the ant community comprised almost exclusively of invasive species (i.e. a synthetic community, see Morrison 1996), with emphasis on inter-specific competition and spatial partitioning. There was no evidence for spatial partitioning via inter-specific competition at the regional scale. Here, the three most common species co-occurred at almost all of the sites, thus it is not surprising that strong patterns of aggregation arose in the null model analysis.

However, an aggregated pattern was also evident from the meta-analysis of local sites, indicating species were not spatially segregated via inter-specific competition. This was unexpected because there are often distinct foraging strategies for ant species based on competitive abilities (Fellers 1987; Hölldobler & Wilson 1990). In general, certain species exploit resources through quick discovery (exploitative competition) but are then excluded from the baits as other species arrive which are behaviourally aggressive (interference competition). In this study there was no such definitive split in discovery or aggression. The discovery ability of most of the species was very similar, and although *P. rugosula* was the most behaviourally aggressive (as measured by numerical dominance, turnovers and monopoly), other species also showed these abilities.

Although aggression and exclusion was observed between species in this study, inter-specific competition does not have a major influence on the ant community. It is possible that inter-specific competition is less important in this community because the environment is not fully saturated with ants. For example, at half of the sites there were only three or fewer ant species. Furthermore, even after 60 minutes only 56% of baits were occupied (on average). The majority of baits were first occupied in the 12 and 24 minute intervals and it appears that concentrated recruitment to these baits occurred rather than the discovery of additional baits. Although inter-specific competition is often regarded as a major structuring force it is perhaps not as important as currently thought. Several recent papers have strongly questioned its importance (Floren & Linsenmair 2000; Ribas & Schoereder 2002; Blüthgen & Stork 2007).

Of major interest to the study of invasive ants in New Zealand is why the urban environment remains relatively unsaturated in terms of ants (both their abundance and species richness). All of the invasive species in this study have been present in New Zealand for many decades (on average >65 years, see Chapter Seven). Given many environments in New Zealand are effectively unoccupied by endemic ant species, why haven’t invasive species been able to fully exploit these new environments? Additionally, very few ants were caught in the arboreal habitat (via vegetation beating), further suggesting that invasive species have not been able to fully exploit a new and unoccupied niche? Population and colony level studies would be useful to examine this issue further.

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Table 5.1 Latitude and longitude (decimal degrees), species diversity estimates and the maximum BIOENV correlation (ant species composition versus environmental variables) for scrub and forest sites.

		Species richness			
Site	**Latitude/Longitude**	**Observed**	**Estimated (Chao 2)**	**% Efficiency**	**BIOENV (ρ)**
Scrub					
Sherwood	36° 51.49S, 174° 38.34E	8	8.0	100	0.788
Chilcott	36° 52.18S, 174° 38.20E	10	10.0	100	0.661
Corban’s	36° 52.67S, 174° 37.56E	6	6.0	100	0.333
Shona	36° 52.23S, 174° 35.41E	12	12.9	92.8	0.706
Forest					
Shona	36° 53.30S, 174° 36.99E	9	9.9	90.7	0.406
Oratia	36° 54.99S, 174° 36.30E	7	7.4	93.8	0.310
Swanson	36° 52.62S, 174° 33.76E	7	7.0	100	0.403
Huapai	36° 47.64S, 174° 29.83E	8	17.1	46.5	0.527

Table 5.2 Endemic and invasive ant species recorded from New Zealand. * - refers to previous history of being invasive in another country. Origins: AF - African, SA – South American, AS – Asian, all others are of Australian origin. Excludes invasive species found only on the Kermadec Islands (*Monomorium floricole* and *Plagiolepis alluaudi*).

Genus + species	**Authority**	**Biostatus**	**First Record**
Amblyopone australis	Erichson 1842:261	Invasive	1876 (Brown 1958)
Amblyopone saundersi	Forel 1892:336	Endemic	
Cardiocondyla minutior	Forel 1899:120	Invasive *, T	2000 (Harris & Berry 2001)
Discothyrea antarctica	Emery 1895:266	Endemic	
Doleromyrma darwiniana	(Forel) 1907:28	Invasive	1959 (Taylor 1959)
Heteroponera brounii	(Forel) 1892:335	Endemic	
Huberia brounii	Forel 1895:41	Endemic	
Huberia striata	(Fr. Smith) 1876:481	Endemic	
Hypoponera eduardi	(Forel) 1894:15	Invasive *, AF	1895 (Brown 1958)
Hypoponera punctatissima	(Roger) 1859:246	Invasive *, AF	2003 (Harris 2003)
Iridomyrmex sp.	undescribed	Invasive	1916 [1]
Linepithema humile	(Mayr) 1868:164	Invasive *, SA	1990 (Green 1990)
Mayriella abstinens	Forel 1902:452	Invasive	1958 (Harris & Berry 2001)
Monomorium antarcticum	(Fr. Smith) 1858:167	Endemic	
Monomorium antipodum†	Forel 1901:377	Endemic	
Monomorium fieldi†	Forel 1910:30	Invasive	1950s [2]
Monomorium pharaonis	(Linnaeus) 1758:580	Invasive *, AS	1941 [1]
Monomorium smithii	Forel 1892:342	Endemic	
Monomorium sydneyense	Forel 1902:442	Invasive	2001 [1]
Ochetellus glaber	(Mayr) 1862:705	Invasive *, AS	1927 [1]
Orectognathus antennatus	Fr. Smith 1853:228	Invasive	1927 (Brown 1958)
Pachycondyla castanea	(Mayr) 1865:69	Endemic	
Pachycondyla castaneicolor	(Dalla Torre) 1893:38	Endemic	
Paratrechina sp.A	undescribed	Invasive	1941 [1]
Paratrechina sp.B	undescribed	Invasive	1941 [1]
Pheidole megacephala	(Fabricius) 1793:361	Invasive *, AF	1942 (Berry et al. 1997)
Pheidole proxima	Mayr 1876:104	Invasive	2004 [2]
Pheidole rugosula	Forel 1902:423	Invasive	1958 (Berry et al. 1997)
Pheidole vigilans	Fr. Smith 1858:166	Invasive	1941 (Berry et al. 1997)
Ponera leae	Forel 1913:175	Invasive	1958 (Harris & Berry 2001)
Prolasius advenus	(Fr. Smith) 1862:53	Endemic	
Rhytidoponera chalybaea	Emery 1901:51	Invasive	1959 (Taylor 1961)
Rhytidoponera metallica	(Fr. Smith) 1858:94	Invasive	1959 (Taylor 1961)
Solenopsis sp.	undescribed	Invasive	2001 [2]
Strumigenys perplexa	(Fr. Smith) 1876:491	Invasive	1876 (Brown 1958)
Strumigenys xenos	Brown 1955:182	Invasive	1955 (Brown 1955)
Technomyrmex albipes	(Fr. Smith) 1861:38	Invasive *, AS	1924 [1]
Tetramorium bicarinatum	(Nylander) 1846:1061	Invasive *, AS	1959 (Taylor 1961)
Tetramorium grassii	Emery 1895:37	Invasive AF	1941 (Taylor 1961)

[1] R. Harris personal communication
[2] S. O'Connor personal communication
† Note Gunawardana (2005) for problems with Monomorium *antipodium*/*fieldi* taxonomy.

Table 5.3 The relationship between exploitative and interference competition for the five most common ant species. Species are ranked in order of overall dominance. See methods for description of dominance categories.

	Numerical Dominance		**Interference Competition**		**Exploitative Competition**
Species	**Mean Occurrence**	**Baits dominated**	**Turnovers**	**Monopoly**	**Discovery**
Pheidole rugosula	0.464	0.514	0.714	0.504	0.467
Paratrechina spp.	0.405	0.263	0.609	0.357	0.434
Iridomyrmex sp.	0.080	0.000	0.500	0.310	0.429
Ochetellus glaber	0.140	0.166	0.500	0.250	0.238
Tetramorium grassii	0.272	0.000	0.190	0.159	0.509

Table 5.4 Meta-analysis of effect sizes for co-occurrence patterns at the local scale for each time interval. Numbers in the lower and upper tails indicate the number of assemblages for which the C-score was respectively less than or greater than predicted by the null model. The number in parentheses indicates the number of assemblages with significant patterns ($p<0.05$, one-tailed test). A one-sample t-test was used to test the hypothesis that the standardized effect size (SES) for the set of assemblages does not differ from zero. See methods for description of meta-analysis. Communities with little co-occurrence should frequently reject the null hypothesis in the upper tail, and the meta-analysis pattern would be an effect size significantly greater than zero.

Time interval	**Lower tail**	**Upper tail**	**Average effect size**	**SD effect size**	**t**	**p**
12 minute	10 (6)	6 (0)	-2.00	3.00	2.66	0.009
60 minute	14 (10)	1 (0)	-4.11	3.84	4.14	<0.001

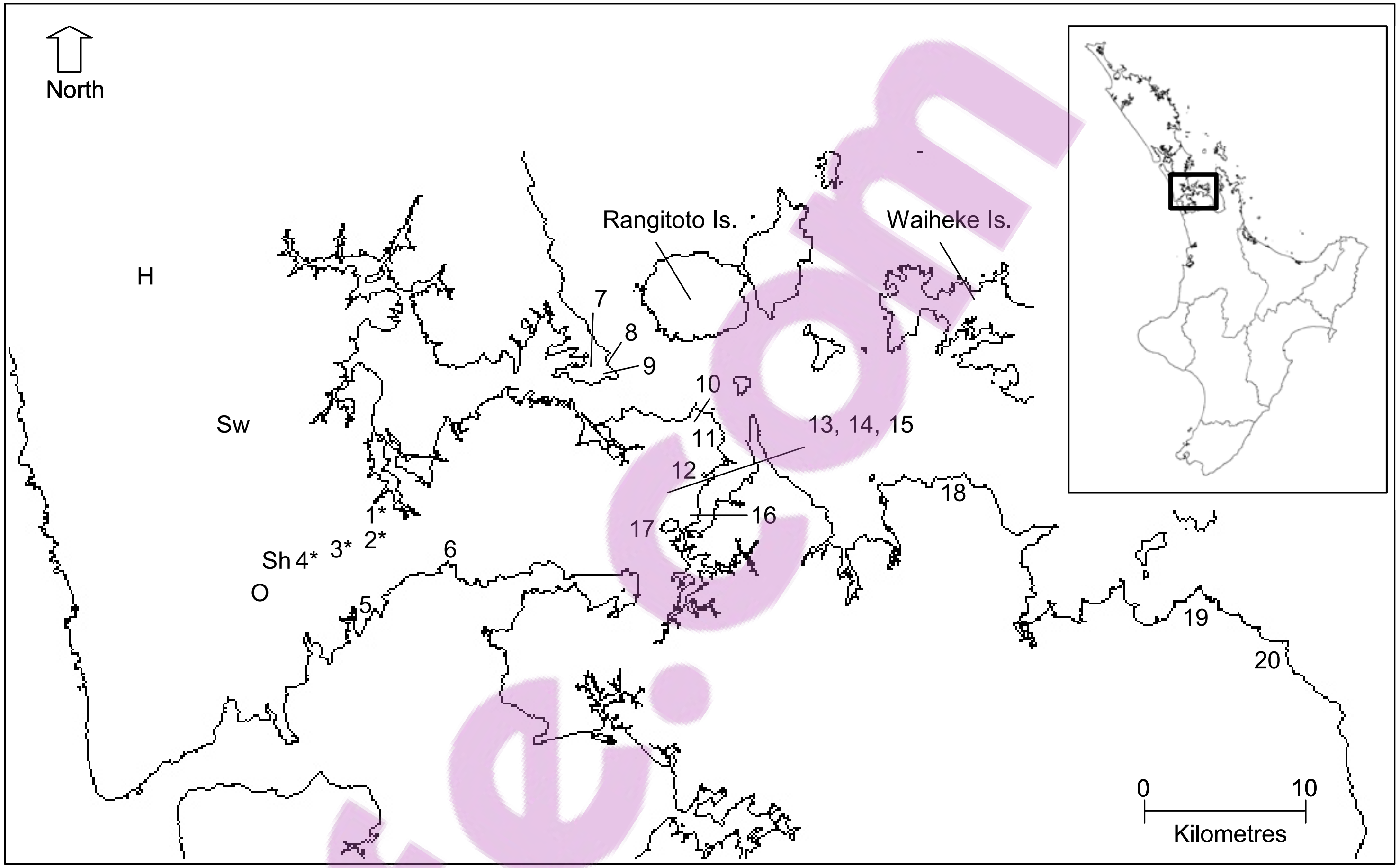

Figure 5.1 Location of study sites in the Auckland region. Sites marked with * were part of the 'Habitat Partitioning' section (scrub sites), and sites with letters are forest sites (H. Huapai reserve, O. Oratia reserve, Sh. Shona reserve, Sw. Swanson reserve). Numbered sites were used for the 'Competitive Interaction' section: 1. Sherwood reserve, 2. Chilcott Brae reserve, 3. Corban's estate, 4. Shona restoration plot, 5. Tangiwai reserve, 6. Lynfield reserve, 7. Rotary reserve, 8. Ngataringa park, 9. Devonport domain, 10. Glover reserve, 11. Churchill park, 12. Pt England reserve, 13. Tamaki campus, 14. Tamaki campus, engineering, 15. Colin Maiden reserve, 16. Mt Wellington War Memorial Reserve, 17. Bertrand reserve, 18. Maraetai, 19. Tapapakana regional park, 20. Orere Point. Inset: the North Island of New Zealand with the location of the Auckland study area (boxed).

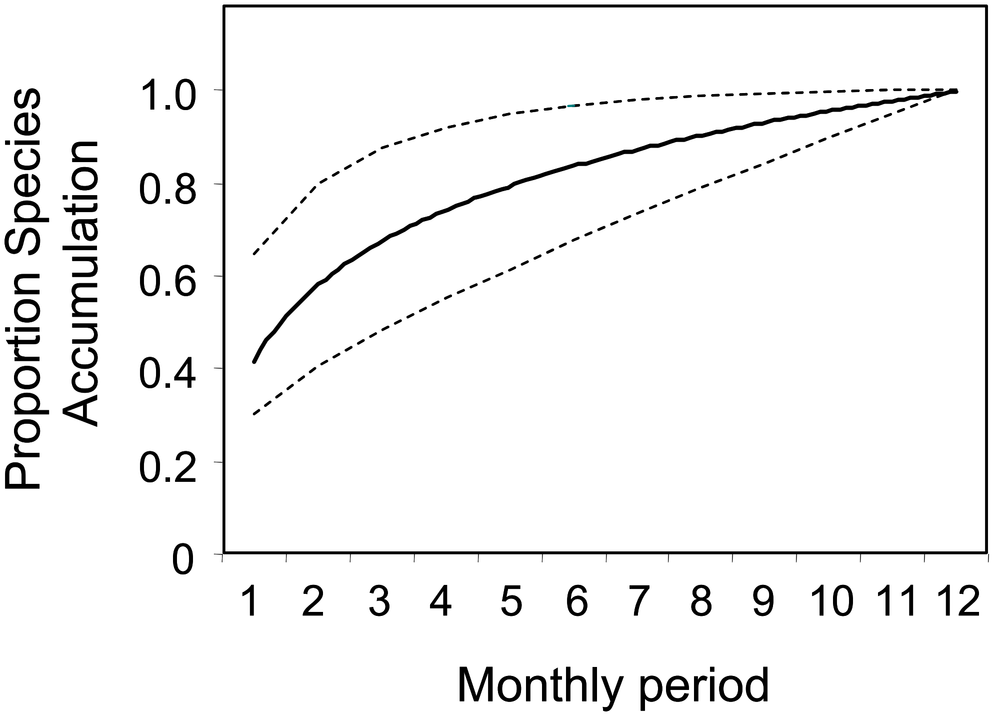

Figure 5.2 The accumulation of species over time. The solid line represents the line of best fit ($y = 0.2342\text{Ln}(x) + 0.4164$, $R^2 = 0.99$) for all sites (scrub and forest), with the dashed lines representing the upper (Sherwood) and lower (Huapai) boundaries of species accumulation.

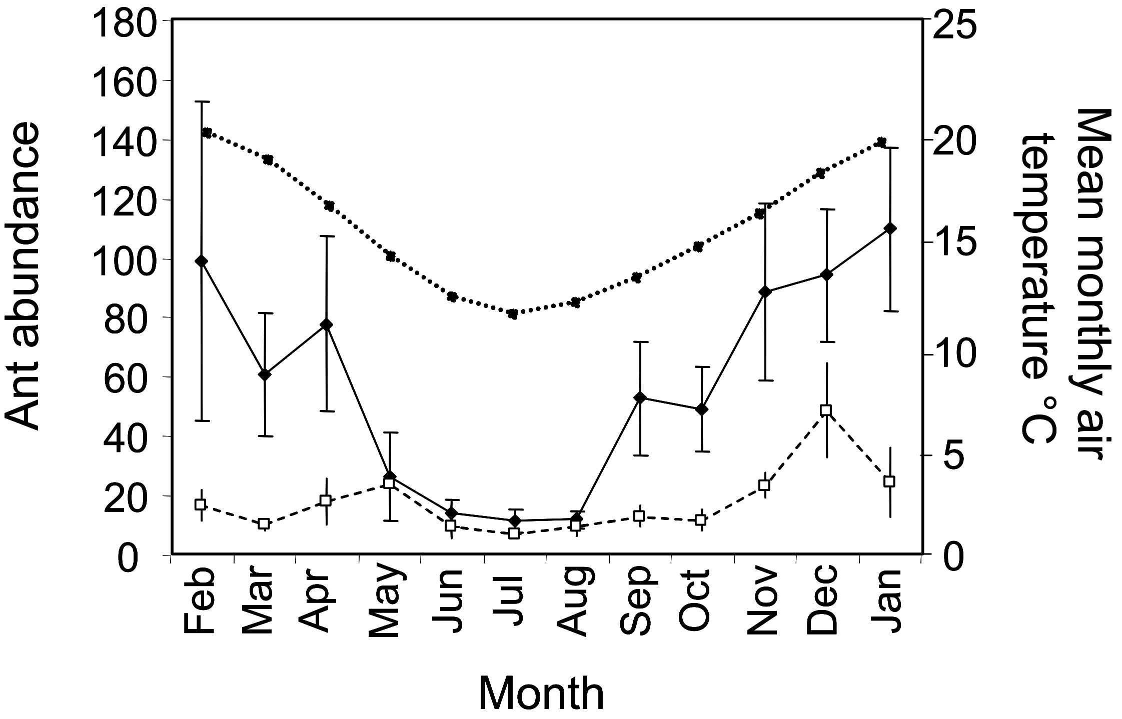

Figure 5.3 The mean monthly abundance (±SD) of ants (all species combined) at scrub sites (solid line) and forest sites (dashed line). Dotted line represent mean monthly air temperature (C). Months indicated by a three letter code.

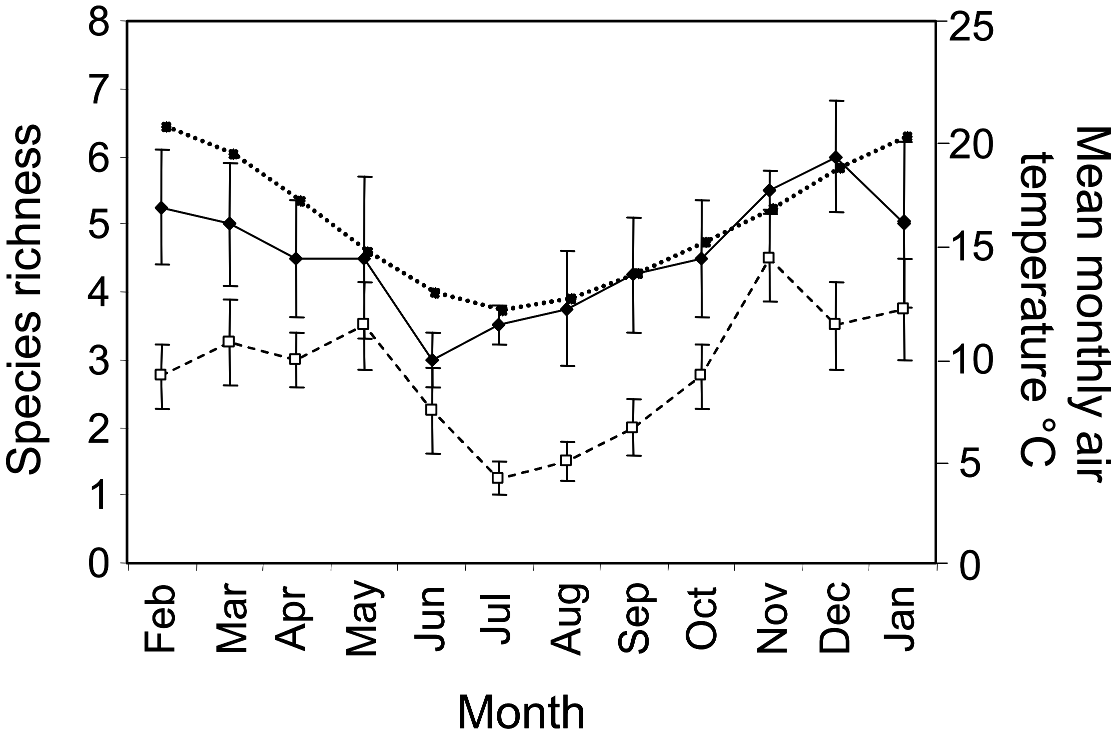

Figure 5.4 The mean monthly species richness (±SD) of ants at scrub sites (solid line) and forest sites (dashed line). Dotted line represent mean monthly air temperature (C). Months indicated by a three letter code.

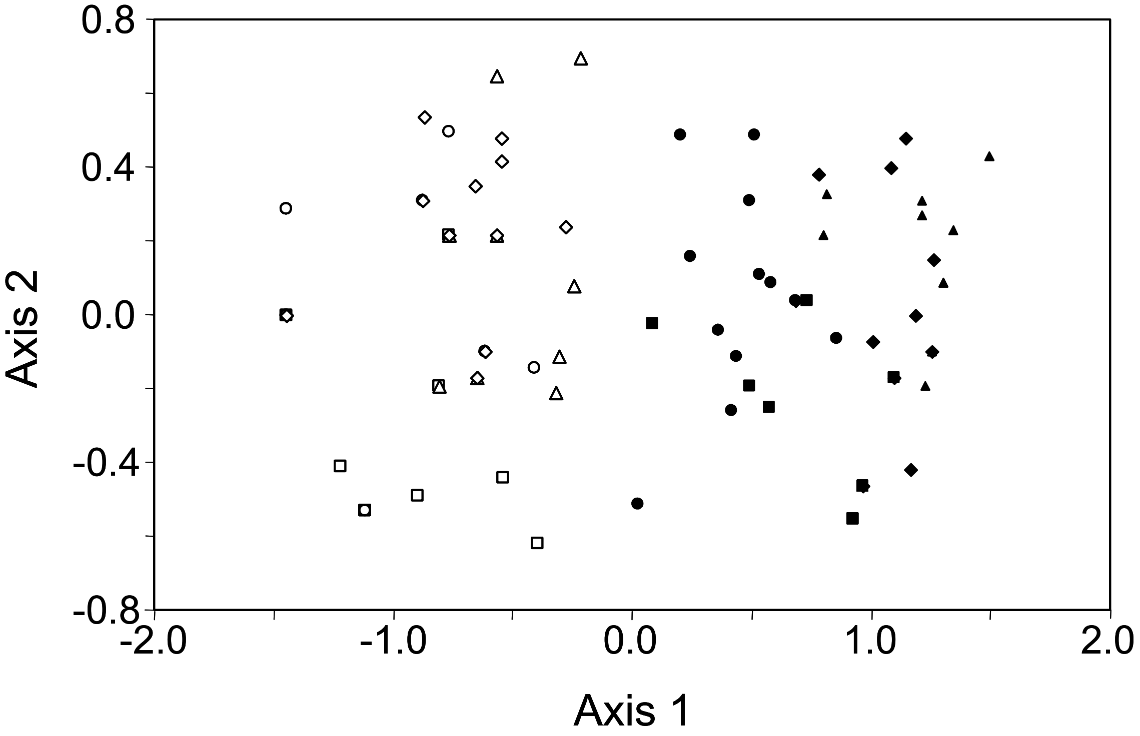

Figure 5.5 The overall composition of ant species at scrub and forest sites for each month. Scrub sites (shaded black); Sherwood (triangle), Chilcott (diamond), Corbans (square) and Shona (circle). Forest sites (shaded white with black edge); Shona reserve (triangle), Swanson (diamond), Huapai (square) and Oratia (circle). Monthly samples are not labelled to improve clarity.

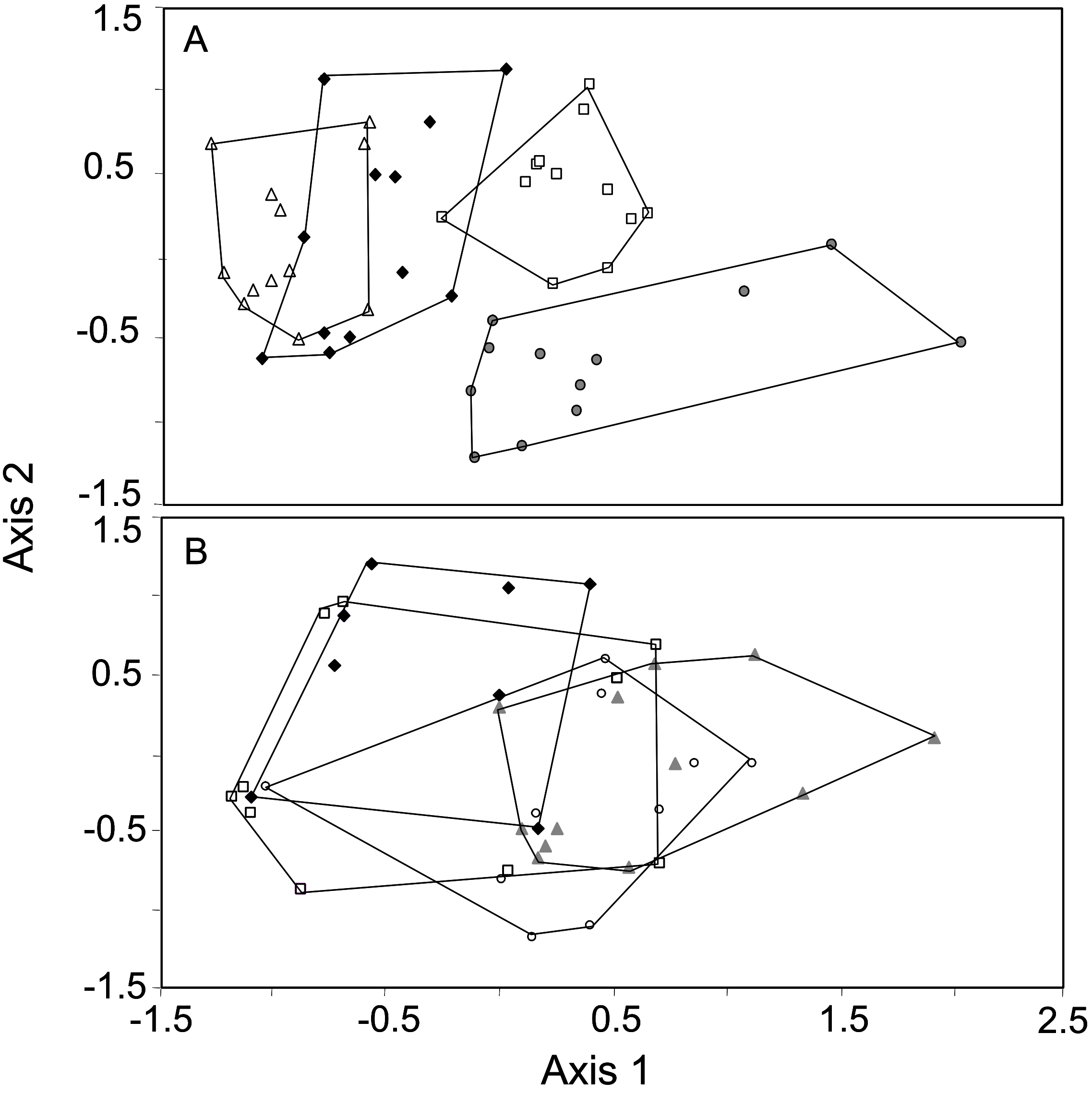

Figure 5.6 The composition of ant species for each month, separating A) scrub and B) forest sites. The boxes bound all points from a site and illustrate overlap between sites. A) Scrub sites; Sherwood (white triangle), Chilcott (black diamond), Corbans (white square) and Shona (grey circle). B) Forest sites; Shona reserve (grey triangle), Swanson (white circle), Huapai (black diamond) and Oratia (white square).

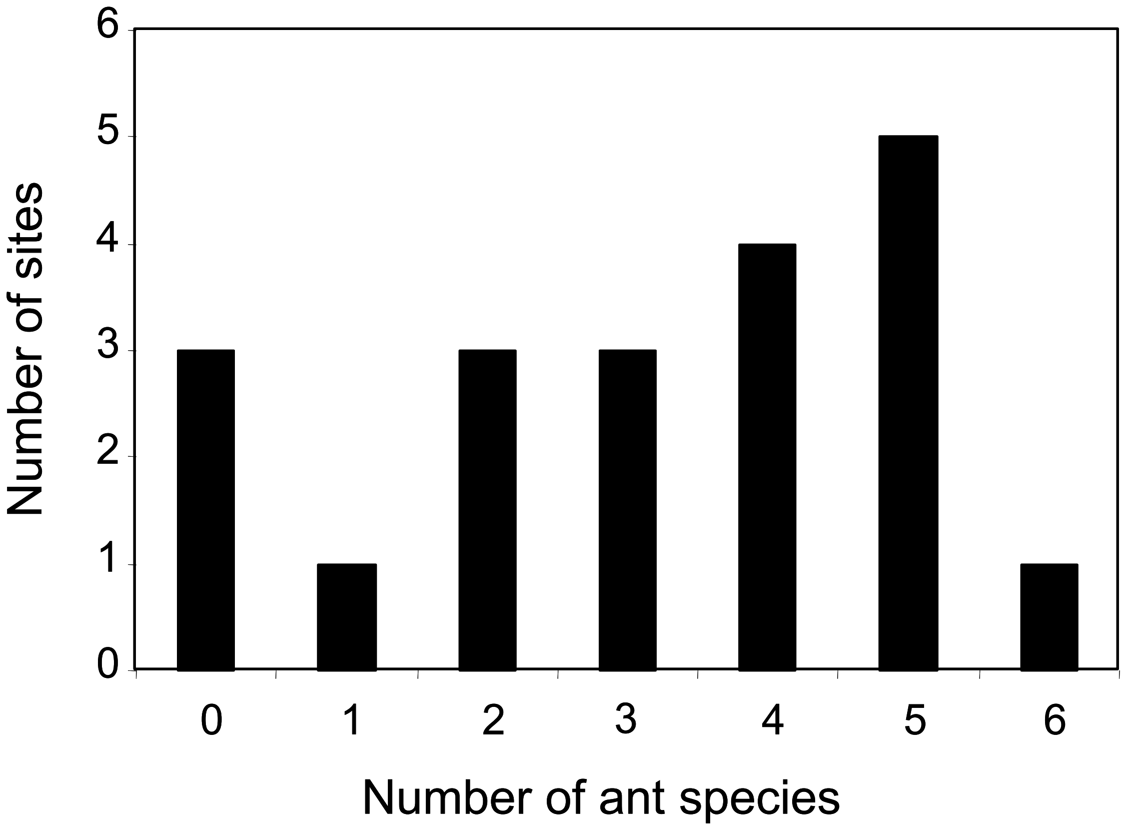

Figure 5.7 The frequency of ant species richness across twenty sites in urban Auckland.

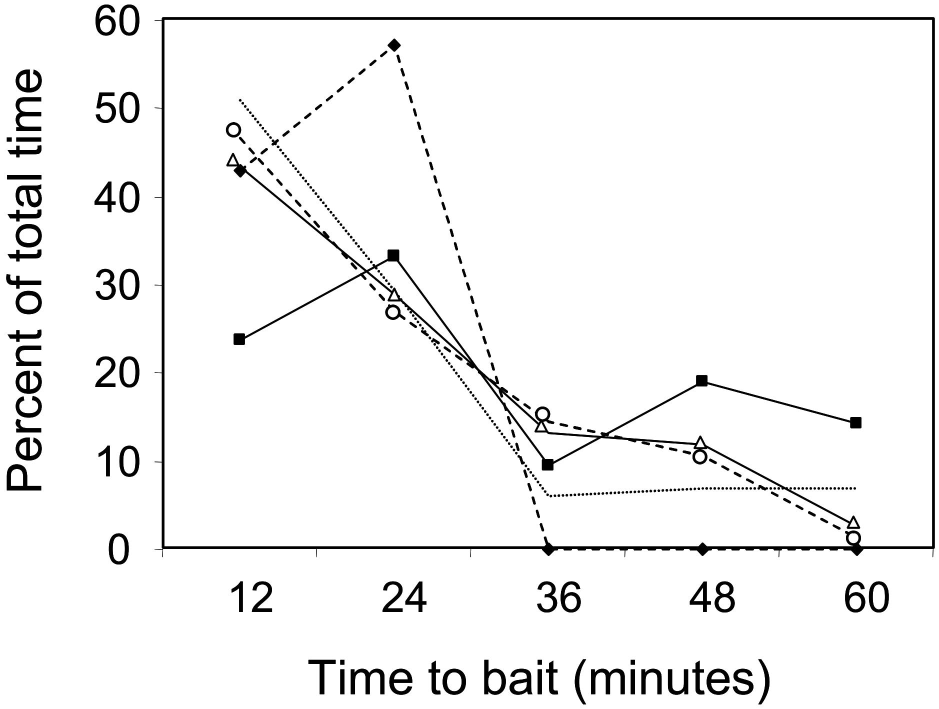

Figure 5.8 The percentage of time taken for each species to arrive at a bait. *Pheidole rugosula* (circle, dashed line), *Paratrechina* spp. (triangle, solid line), *Iridomyrmex* sp. (diamond, dashed line), *Ochetellus glaber* (square, solid line), and *Tetramorium grassii* (no marker, dotted line).

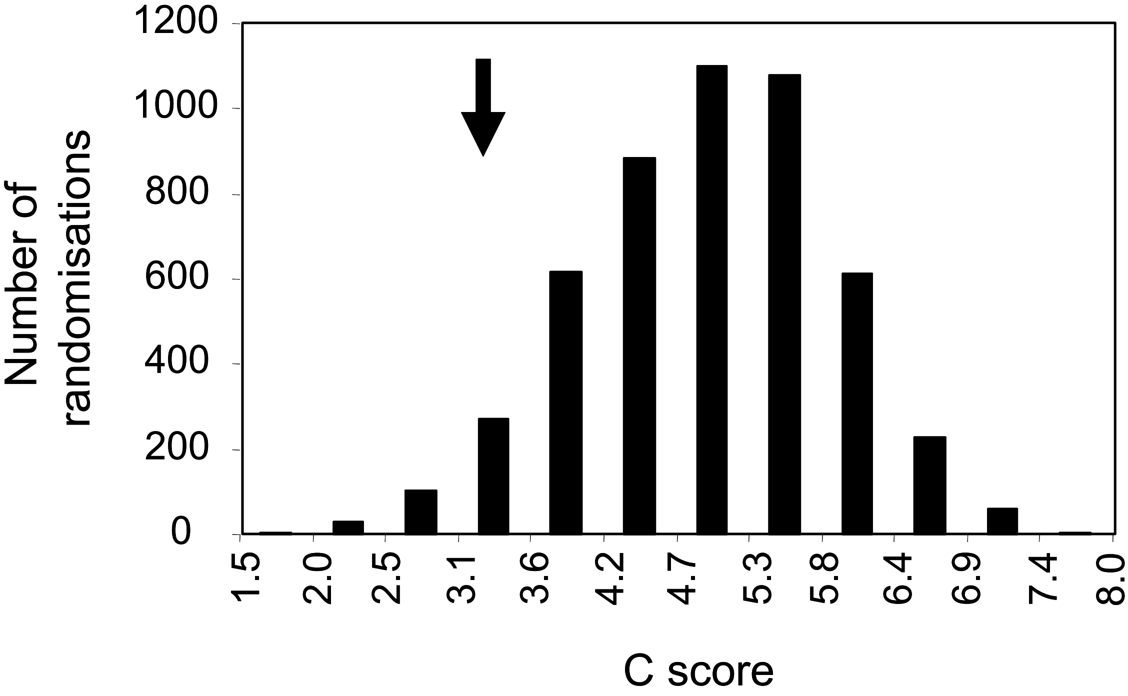

Figure 5.9 Histogram of the frequencies of simulated C-scores from EcoSim null models (5000 randomisations) at the regional scale (p = 0.055 for aggregation). The observed regional C-score is indicated by the arrow.

Transferability of Distribution Models for Two Invasive Ant Species

6

Abstract

An important step to understanding and managing invasive species is determining the factors responsible for their current and potential distribution. Species distribution modeling (SDM) aims to predict areas that describe where environmental conditions are suitable for the survival of a species. It is often assumed that models fitted in one region will be applicable to another region, that is, the models are transferable. However, recent work has suggested this is not always the case, and model transferability has received relatively little attention. In this study the transferability of distribution models of two invasive ant species, *Anoplolepis gracilipes* (Smith) and *Wasmannia auropunctata* (Roger), is examined using their native and introduced ranges across the globe. The DOMAIN modeling approach was used in DIVA-GIS software with 11 climate variables at a spatial resolution of 10 minutes. Each of 10 native range and 10 introduced range models were evaluated individually by internal evaluation. Evaluation was also carried out using native records to evaluate models produced by introduced records, and vice versa (i.e. external evaluation). Although both species are already widespread, SDMs predicted a large potential global range where both species could spread, establish and become invasive. In relation to their native ranges, a number of climate variables associated with the introduced range of both species showed reduced seasonality. For both species, the internal evaluation of models was generally very good with high AUC and Kappa values, although omission error was outside the *a priori* criteria of <0.05. However, external evaluation was poor, particularly for omission error, which was very high >0.40. Thus, both the native and introduced models failed transferability. That is, native models did not successfully predict the introduced range, and vice versa. Both native and introduced models under-predicted the corresponding reciprocal ranges. Poor transferability has widespread implications for the prediction of species potential distributions in a range of different applications. However, several methodological issues with model transferability need further investigation, including the use of different evaluation statistics, the implications of including/excluding outlying locality records, and the importance of selecting the climate variables that have the most proximal effects on a species distribution.

6.1 Introduction

Invasive species are a global problem, affecting productive agroforestry sectors, human health and natural ecosystems (Mooney & Drake 1986; Drake et al. 1989; Sandland et al. 1999; Mack et al. 2000). Fundamental to understanding and managing invasive species is the identification of their current and potential distribution, and also the factors responsible for this distribution. Such information is important in planning and prioritising areas for surveillance and for the success of control programs. Thus, understanding, and being able to predict, the distribution of a species represents an important tool for invasive species management (Anderson et al. 2003).

Species distribution modeling (SDM) aims to predict areas that describe where environmental conditions are suitable for the survival of the species. In general, these modeling methods combine species locality data (geo-referenced coordinates of latitude and longitude from confirmed presence and/or absence) with environmental variables to create a model of the species requirements (Anderson et al. 2003). There has been a large number of recent papers providing an overview of species distribution modeling, a comparison of modeling methods, and ways to minimise errors (Fielding & Bell 1997; Guisan & Zimmermann 2000; Zaniewski et al. 2002; Anderson et al. 2003; Segurado & Araújo 2004; Guisan & Thuiller 2005; Araújo & Guisan 2006; Elith et al. 2006; Hartley et al. 2006; Phillips et al. 2006; Pearson et al. 2006; Randin et al. 2006). One major issue for the study of invasive species is whether the native ecological niche of an invasive species is conserved in its introduced range, that is, niche conservatism (Peterson et al. 1999; Weins & Graham 2005). If a species niche is conserved, then the species should only be able to invade regions that have similar niche conditions to that of their native range (Wiens & Graham, 2005). In terms of species distribution modeling, it is often assumed that models fitted in one region will be applicable in another region. That is, the models are transferable from one region to another (Fielding & Haworth 1995; Kleyer 2002; Randin et al. 2006). Transferability is an important feature of SDMs, particularly for invasive species where a significant part of invasive species management is to make projections into new areas where species may become invasive (i.e. transferability in space).

Niche conservatism and model transferability can be determined through species distribution modeling (Peterson et al. 1999; Weins & Graham 2005). For an invasive species, SDMs are created with data from the native range and the invaded range separately. Then reciprocal predictions and evaluations are made, for example, using data from the native range onto invaded range models, and vice versa. Despite the potential importance of niche conservatism and the transferability of SDMs to understanding species distributions, these concepts have received relatively little attention (Weins & Graham 2005; Randin et al. 2006).

However, several recent papers have examined niche conservation with contrasting views. For example, Randin et al. (2006) studied 54 alpine plant species in Switzerland and Austria and showed transferability failed for 53-68% of species depending on the model used. Overall they found limited geographical transferability and called for caution when using niche-based models. Fitzpatrick et al. (2007) used occurrence data of the red imported fire ant (*Solenopsis invicta*) from its native range in South America and the introduced range in the USA to examine limits to its distribution. They found that, although there was some geographical overlap in predictions, species distribution models were generally not transferable between the native and introduced ranges and did not predict similar distributions. Furthermore, in the initial stages of invasion into the USA, fire ants occupied environments similar to their native range, but subsequently invaded harsher (colder, drier) environments; evidence against the niche conservatism concept. Finally, Roura-Pascual et al. (2006), examined the native and introduced distribution of the Argentine ant (*Linepithema humile*) and found its ecological niche did not differ markedly between its native and invaded ranges; demonstrating evidence for the conservatism of species ecological niches.

The aim of this study is to further examine niche conservatism and the transferability of SDMs between the native and introduced ranges of two well known invasive ant species, *Anoplolepis gracilipes* (Smith) and *Wasmannia auropunctata* (Roger).

6.2 Methods

6.2.1 Modeling approach

The DOMAIN modeling approach was used to predict the distribution of each invasive ant species. DOMAIN uses a distance-based measure (the Gower metric) to assess new sites in terms of their environmental similarity to sites of known presence (Carpenter et al. 1993). DOMAIN was implemented in DIVA-GIS software (version 5.2, http://www.diva-gis.org), which produces an index on a continuous scale (maximum score = 100), where higher scores represent areas of higher suitability. For example, an area with a score of 90 would have an average variation in climate of no more than 10% of the range of a known occurrence record.

6.2.2 Model inputs

Species modeled

Two species are modeled, *Anoplolepis gracilipes* (Smith), commonly known as the yellow crazy ant or the long-legged ant; and *Wasmannia auropunctata* (Roger), commonly known as the little fire ant. Both these species have good quality locality data for modeling and they also represent invasive ant species which are of particular concern in the Pacific (Jourdan 1997; Wetterer 2002, 2005; Wetterer & Porter 2003; Wetterer & Vargo 2003; Lester & Tavite 2004). Geo-referenced locality records (from sites of confirmed presence) for the native and introduced ranges of both species were obtained from Landcare Research (2007), Wetterer (*pers. comm.*) and for *A. gracilipes*, unpub data (D. Ward). For *A. gracilipes,* several records were excluded from modeling because they represent recent introduced populations that have been eradicated (e.g. New Zealand, eastern Australia), or have most likely not perisisted (e.g. South Africa, Chile); see Wetterer (2005) for further discussion of these specific records. For *W. auropunctata*, records were excluded from modeling because they represent populations persisting in unsuitable environments only because of conditions artificially created by humans (e.g. glasshouses in Canada and England). Records of *W. auropunctata* from Fiji were also excluded as these are erroneous (Ward & Wetterer 2006).

Environmental variables

Climate data was obtained from WORLDCLIM (version 1.3, http://www.worldclim.org), which is explained in detail in Hijmans et al. (2005). WORLDCLIM contains climate data (monthly precipitation and monthly mean, minimum and maximum temperature) at a spatial resolution of 10 minutes (~18 x 18 km resolution) obtained by interpolation of climate station records from 1950-2000. From this baseline climate data, a number of climate variables are derived, of which 11 are used in this study (Table 6.1, 6.2). The climate variables represent a combination of monthly and annual trends, seasonality and extreme environmental conditions. For each species, a principal component analysis (PCA) was used (PRIMER v5.0, Clarke & Warwick 2005) to analyse locality records in relation to environmental data, for both the native and introduced ranges.

6.2.3 Model building and evaluation

Coordinates for species locality records were converted to decimal latitude and longitude in DIVA-GIS. Locality records were ‘cleaned’ in DIVA-GIS where duplicate records were deleted and only one species occurrence record per grid cell was allowed.

Two types of datasets were used to produce models, one using only native range locality records, and the other using only introduced range locality records. For each dataset, locality records were randomly split into 10 partitions, each with 50% of the original records. For each partition, models were built on 75% of the locality records with the remaining 25% used in model evaluation. Models were projected onto a global map using DIVA-GIS for visual interpretation. A composite model was also created by summing all the 10 individual models (thus 10 models x a maximum score of 100 = 1000).

Models were evaluated by examining the Kappa statistic, omission error and the area under the Receiver Operating Characteristic curve (AUC). These evaluation statistics compare prediction errors using combinations of true/false and presence/absence. Omission error (false negatives, under-prediction) results in areas being classified as climatically unsuitable when they are suitable. Conversely, commission error (false positives, over-prediction) results in areas being classified as climatically suitable when they are unsuitable. For invasive species it is more important to minimise false negatives. That is, it is better to predict that an invasive species will occur in a area (but it never happens) than to predict an invasive will not occur in an area, when it actually could. Models that have a low omission error (false negative rate) should be preferred. For omission error a threshold was applied (DOMAIN score = 90) to determine what values represent true presence and true absence. Pseudo-absences were generated in DIVA-GIS at random in a 1:1 ratio with the number of presence records. A maximum Kappa was calculated in DIVA-GIS providing an index that considers both omission and commission errors (Elith et al. 2006).

AUC measures the ability of a model to discriminate between sites where a species is present versus those where it is absent (Fielding & Bell 1997; Elith et al. 2006). It provides a single measure of overall accuracy that is not dependent upon a particular threshold (Fielding & Bell 1997). AUC ranges from 0 to 1, where a score of 1 indicates perfect discrimination; a score of 0.5 implies discrimination that is no better than random. A value of 0.8 for the AUC means that there is a 80% probability that a random selection from the presence records will have a model score greater than a random selection from the absence records.

Models were evaluated by following a similar approach to Randin et al. (2006). Models were evaluated within (internal evaluation and prediction) and between (external evaluation and prediction) the native and introduced ranges. Each of the 10 native range and the 10 introduced range models were evaluated individually by internal evaluation. Evaluation was also carried out using reciprocal (native/introduced) locality records and models (external evaluation). That is, native range locality records were used to evaluate models produced by introduced range locality records, and vice versa. For these evaluations all available locality records were used to evaluate the composite models. Models are considered to have very good discriminatory value if AUC values are >0.9 (Swets 1988) and Kappa >0.7 (Monserud & Leemans 1992), and omission error is <0.05 (Anderson et al. 2003). Models were considered to have failed transferability if evaluation statistics were not in these ranges.

6.3 Results

6.3.1 Environmental variables associated with current distribution

The first two principle component axes accounted for approximately 66% of the total variation in the environmental variables associated with the current distribution of both species (Table 6.1, 6.2, Figures 6.1, 6.2). The first principle component (PC1) was related to several aspects of the seasonality of temperature, whereas PC2 was related to annual mean temperature and maximum temperature of the warmest month. There were also significant differences between the native and introduced ranges for many environmental variables (Table 6.1, 6.2). In general, environmental conditions associated with the introduced range of both species showed reduced seasonality in a number of variables. In particular, maximum values were lower, and minimum values were higher, as well as several measurements of seasonality being lower overall in the introduced range (Table 6.1, 6.2).

6.3.2 Model predictions

Anoplolepis gracilipes

A total of 360 locality records were obtained for *A. gracilipes*, 164 records from the native range and 196 from the introduced range. The predicted geographic distributions of *A. gracilipes* from models using the native range and introduced ranges are shown in Figures 6.3 and 6.4, respectively.

Areas of high suitability (DOMAIN score of >900 from the composite model) for *A. gracilipes* predicted by native models included much of south and central America, tropical and southern Africa, tropical Asia and northern Australia (Figure 6.3). In general terms, areas of high suitability for *A. gracilipes* predicted by introduced models were more restricted in their predictions, with many parts of the above regions being less suitable (Figure 6.4). However, introduced models predicted greater suitability in eastern and southern Africa (Angolia, Namibia, Zambia, Zimbabwe, Mozambique and Madagascar).

The internal evaluation of models was generally very good (Table 6.3). Both native and introduced models had a very good discriminatory value with high AUC and Kappa values. However, omission error was higher than the <0.05 criteria considered to represent good models. For internal evaluation, introduced models performed better than native models with significantly higher AUC ($W = 55.5$, $p < 0.001$) and Kappa ($W = 71.5$, $p < 0.05$). Omission error ($W = 94$, $p < 0.427$) was not significantly different between introduced and native model in internal evalaution.

However, external evaluation results were very poor for both the introduced (evaluated by native data) and the native model (evaluated by introduced data). For both, models were considered to have failed transferability as evaluation statistics were outside the ranges of AUC >0.9, Kappa >0.7, and omission error was extremely high (Table 6.3). The native model, although poor, did perform better than the introduced model (Table 6.3). The extent of poor model transferability can also be examined by the variation in native and introduced model predictions (Figure 6.5). The introduced model had higher DOMAIN scores (greater suitability) in Mexico, southern Africa, north Africa, Arabia, the Middle East, inland parts of Australia and the Pacific Islands. The native model predicted greater suitability in colder areas and tropical areas.

Wasmannia auropunctata

A total of 252 locality records were obtained for *W. auropunctata*, 120 records from the native range and 142 from the introduced range. The predicted geographic distributions of *W. auropunctata* from models using the native range and introduced ranges are shown in Figures 6.6 and 6.7, respectively.

Areas of high suitability (DOMAIN score of >900 from the composite model) for *W. auropunctata* predicted by native models included most of south and central America, tropical and southern Africa, tropical Asia, Australia, and coastal areas with warm temperate and Mediterranean climates (Figure 6.6). In general terms, areas of high suitability for *W. auropunctata* predicted by introduced models were much more restricted in their predictions, with most parts of the above regions being less suitable (Figure 6.7). Introduced models predicted very few regions of greater suitability compared to native models (Figure 6.8). Not surprisingly, the greatest differences are associated with records of invasion (e.g. Caribbean, eastern Pacific).

For *W. auropunctata*, the internal evaluation of models was generally good (Table 6.3). Both native and introduced models had a very good discriminatory value with high AUC and Kappa values.

However, omission error was higher than the <0.05 criteria considered to represent good models. For internal evaluation, introduced models performed better than native models with higher AUC (W = 79, p = 0.054) and Kappa (W = 80, p = 0.064), although these values were not significant at the 0.05 level of significance. Omission error (W = 102.5, p < 0.879) was not significantly different between introduced and native models for internal evaluation.

For external evaluation, the native model failed transferability as all evaluation statistics were outside the ranges of AUC >0.9, Kappa >0.7, and omission error was extremely high (Table 6.3). The ranges of AUC and Kappa were within the success range for the introduced model, however, there was extremely high omission error associated with this model. Compared with *A. gracilipes*, there was relatively little variation between the native and introduced model predictions for *W. auropunctata* (Figure 6.8).

6.4 Discussion

6.4.1 Model predictions

Both *A. gracilipes* and *W. auropunctata* are significant global pests (Jourdan 1997; Wetterer 2002, 2005; Wetterer & Porter 2003; Wetterer & Vargo 2003; Lester & Tavite 2004). The introduced ranges of both species are spread across a large portion of the globe and their predicted distributions (Figures 6.3, 6.4, 6.6, 6.7) highlight the extent to where they could spread, establish and become invasive. It is likely that both species will continue to spread, assisted largely by the movement of goods by human trade.

For both species, the internal evaluation of models was generally very good with high AUC and Kappa values. Despite omission error being outside than the <0.05 criteria (suggested by Anderson et al. 2003), these internal omission errors were substantially less compared to the external omission error. Both the native and introduced models failed transferability. That is, native models did not successfully predict the introduced range, and vice versa. Both native and introduced models under-predicted the corresponding reciprocal ranges.

There were several consistencies between the two species in this study. PCA results showed that a similar set of environmental variables were associated with the current distribution of both species. Furthermore, the environmental variables associated with the introduced ranges showed evidence of reduced seasonality for both species. In terms of model evaluation, trends were also similar for both species. There was good internal evaluation but poor external evaluation (lower AUC and Kappa, and very high omission error). The external evaluation of both species showed that the native models produced lower omission error, suggesting native models were better at predicting distribution than the introduced models (although both were poor and failed transferability).

6.4.2 Issues affecting the transferability of models

Reasons for niche differences between the native and invaded ranges of a species fall under three main categories: differences in environments, adaptation and methodological issues.

First, SDMs assume that climatic conditions and species tolerances are the primary determinant of distribution. However, differences in the local environments between the native and introduced ranges can affect transferability. For example, differences in the geography of the areas (e.g. north–south vs. east–west orientation), the existence of ecotypes, differences in the ranges of climate predictors, and in land-use history (Randin et al. 2006) could be more important than broad-scale climate conditions. Dispersal limitation could also play an important role in determining distribution, especially if dispersal is tied to particular biotic factors (competition, predation) or the abundance of the species in different environments (see Randin et al. 2006).

Second, differences in distribution between the native and introduced ranges could reflect the adaptation of a species to a new environment. In particular there is evidence that a release from competitors and enemies has occurred for several invasive ant species (Porter et al. 1997; Holway 1999; Holway et al. 2002). For example, Porter et al. (1997) conclude that differences in fire ant abundance (*Solenopsis* species) are due to the absence of natural enemies in the introduced range, and not a result of differences in sampling conditions, seasonal variability, habitat differences, or the frequency of polygyny.

Third, there are also several serious methodological issues that affect interpretation of transferability and warrant further investigation. The use of different evaluation statistics, criteria for successful transferability, and setting threshold values are important issues for the transferability of SDMs. For many statistics, a threshold is needed to correctly classify cases as presence/absence in models (Fielding & Bell 1997). However, some evaluation statistics overcome the issue of requiring a set threshold. For example, the area under the ROC function (AUC) provides a single measure of overall accuracy and is thus not dependent upon a particular threshold (Fielding & Bell 1997).

In this paper, AUC and maximum Kappa values are outside the *a priori* criteria of Monserud and Leemans (1992), for three of the four external models. However, if a more relaxed transferability criteria had been adopted then these models would have been judged to have been successfully transferred. For example, Randin et al. (2006) uses a much lower success criteria of AUC < 0.7 and Kappa < 0.4 to evaluate model transferability. For *A. gracilipes* and *W. auropunctata*, it is omission error that most strongly indicates that external models have failed transferability. Omission error relies on a setting a threshold value to determine whether or not the models are correctly classifying presence/absence. Lowering the threshold value essentially results in a lower omission error. However, if thresholds are set too low, then the utility of models are diminished, as the extent of where models predict suitability increases. High omission error (false negatives, under-prediction) results from areas being classified as unsuitable for the species when they are suitable. For invasive species it is important to minimise omission error because it is better to predict that an invasive species will occur in a area (but it never happens) than to predict an invasive will not occur in an area, when it actually could. Thus, omission error should be evaluated as part of any examination of SDM and of model transferability for invasive species.

One major issue for SDM is the inclusion/exclusion of locality records. The aim of SDM is to predict areas that describe where environmental conditions are suitable for the survival of the species. This essentially equates to Chase & Leibold's (2003) definition of a niche: the environmental conditions that allow a species to satisfy its minimum requirements so that birth rate is equal to or greater than its death rate. Locality records are used to define and model this niche. However, often the only information available for a species at a locality is its confirmed presence. There is almost always no information on population density or population growth. Thus, for some locality records it can be unclear whether the locality actually meets the requirements for species persistence. Furthermore, these problematic locality records are at the extreme end of environmental conditions - the same conditions which SDM is trying to determine whether are suitable or not. For example, tropical ant species have often been recorded living in greenhouses in cold temperate regions (Harris et al. 2005). Anecdotal evidence for several species also supports the idea that a species may perist in urban environments where through the urban heat-effect (concrete, heated buildings) species are buffered from cold conditions. Irrigation has shown to be an important factor in determining the abundance of Argentine ants in seasonally dry environments in California (Menke & Holway 2006).

A case in point is the locality records of *A. gracilipes* in Mexico (Baja Peninsula). Compared to other introduced records of *A. gracilipes*, these Mexican locality records are associated with very low precipitation and high seasonality (in the extreme right of Figure 6.1). Consequently, introduced models (that include Mexican records) predicted greater suitability in a number of semi-arid and arid areas (e.g. Mexico, southern Africa, North Africa, Arabia, the Middle East, inland parts of Australia). Wetterer (2005) has previously noted that Mexican records of *A. gracilipes* are not typical of the habitats usually occupied by *A. gracilipes*, that is, tropical rainforest. Thus, their inclusion/exclusion can drastically change SDM predictions. In this paper, locality records which were thought to represent unsuitable environments or those artificially created by humans were excluded prior to modeling (see methods). A related problem for SDMs is working with incomplete distribution data. That is, where there has been an absence of survey data in a region. However, this is more of a problem when there has been over-prediction, that is, a species is predicted to occur but is not there, possibly because of incomplete data. In the present study, under-prediction occurred, so incomplete distribution data was not the reason for poor transferability.

Finally, another issue is the quality of the predictor (i.e. climate) variables used in SDMs, a issue recently highlighted by Randin et al. (2006). Given climate variables are fundamental to most SDMs, there has been surprisingly little attention examining their importance (Beaumont et al. 2005). Further work is needed on selecting the number and the type of climate variables, the combinations of individual variables, and most importantly identifying the variable(s) that have the most causal effects on a species distribution.

Poor transferability of models has widespread implications for the prediction of potential distribution, not just for invasive species, but also for the selection of biological control agents and the conservation of threatened species. If poor transferability is the rule rather than the exception, then considerable caution needs to be taken when projecting SDMs into new environments.

6.5 References

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Table 6.1 Principal components analysis of environmental conditions associated with the presence of *A. gracilipes*. Median values of environmental variables for the native and introduced ranges are compared using a two sample Wilcoxon test. * $P < 0.05$, ** $P < 0.01$, ^{NS} Not significant.

		Principal Component Axis		**Median values**	
Variable	**Abbrevation**	**PC-1**	**PC-2**	**Native range**	**Introduced range**
Annual mean temperature	MAT	-0.271	-0.494	25.9	25.4 ^{NS}
Mean monthly temperature range	MMTR	0.268	-0.202	8.5	6.1 **
Isothermality	ISO	-0.335	-0.080	67.3	68.0 *
Temperature seasonality	TSEAS	0.367	0.121	104.3	102.3 *
Maximum temperature of warmest month	MXTWM	0.060	-0.635	31.7	30.0 **
Minimum temperature of coldest month	MTCM	-0.379	-0.230	19.9	21.3 **
Annual temperature range	TAR	0.395	-0.066	12.0	8.8 **
Annual precipitation	APR	-0.302	0.050	2210	2211 ^{NS}
Precipitation of wettest month	PWM	-0.122	-0.226	337	326 *
Precipitation of driest month	PDM	-0.319	0.243	27.0	86.0 **
Seasonal precipitation	PSEAS	0.311	-0.349	72.9	41.7 **
Eigenvalue		8.51	4.16		
Percentage variance		44.8	21.9		
Cumulative percentage variance		44.8	66.7		

Table 6.2 Principal components analysis of environmental conditions associated with the presence of *W*. *auropunctata*. Median values of environmental variables for the native and introduced ranges are compared using a two sample Wilcoxon test. * P < 0.05, ** P < 0.01, ^{NS} Not significant.

		Principal Component Axis		**Median values**	
Variable	**Abbrevation**	**PC-1**	**PC-2**	**Native range**	**Introduced range**
Annual mean temperature	MAT	-0.214	-0.521	24.3	23.7 ^{NS}
Mean monthly temperature range	MMTR	0.263	0.060	9.9	7.7 **
Isothermality	ISO	-0.337	0.019	74.6	60.8 **
Temperature seasonality	TSEAS	0.393	0.059	82.8	164.7 **
Maximum temperature of warmest month	MXTWM	0.078	-0.488	31.4	30.6 *
Minimum temperature of coldest month	MTCM	-0.364	-0.364	16.3	16.9 ^{NS}
Annual temperature range	TAR	0.410	0.061	12.2	12.8 ^{NS}
Annual precipitation	APR	-0.341	0.235	1765.0	1475.0 ^{NS}
Precipitation of wettest month	PWM	-0.316	0.100	258.0	225.5 *
Precipitation of driest month	PDM	-0.276	0.365	55.0	55.5 ^{NS}
Seasonal precipitation	PSEAS	0.132	-0.385	49.1	44.9 ^{NS}
Eigenvalue		4.85	2.4		
Percentage variance		44.1	21.9		
Cumulative percentage variance		44.1	66.0		

Table 6.3 Model evaluation statistics for *A. gracilipes* and *W. auropunctata*. For internal evaluations, statistics were based on an average (standard deviation) of the 10 individual models. There was only one external model to evaluate. Training records for the composite (external) model were based on the summation of the 10 individual models, but all records were used in the testing of the model.

Species/model	**Number of records Train/Test**	**Evaluation**	**AUC**	**Omission error**	**Kappa (max)**
A. gracilipes					
Native data on native models	62/20	Internal	0.930 (0.05)	0.110 (0.05)	0.792 (0.05)
Introduced data on introduced models	73/25	Internal	0.980 (0.01)	0.090 (0.03)	0.853 (0.04)
Native data on introduced model	na /163	External	0.847	0.883	0.607
Introduced data on native model	na /195	External	0.861	0.495	0.679
W. auropunctata					
Native data on native models	45/15	Internal	0.947 (0.02)	0.132 (0.10)	0.812 (0.06)
Introduced data on introduced models	53/18	Internal	0.968 (0.02)	0.148 (0.13)	0.874 (0.07)
Native data on introduced model	na/120	External	0.923	0.660	0.745
Introduced data on native model	na/142	External	0.808	0.436	0.628

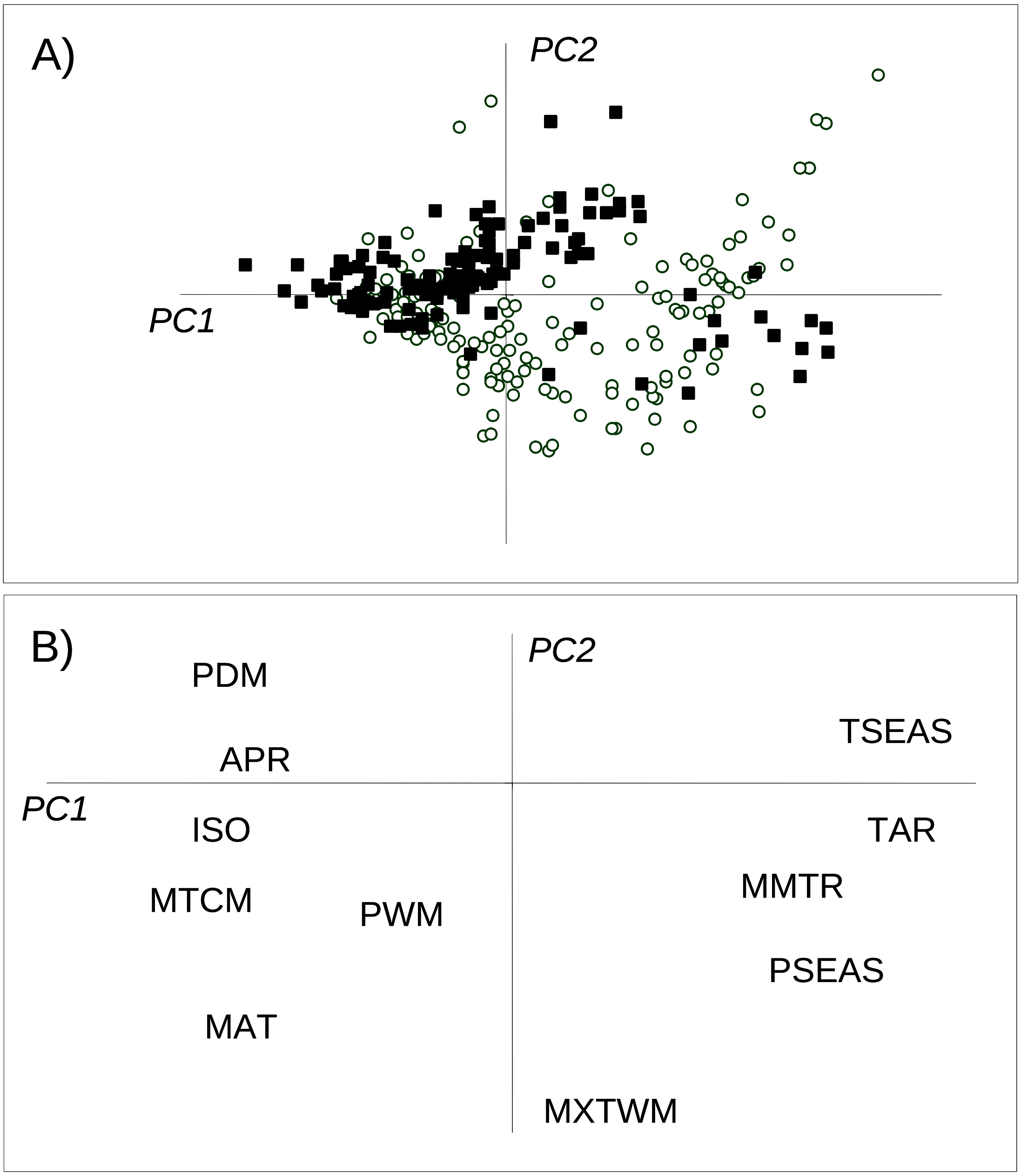

Figure 6.1 PCA ordination of environmental variables associated with the locality records of *A. gracilipes*. A) Open circles represent the native range and black squares represent the introduced range. B) Contribution of environmental variables in relation to the native and introduced ranges. Abbreviations of environmental variables are given in Table 6.1.

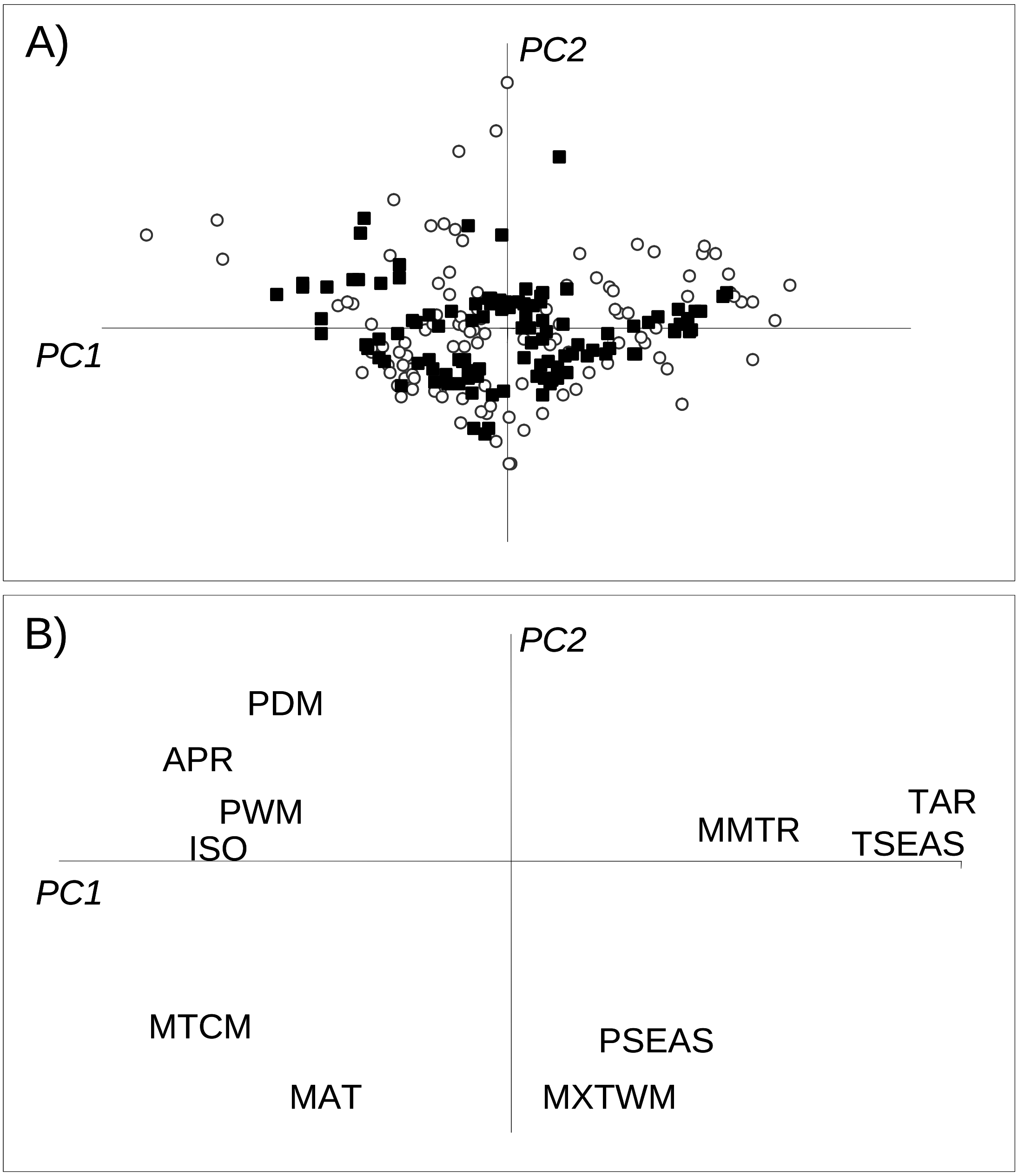

Figure 6.2 PCA ordination of environmental variables associated with the locality records of *W. auropunctata*. A) Open circles represent the native range and black squares represent the introduced range. B) Contribution of environmental variables in relation to the native and introduced ranges. Abbreviations of environmental variables are given in Table 6.2.

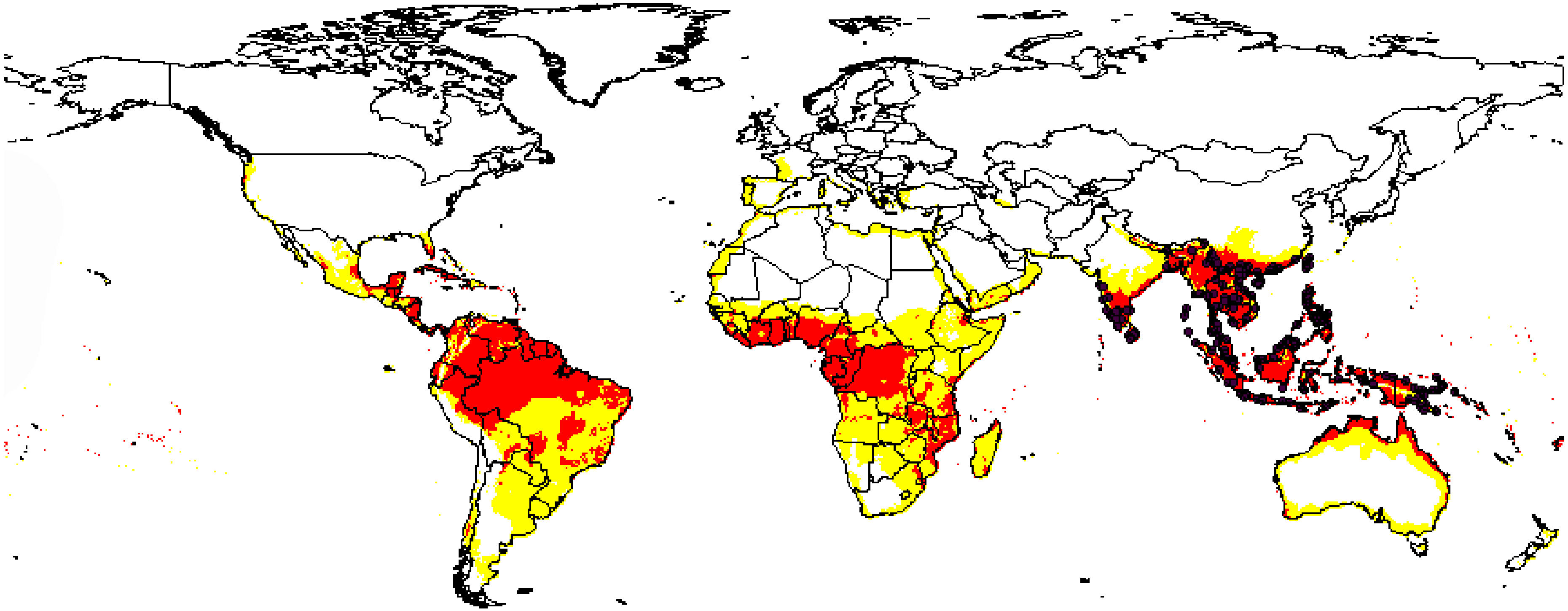

Figure 6.3 The potential geographic distribution of *A. gracilipes* predicted by native range data. Species presence points are marked by black dots. The map is a composite of 10 individual models (each with a maximum DOMAIN score of 100). Categories are: white = <800 (unsuitable), yellow = 800-899 (marginal), red = 900-1000 (highly suitable).

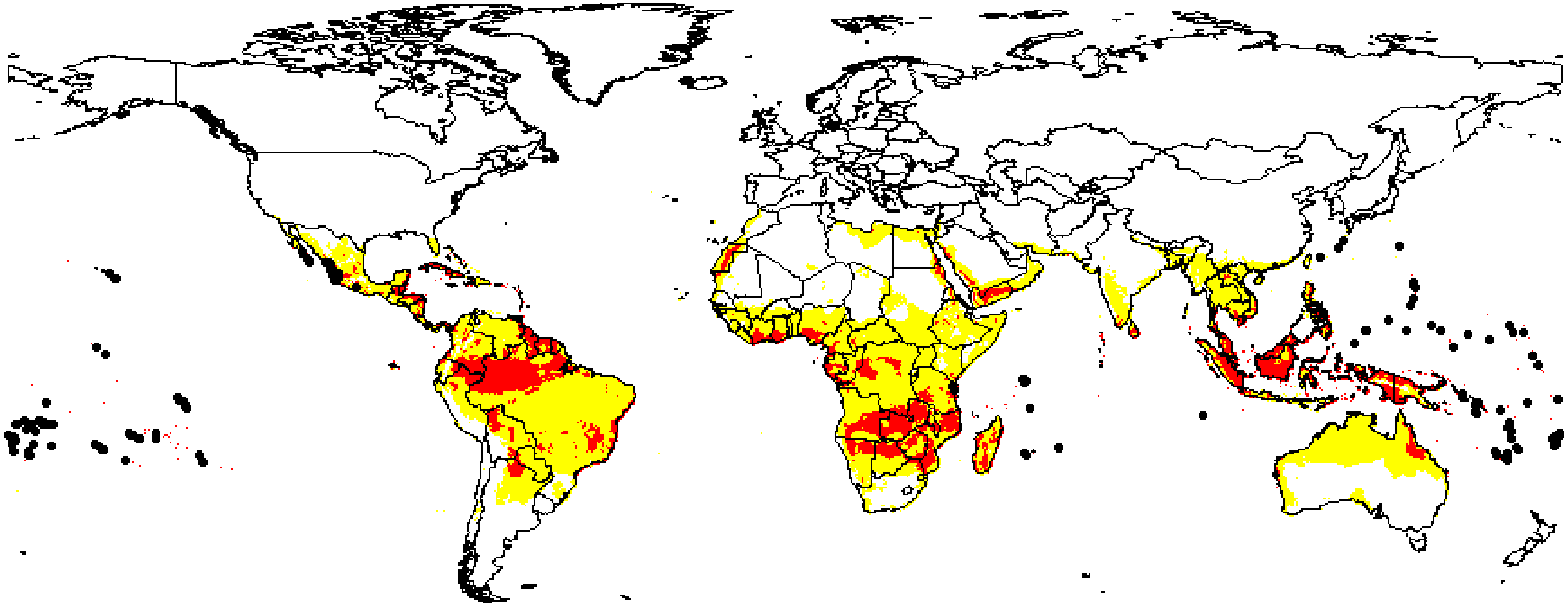

Figure 6.4 The potential geographic distribution of *A. gracilipes* predicted by introduced range data. Species presence points are marked by black dots. The map is a composite of 10 individual models (each with a maximum DOMAIN score of 100). Categories are: white = <800 (unsuitable), yellow = 800-899 (marginal), red = 900-1000 (highly suitable).

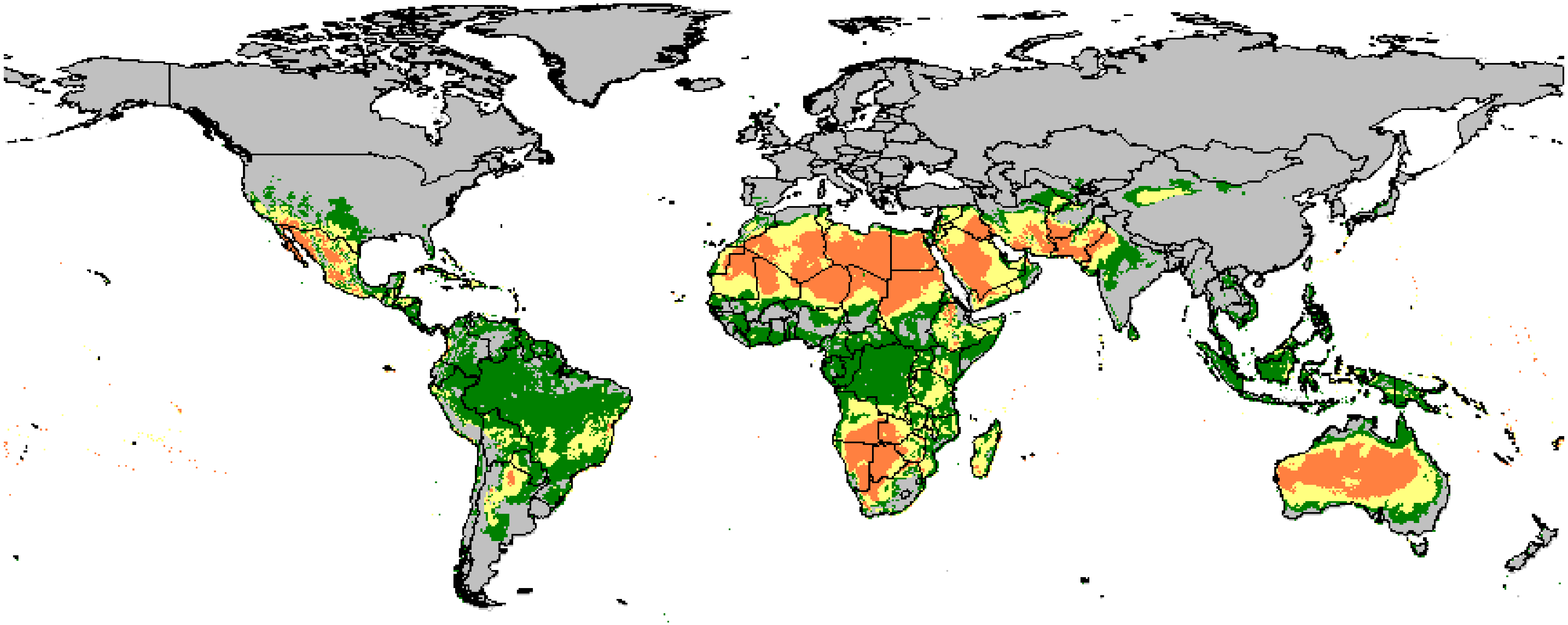

Figure 6.5 Variation between native and introduced models in their respective DOMAIN scores for *A. gracilipes*. Introduced models have a higher score in regions coloured orange and yellow. Native models have a higher score in areas coloured green and grey. Areas of closest agreement between models are in yellow and green and scores are of greatest different with orange to grey. Scores are: orange = >-50, yellow = -50-0, green = 1-50, grey = >51.

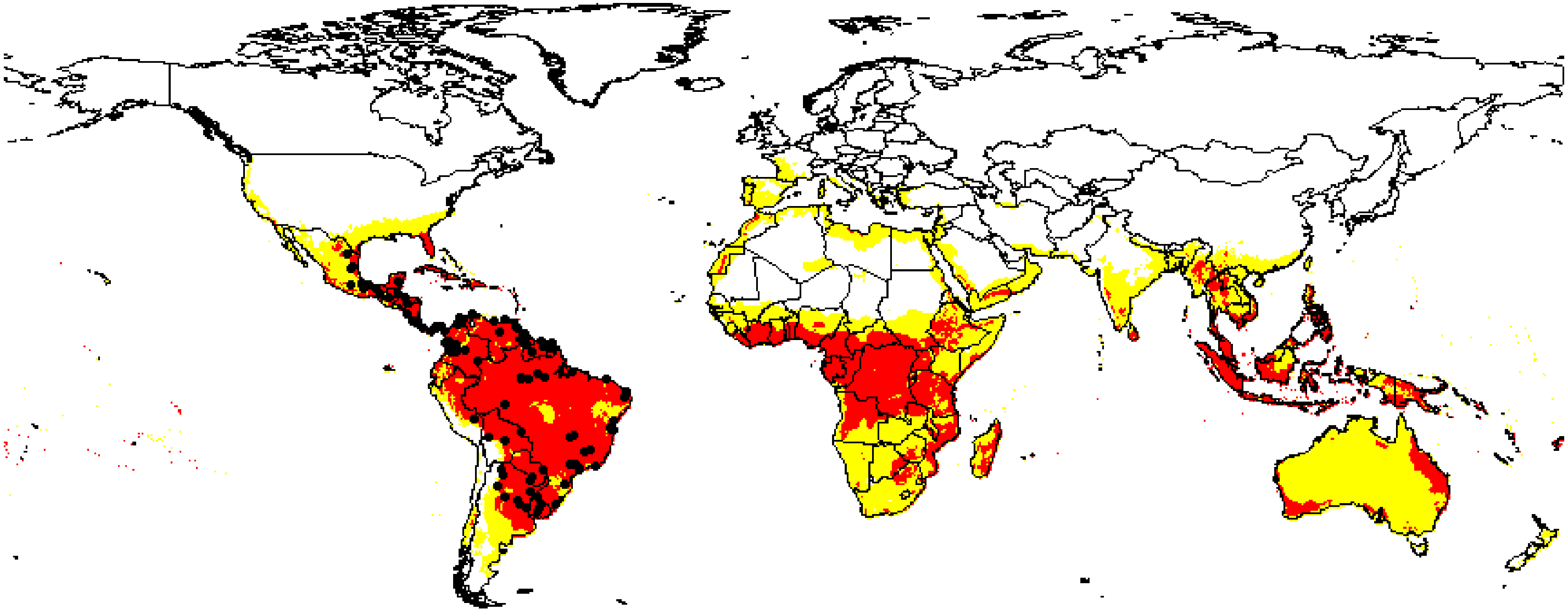

Figure 6.6 The potential geographic distribution of *W. auropunctata* predicted by native range data. Species presence points are marked by black dots. The map is a composite of 10 individual models (each with a maximum DOMAIN score of 100). Categories are: white = <800 (unsuitable), yellow = 800-899 (marginal), red = 900-1000 (highly suitable).

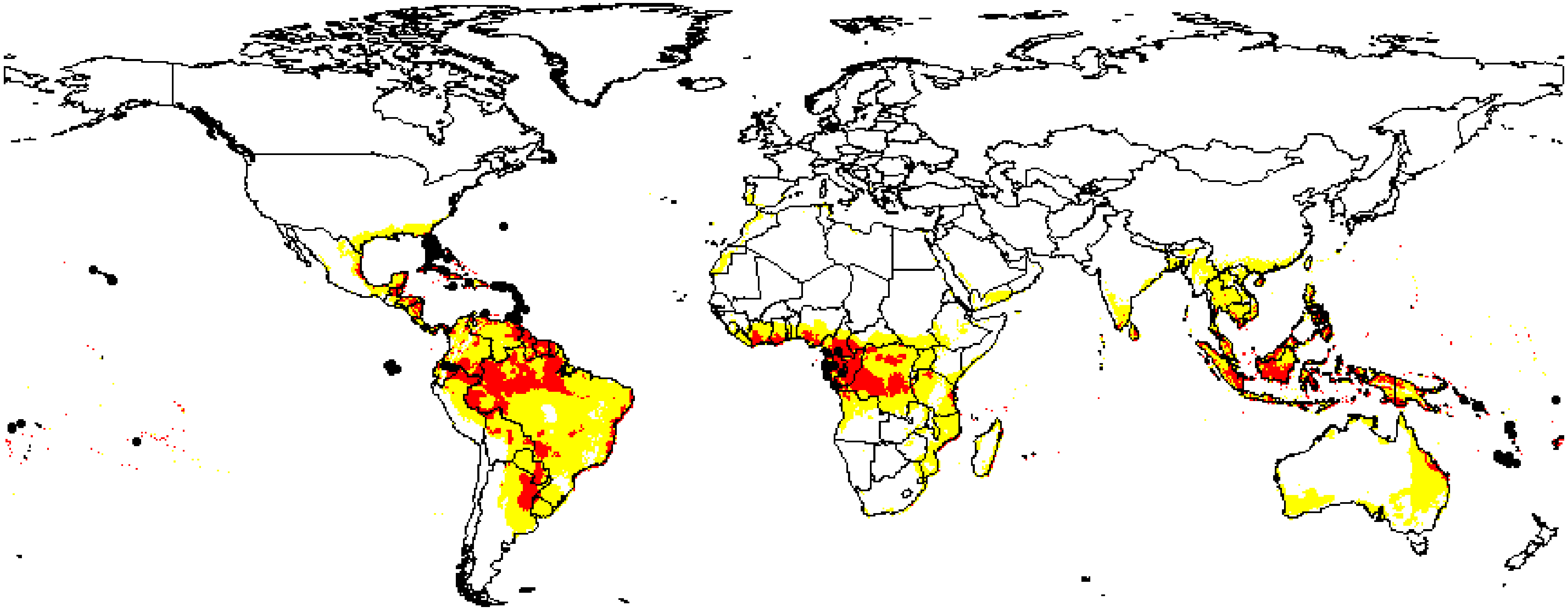

Figure 6.7 The potential geographic distribution of *W. auropunctata* predicted by introduced range data. Species presence points are marked by black dots. The map is a composite of 10 individual models (each with a maximum DOMAIN score of 100). Categories are: white = <800 (unsuitable), yellow = 800-899 (marginal), red = 900-1000 (highly suitable).

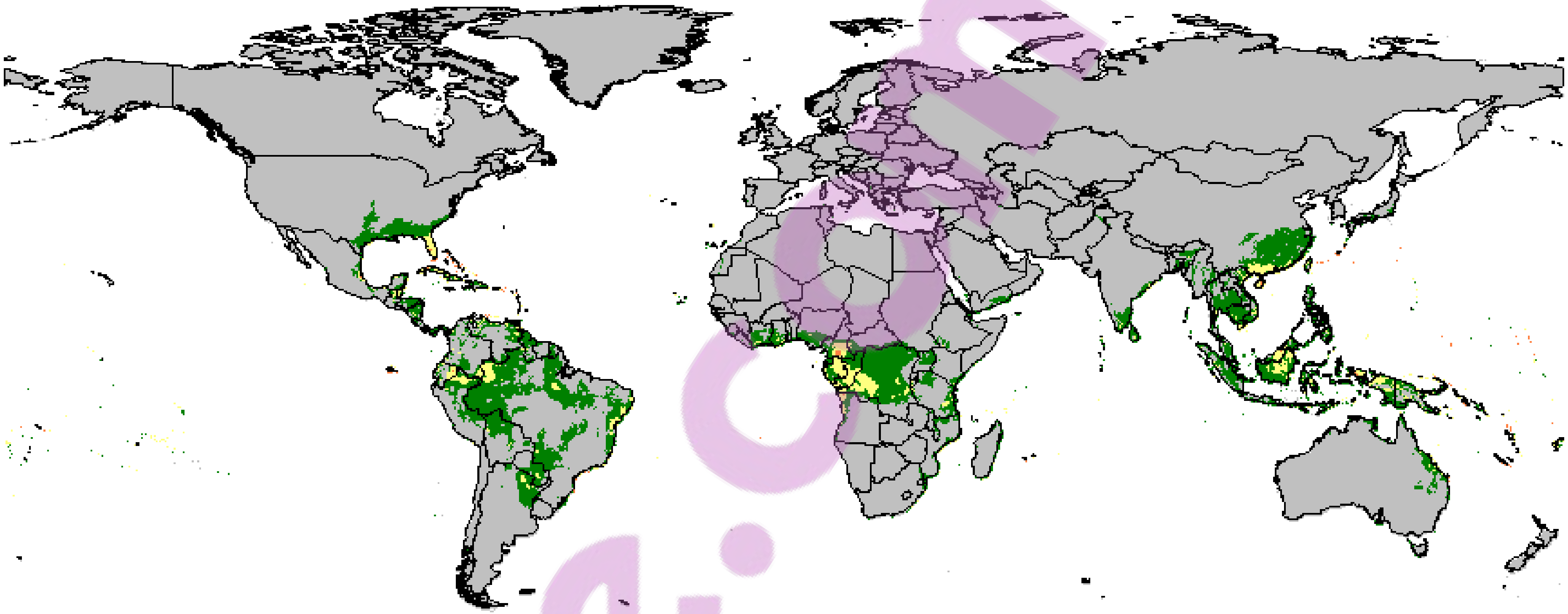

Figure 6.8 Variation between native and introduced models in their respective DOMAIN scores for *W. auropunctata*. Introduced models have a higher score in regions coloured orange and yellow. Native models have a higher score in areas coloured green and grey. Areas of closest agreement between models are in yellow and green and scores are of greatest different with orange to grey. Scores are: orange = >-50, yellow = -50-0, green = 1-50, grey = >51.

Modeling the Potential Geographic Distribution of Invasive Ant Species in New Zealand

7

Abstract

Despite their economic and environmental impacts, there have been relatively few attempts to model the distribution of invasive ant species. In this study, the potential distribution of six invasive ant species in New Zealand are modeled using three fundamentally different methods (BIOCLIM, DOMAIN, MAXENT). Species records were obtained from museum collections in New Zealand. There was a significant relationship between the length of time an invasive species had been present in New Zealand and its geographic range. This is the first time such a time lag has been described for invasive ant species, and shows there is a considerable time lag in their spread. For example, it has taken many species several decades (40-60 years) to obtain a distribution of 17-25% of New Zealand regions. For all six species, BIOCLIM performed poorly compared to the other two modeling methods. BIOCLIM had lower AUC scores and higher omission error, suggesting BIOCLIM models under-predicted the potential distribution of each species. Omission error was significantly higher between models fitted with all 19 climate variables compared to those models with fewer climates variables for BIOCLIM, but not DOMAIN or MAXENT. Widespread species had a greater commission error. A number of regions in New Zealand are predicted to be climatically suitable for the six species modeled, particularly coastal and lowland areas of both the North and South Islands.

7.1 Introduction

Invasive species are a global problem, affecting agriculture, forestry, fisheries, human health and natural ecosystems (Drake et al. 1989; Mooney & Drake 1986; Sandland et al. 1999; Mack et al. 2000). A fundamental approach to understanding and managing invasive species is to determine their current and potential distribution. There have been a number of recent papers providing an overview to species distribution modeling, or a comparison of modeling methods (Fielding & Bell 1997; Guisan & Zimmermann 2000; Zaniewski et al. 2002; Anderson et al. 2003; Segurado & Araújo 2004; Guisan & Thuiller 2005; Elith et al. 2006; Phillips et al. 2006). Essentially, species distribution modeling aims to predict areas that describe where environmental conditions are suitable for the survival of the species. That is, the potential distribution or fundamental niche (Anderson et al. 2003; Peterson 2003; Guisan & Thuiller 2005).

In general, these modeling methods combine species locality data (geo-referenced coordinates of latitude and longitude from confirmed presence) with environmental variables to create a model of a species requirements for the examined variables (Anderson et al. 2003). The resulting model is then projected onto a GIS map (termed a habitat suitability map), of the study region showing the potential geographic distribution of a species. For invasive species management, habitat suitability maps identify areas where 1) invasive species may actually be present (but are as yet undetected), and 2) where invasive species may disperse to in the future, thus providing assistance for planning and prioritising areas for surveillance. Such information can also assist in determining the extent, cost and likelihood of success of a control program. Thus, predictive modeling of a species distribution represents an important tool for invasive species management (Anderson et al. 2003).

Invasive ant species are currently receiving considerable attention from around the globe, with increasing evidence of economic and agricultural impacts, health effects on humans, and disruption to natural ecosystems (Williams 1994; Christian 2001; Holway et al. 2002; O'Dowd et al. 2003; Ward & Harris 2005). Although only a handful of invasive ant species are well studied (Holway et al. 2002), there are many other ant species with the opportunity to become invasive. For example, at least 150 species of ants have been accidentally transported by humans to new regions through global trade (McGlynn 1999). However, this number is almost certainly an under-estimate (Suarez et al. 2005; Ward et al. 2006).

Climatic variables, especially temperature, rainfall and humidity, play a large role in determining the distribution of ant species. Hölldobler and Wilson (1990) state that every ant species operates within a temperature-humidity envelope, however, this climate envelope is more apparent at large spatial scales. At local levels distribution is strongly shaped by species microhabitat specialisation and strategies to avoid inter-specific competition (Hölldobler & Wilson 1990). On large spatial scales ant abundance is strongly correlated with net primary productivity (a function of solar radiation and rainfall) (Kaspari et al. 2000). Temperature also plays an important role in the abundance of ants by restricting foraging activity and regulating seasonal productivity (Kaspari et al. 2000). Environments with high rainfall reduce the time spent foraging (Vega & Rust 2001). Conversely, in xeric habitats, the lack of water and soil moisture can also limit the distribution of some species (Holway & Suarez 2006).

At the level of the colony, the location and construction of nests play an important role in regulating temperature and humidity (Hölldobler & Wilson 1990). For example, nests can also provide a thermal refuge in hot environments, allowing workers to retreat to a cool nest in the hottest part of the day. Temperature primarily controls the development of the eggs, larvae and pupae (Hartley & Lester 2003). Some ant species are known to move brood vertically within the nest to keep them at the optimum temperature for development (Hölldobler & Wilson 1990). Extremes of temperature are known to severely limit, or stop, the production of workers and reproductive castes, which can ultimately kill the colony (Korzukhin et al. 2001).

Despite the importance of climate variables to the survival and distribution of ants, there have been relatively few attempts to model the distribution of invasive ant species. Hartley and Lester (2003) used climate station records and a degree-day model for each life stage of the Argentine ant, *Linepithema humile*, to examine its potential distribution in New Zealand. Roura-Pascual et al. (2004)

also examined the potential distribution of *L. humile* on a global distribution and under climate change scenarios using a genetic algorithm for rule-set prediction (GARP) model.

Pimm and Bartell (1980) provided one of the first distribution models for the red imported fire ant, *Solenopsis invicta*, an invasive species in the south-eastern USA. They used a principal coordinate analysis to model the distribution in Texas on two environmental axes (temperature and rainfall). However, they overestimated the extent of expansion under dry conditions (Korzukhin et al. 2001). Stoker et al. (1994) used a complex mechanistic model to simulate population and colony growth of *S. invicta* at different temperature and rainfall regimes. More recently Korzukhin et al. (2001) has provided a simulation model for *S. invicta* based on colony growth as a function soil temperature. The production of female alates (reproductive) of a colony was estimated and this provided an assessment of whether *S. invicta* could survive in different locations. The model of Korzukhin et al. (2001) has also been applied on a global scale by Morrison et al. (2003). Sutherst and Maywald (2005) have also modeled *S. invicta* at a global scale using colony growth and stress parameters in the program CLIMEX.

These models have allowed the identification of areas that are climatically suitable, as well as providing insight into the factors that may limit the expansion of these two invasive species. In this study, the potential distributions of six invasive ant species in New Zealand are modeled using three fundamentally different methods. New Zealand has a very small endemic ant fauna of 11 species (Ward 2005). As a consequence, the establishment and subsequent spread of invasive ant species in New Zealand is less likely to be determined by inter-specific competition from endemic ant species. Thus, climate variables are most likely to be the primary factor in restricting the occurrence of invasive ant species on a large-scale in New Zealand.

7.2 Methods

7.2.1 Species records

Records of all invasive species established in New Zealand were obtained from an online database (Landcare Research 2006). The database represents records from a 90 year period (from the early 1900s to 2004) of specimens held in museums throughout the country. Specimens are collections made by professional scientists (from Universities and government institutions), amateur entomologists, and members of the public. All records contained information of locality, year of collection, and the majority (>90%) of records contained information on habitat, collector, and a map reference. The database consists of over 2000 species-locality records.

7.2.2 Spread since arrival

The geographical spread since the arrival of a species was estimated by using the date of the first recorded presence in New Zealand and the number of coded regions (‘Crosby codes’) each species has been recorded within. Crosby codes are equal-sized regions throughout New Zealand and are primarily used for the retrieval and documentation of entomological specimens in New Zealand collections (Crosby et al. 1998). They are used here as a measure of distribution. There are 29 Crosby regions for New Zealand.

7.2.3 Modeling potential distribution

Data sources

Not all invasive species in New Zealand were modeled. Many species are known from very few records or are very recent establishments. Six invasive species were chosen to be modeled: *Iridomyrmex* sp. (undescribed), *Ochetellus glaber, Paratrechina* spp. (undescribed), *Pheidole rugosula*, *Technomyrmex albipes*, and *Tetramorium grassii* (Table 7.1). These species have been in New Zealand for many decades, are among the most geographically widespread and are increasingly found in native ecosystems.

Environmental data was obtained from WORLDCLIM (version 1.3, http://www.worldclim.org) which is explained in detail in Hijmans et al. [2005]). WORLDCLIM contains climate data (monthly precipitation and monthly mean, minimum and maximum temperature) at a spatial resolution of 30 arc seconds (~1 x 1 km resolution) obtained by interpolation of climate station records from 1950-2000. From this climate data, 19 climate variables are derived: annual mean temperature [1], mean monthly temperature range [2], isothermality [3], temperature seasonality [4], maximum temperature of warmest month [5], minimum temperature of coldest month [6], temperature annual range [7], mean temperature of wettest quarter [8], mean temperature of driest quarter [9], mean temperature of warmest quarter [10], mean temperature of coldest quarter [11], annual precipitation [12], precipitation of wettest month [13], precipitation of driest month [14], precipitation seasonality [15], precipitation of wettest quarter [16], precipitation of driest quarter [17], precipitation of warmest quarter [18], and precipitation of coldest quarter [19]. For further detail see (http://www.worldclim.org, or Hijmans et al. [2005]). The same climate variables were used in each modeling method. The climate variables represent a combination of annual trends, seasonality and extreme environmental conditions.

Modeling methods

Three different modeling methods were used. First, BIOCLIM (Nix 1986) uses a climate envelope (a rectilinear volume in environmental space) to summarise the climate at locations where a species has been recorded. BIOCLIM predicts suitable conditions for a species where values of the climate variables fit within the extreme values determined by the set of known locations. Locations where the values lie within the 5-95th percentile of the climate envelope are traditionally classified as 'core' regions of suitability. The second method, DOMAIN (Carpenter et al. 1993), uses a distance-based method (the Gower metric) to assess new sites in terms of their environmental similarity to sites of known presence. DOMAIN produces an index of habitat suitability on a continuous scale (0-100), where higher scores (e.g. >90) are considered highly suitable. Both BIOCLIM and DOMAIN modeling methods were implemented in DIVA-GIS software (version 5.2, http://www.diva-gis.org).

The third method is maximum entropy species distribution modeling (MAXENT, version 2.2), a general-purpose machine learning method (Phillips et al. 2006). Entropy in the context of probability theory and statistics measures the amount of information that is contained in a random variable or unknown quantity. The idea of MAXENT is to estimate the target probability distribution by finding the probability distribution of maximum entropy, that is, the closest to uniform. This is equivalent to finding the maximum likelihood Gibbs distribution. MAXENT software and further information on this method are available from http://www.cs.princeton.edu/~schapire/maxent (or see Phillips et al. 2006).

The three modeling methods differ in their theoretical assumptions, modeling procedures, novelty and performance. BIOCLIM is an established method and has been widely used for species distribution modeling (Téllez-Valdés & Dávila-Aranda 2003; Meynecke 2004; Beaumont et al. 2005), DOMAIN has not been widely used (Loiselle et al. 2003), and MAXENT has only recently been applied to modeling species distributions (Phillips et al. 2006). Despite using three very different modeling methods, all use the same basic set of information to model the distribution of a species. That is, a set of samples (species presence) is available from a geographical region, which is linked to a set of features (e.g. climatic variables).

Model building and evaluation

For each species, 10 random partitions were made of species records by bootstrapping. Each partition was created by randomly selecting 75% of the species records as training data. The remaining 25% of species records were set aside for testing the resulting models. This is a split-sample approach (Guisan & Zimmerman 2000). Ten partitions were made to assess the variability of each method and to allow statistical testing of differences in performance (see Phillips et al. 2006). Data was 'cleaned' in DIVA-GIS where duplicates records were deleted and only one species occurrence record per grid cell was allowed. Coordinates for species records in the online database are listed as New Zealand map grid references; these were converted to decimal latitude and longitude in DIVA-GIS.

Species records consist of individual point-locality data, that is, presence-only data. However, in order to evaluate models on the basis of error rates, absence data is needed. To overcome the lack of absence data, 'pseudo-absence' data is generated which uses random points throughout the study area as assumed absences (Zaniewski et al. 2002). For BIOCLIM and DOMAIN pseudo-absence records were generated at random in a 1:1 ratio with the number of presence records. MAXENT uses 10000 random background points in the study area to define the probability distribution and evaluate model predictions.

In presence/absence models there are two types of prediction errors (Fielding & Bell 1997). False negatives (omission error, under-prediction) result in areas being classified as climatically unsuitable when they are suitable. Conversely, false positives (commission error, over-prediction) result in areas being classified as climatically suitable when they are unsuitable. For invasive species it is more important to minimise false negatives. That is, it is better to predict that an invasive species will occur in a area (but it never happens) than to predict an invasive will not occur in an area, when it actually could. Models that have a high proportion of presences correctly predicted (i.e. model sensitivity) and a low omission error (false negative rate) should be preferred. Commission error are likely to result from the species not yet having colonised all climatically suitable locations and dispersal limitations (Guisan & Thuiller 2005), and for presence-only modeling apparent commission error will exist, where the species is present in an area but surveys have not been undertaken to confirm this (Anderson et al. 2003).

Omission error was determined through a confusion matrix (Fielding & Bell 1997). A threshold was applied to each modeling method because an upper limit is needed to determine what values represent true presence and true absences (BIOCLIM = 25, DOMAIN = 90, MAXENT = 1, see Phillips et al. 2006). Optimal models were defined as ‘omission error <0.05’ by the criteria of Anderson et al. (2003). The area under the Receiver Operating Characteristic curve (AUC) was also used to examine model performance. AUC measures the ability of a model to discriminate between sites where a species is present versus those where it is absent (Fielding & Bell 1997, Elith et al. 2006). It provides a single measure of overall accuracy that is not dependent upon a particular threshold (Fielding and Bell 1997). AUC ranges from 0 to 1, where a score of 1 indicates perfect discrimination; a score of 0.5 implies discrimination that is no better than random. A value of 0.8 for the AUC means that there is an 80% probability that a random selection from the presence records will have model scores greater than a random selection from the absence records.

Another issue in the modeling of species distributions is the number of climatic variables used in modeling (Kriticos & Randell 2001; Beaumont et al. 2005). Using too few, or too many, climatic variables may result in incorrect predictions. To examine the influence on the number of climate variables on model performance climate data was generated for each species record in DIVA-GIS. Principle co-ordinate analysis (PCA) within PRIMER v5.0 software (Clarke & Warwick 2005) was used to examine the similarity between the climate variables. Collinearity was examined through a Pearson correlation matrix and subsets of variables with a high average correlation (>90%) were reduced to a single variable (recommended by Clarke & Warwick 2005). To assist in the interpretation of results the same variables were retained for each species from the PCA. The Wilcoxon signed-rank test was used to examine differences in omission error between models generated from all 19 climate variables (e.g. BIOLCIM-all) and between models with only a ‘select’ number of climate variables (e.g. BIOCLIM-select).

Thus, 360 models were created, using 6 species, 3 modeling methods, 10 partitions, and 2 options (number of climatic variables).

7.3 Results

7.3.1 Invasive ant species in New Zealand

There are 28 invasive ant species present in New Zealand (Ward 2005). Invasive species are predominantly found in the northern regions of the North Island, and to a lesser extent in the coastal lowland regions of the North Island and the northern region of the South Island (Figure 7.1). These areas generally represent the warmer areas of New Zealand. The greatest numbers of invasive species are concentrated in the cities with a large port: Auckland, Tauranga and Napier.

There has been a relatively constant arrival of invasive species to New Zealand from the late 1800's to the present (Figure 7.2). The oldest records of invasive species date from before the 1870s and are thought to have been associated with soil ballast of ships arriving during the early days of European settlement (Brown 1958). The presence of four new species in the last five years also serves to highlight the relatively regular establishment of ant species in New Zealand. There was a significant correlation ($r^2 = 0.436$, $p < 0.01$) between the length of time an invasive species has been present in New Zealand and the extent of its current distribution (Figure 7.2).

The six species (which are being modeled in the following section) have been in New Zealand an average of 65.5 years (SE ± 6.2; range 42-84), and occupy an average of 10.2 Crosby regions (SE ± 1.3; range 7-16), for an average spread of 6.8 years for every Crosby region occupied (SE ± 0.9; range 5-11).

7.3.2 Potential distribution

Selection of climatic variables

The first three PCA axes consistently explained ~90% of the variation within climate data for each species (Table 7.1). The first PCA axis always represented temperature variables and the second precipitation variables. The number of variables selected was relatively consistent for each species, reduced from the original 19, to approximately four variables (range 4–7, Table 7.1). Across all species, the climate variables selected were: annual mean temperature, mean monthly temperature range, isothermality, temperature seasonality, maximum temperature of warmest month, temperature annual range, mean temperature of warmest quarter, annual precipitation, precipitation of driest month, precipitation of wettest quarter. However, it should be remembered, where high average collinearity existed within groups of variables, the same variable for each species was consistently selected to represent this group.

For each modeling method, the omission error from models of ‘all variables’ was compared to ‘selected variables’ derived from the PCA. For DOMAIN and MAXENT methods there were no significant differences between the average omission error of models with ‘all variables’ compared to ‘selected variables’ (Wilcoxon signed rank test, all species, $p > 0.125$). For BIOCLIM, omission error was significantly higher for models fitted with all 19 climate variables compared to those with fewer climates variables. This was consistent for all species; *Ochetellus glaber* and *Pheidole rugosula* ($p < 0.05$), *Iridomyrmex* sp., *Paratrechina* spp., *Technomyrmex albipes*, *Tetramorium grassii* ($p < 0.01$).

Model performance

From a plot of omission versus commission error, the performance of methods and each model ($n = 360$) can be compared (Figure 7.3). BIOCLIM models generally cluster in the upper left, represented by high omission and low commission, suggesting that these models are under-predicting species distributions. DOMAIN and MAXENT models mix together, and 91% of these models have an omission error less than 0.10.

Of models with an omission error of less than 0.05, there were significantly fewer BIOCLIM models ($n = 2$) represented compared to DOMAIN ($n = 76$) and MAXENT ($n = 96$) models (Chi-square = 85.31, d.f. = 5, $p <0.001$). Further examination of these models revealed that species were not spread evenly across the range of observed commission error (Figure 7.4). This is a consequence of widespread species having greater commission error (Anderson et al. 2003). The average commission error of these species (for models with omission error of less than 0.05) is highly correlated with the number of Crosby regions ($r^2 = 0.865$), a measure of New Zealand wide distribution, but not with the number of training records ($r^2 = 0.467$).

For each species, MAXENT and DOMAIN consistently performed better than BIOCLIM, with higher average AUC scores (Figure 7.5A). AUC scores were not significantly correlated with the number of training records for any modeling method (all methods, $p > 0.50$). Omission errors parallel AUC values, with BIOCLIM having higher average omission error than either DOMAIN or MAXENT (Figure 7.5B). Omission error was not significantly correlated with the number of training records for BIOCLIM for MAXENT methods, but it was for DOMAIN ($r^2 = 0.783$, $p < 0.05$).

Habitat suitability maps

For each species a single model was selected to create a habitat suitability map of the predicted geographic distribution (Figures 7.6 – 7.11). Habitat suitability maps with presence-only data do not predict the probability of presence, but provide relative index of suitability (Anderson et al. 2003). The criteria of selecting ‘optimal models’ from Anderson et al. (2003) was used, that is, the model which was closest to the average commission (of all models with omission error of less than 0.05). For each species, a DOMAIN model was closest to these criteria. However, it should be noted that there were a number of DOMAIN and MAXENT models that could have been used, and the selection of this single model is not meant to imply that DOMAIN out-performed MAXENT. The number of Crosby regions occupied was counted for the current distribution and was compared to predicted potential distribution for each species. On average, the current distribution was 47.9% of potential distribution, which was consistent for each species *Iridomyrmex* sp. (50.0%), *Ochetellus glaber* (47.8%), *Paratrechina* spp. (45.5%), *Pheidole rugosula* (40.9%), *Technomyrmex albipes* (59.3%), *Tetramorium grassii* (43.8%).

7.4 Discussion

7.4.1 Presence-only modeling

Museum records have great potential for ecological research, conservation issues, and in the study of invasive species (Loiselle et al. 2003; Suarez & Tsutsui 2004). Several recent studies on the invasive Argentine ant, *Linepithema humile*, have relied on museum collections to track its dispersal and model the potential distribution across local, regional and global scales (Suarez et al. 2001; Roura-Pascual et al. 2004; Ward et al. 2005). Museum records are particularly useful because the records consist of individual point-locality information, which are readily transferable as input data for species distribution modeling methods. However, museum records represent presence-only data. There is almost always no information on where a species is absent. This represents several drawbacks for modeling (Zaniewski et al. 2002); absence data is a necessary component of many modeling methods, there may be unknown biases associated with *ad hoc* or non-systematic data samples, and rare species are often disproportionably present in presence-only records. These generally make presence-only data more difficult to model than systematically gathered presence-absence data (Zaniewski et al. 2002).

However, results from a recent comprehensive comparison of modeling methods found that, although presence-absence data generally outperform presence-only methods, models with presence-only were sufficiently accurate for modeling potential species' distributions and thus for applied use (Elith et al. 2006). Furthermore, there can also be problems with obtaining accurate absence data, especially when the study species is mobile or cryptic (Guisan & Thuiller 2005). These issues are particularly important for ant species, which may frequently move nesting sites and are often very cryptic, with nests underground or under logs. In addition, many ant species in temperate regions show a strong seasonal activity pattern, with less (or no) workers actively foraging in colder periods. Sampling effort also plays an important role in determining whether or not a absence is accurate. In this study, a 1x1 km grid was used to classify either presence or absence of a species, however, ant sampling is typically undertaken over a much smaller area (e.g. a 20x 20m grid). Thus, insufficient effort or inappropriate sampling can relatively easily result in a false absence.

There are also theoretical reasons for the justification of using presence-only modeling. Presence-only modeling is strongly linked with the fundamental niche of a species (Guisan & Zimmerman 2000; Phillips et al. 2006). Presence-only modeling determines potential habitat suitability, the inclusion of absence data will restrict habitat suitability as the result of historical restrictions, dispersal limitations, extinction and biological interactions (Anderson et al. 2003). Absence data is more useful in determining the realised niche (Guisan & Zimmerman 2000; Anderson et al. 2003; Phillips et al. 2006). Modeling the fundamental niche is more appropriate for invasive species, which may be less restricted by biotic interactions, and because pest management authorities are interested in determining the 'maximum' potential distribution of an invasive species. Furthermore, in New Zealand, determining the fundamental niche of invasive ant species may equate closely to the realised niche. This is a consequence of New Zealand having very few endemic ant species (Ward 2005), and thus invasive ant species are unlikely to be limited by competition with endemic species.

7.4.2 Model performance and climatic variables

In this study, two measurements of model performance were examined. For each species, MAXENT and DOMAIN consistently perform better than BIOCLIM, with higher average AUC scores and lower omission error. Although AUC scores provide a single measure of performance that is independent of a classification threshold, for invasive species omission error also needs to be given significant consideration. For invasive species, high omission errors are considered to be a serious flaw (Guisan & Thuiller 2005), as they result in areas being classified as climatically unsuitable when they are not. Hence, the importance given to omission error in this study.

There are several recent studies which have compared modeling methods involving BIOCLIM, DOMAIN or MAXENT. Loiselle et al. (2003) compared five methods, including BIOCLIM and DOMAIN, to assess the conservation of 11 bird species in Brazil. DOMAIN models were amongst the best performing models, with the highest kappa values, low false-positives and included the greatest number of key areas in reserve designs. In contrast, BIOCLIM performed relatively poorly (Loiselle et al. 2003). In a major comparison of modeling methods, regions and taxa, Elith et al. (2006) reported a general progression of performance (poor to best) from BIOCLIM to DOMAIN to MAXENT (Elith et al. 2006). MAXENT was consistently one of the best performing models.

In this study BIOCLIM under-predicted the potential distribution of invasive ant species in New Zealand. BIOCLIM had substantially higher omission error than DOMAIN and MAXENT, even when a number of different thresholds were examined within BIOCLIM. A major criticism of BIOCLIM is how locality records and climatic variables are characterised into an 'environmental envelope' in Euclidean space (Carpenter et al. 1993; Kriticos & Randell 2001). As more climatic variables are added, a progressively smaller potential distribution occurs. Consequently, BIOCLIM may tend to under-predict the potential distribution species. In this study, the inclusion of fewer variables led to a larger potential distribution area and thus improved the omission error of models (as more actual presence records were encompassed). Therefore, the number of climate variables included in a model is an important consideration because using too few, or too many, may result in incorrect predictions (Beaumont et al. 2005).

Choosing the right climate variables based on the biology of the study species also plays an important role in robust modeling (Beaumont et al. 2005, Guisan & Thuiller 2005). Although the number of environmental variables currently available as digital environmental layers is relatively few, they provide many of the variables that are strongly thought to commonly influence species macro-distributions (Anderson et al. 2003). Several climate variables are known to play a key role in the biology of ant species (Kaspari et al. 2000; Vega & Rust 2001; Holway & Suarez 2006). At large spatial scales, the tolerances of ant species are generally correlated with climate and major habitat (Hölldobler & Wilson 1990). Microhabitat specialisation and inter-specific competition play an increasing role at finer scales.

7.4.3 Distribution of invasive ants in New Zealand

Detailed studies of newly arrived invasive species and their subsequent spread are greatly lacking in the invasion biology literature (Puth & Post 2005). The continued study of these early introductions may provide useful insights into the process of invasion for ant species. This is the first time such a time lag has been described for invasive ant species, and suggests there is a considerable time lag in their spread. For example, it has taken many species several decades (40-60 years) to obtain a distribution of 5-8 Crosby regions (17-25% of all regions). Even after 100 years, the number of Crosby regions occupied is ~50% of maximum.

There are several caveats to this approach; primarily, the reliability of the year of introduction, the completeness of distribution records, and whether all species would reach the maximum number of Crosby regions. It is also likely that some species will spread faster than others, as a consequence of human-mediated spread. The Argentine ant (point x, y; 1990, 11; Figure 7.2) is one such species (Ward et al. 2005). A recent analysis of weeds in New Zealand has also shown a linear increase in distribution with the number of years since the species naturalised (Williams & Cameron 2006). Such data suggests that it takes most naturalised plants more than a century after naturalisation to appear in all environmentally suitable regions (Williams & Cameron 2006).

The six ant species modeled are predicted to be ubiquitous in the northern regions of the North Island, although areas with large stands of Kauri forest appear not to be suitable. Coastal lowland regions of the North Island are highly suitable for all species, although *Technomyrmex albipes* and *Ochetellus glaber* have the potential to extend inland and inhabit considerable areas of the middle and lower North Island. The suitability of the South Island is low for *Iridomyrmex* sp. and *Tetramorium grassii*, and these species should remain restricted to the very upper regions of the South Island. However, the other four species have the potential to inhabit sizeable areas of the South Island, particularly the eastern lowland (drier) areas of Canterbury. These distributions correspond very well to an intolerance of cooler mountainous regions. The distribution of these species in the South Island is more problematic because there are fewer occurrence records and there is greater uncertainty whether these records are permanent self-sustaining populations.

Comparing the number of Crosby regions of current and predicted distribution suggests that each species is currently distributed in only half the number of regions is could potentially inhabit. Thus, it will take many more decades before these species have reached equilibrium in their regional-scale distribution (assuming these species are not already present in these areas but are undetected).

7.4.4 Conclusions

Invasive ant species are potentially a significant threat to the New Zealand biota, which has evolved in the absence of a large and dominant native ant fauna. Thus, the continued study of invasive ants in New Zealand is warranted, particularly the potential distribution of species and their ecological impacts. At present there is no information regarding the ecological impact of invasive ant species in New Zealand and scant information on other aspects of their biology. Several avenues exist to improve the accuracy and value of habitat suitability maps for invasive ant species in New Zealand. The inclusion of soil moisture and temperature information are likely to be particularly useful as this has been an important variable in *Solenopsis invicta* modeling (Korzukhin et al. 2001), but such information is still being developed for New Zealand. Overlays of other environmental data could also prove useful to improve predictions, particularly vegetation coverage. However, there is also the need for widespread surveys for the presence of invasive ant species in several areas of the country. Such information will help evaluate modeling performance and also reduce apparent commission error, areas where there are no records but the species is actually present. Colony level information on the development of different life stages and nesting behaviour would also greatly assist in determining the environmental tolerances of invasive ant species.

7.5 References

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Table 7.1 The six invasive ants species modeled and the number of training records used in each partition. PCA 1-3 refers to the contribution of the first, second and third PCA axis in explaining the cumulative percentage variation in climate variables. The selected climate variables refer to variables used in comparison to ‘all variables’, numbered variables are given in the methods. The number of Crosby regions is a measure of the extent of a species distribution in New Zealand (maximum 29).

Species	**Training records**	**PCA 1**	**PCA 2**	**PCA 3**	**Selected variables**[1]	**Crosby Regions**
Iridomyrmex sp.	143	40.5	75.4	87.2	1, 3, 5, 12	8
Ochetellus glaber	125	43.1	76.7	87.1	1, 2, 3, 12	11
Paratrechina spp.	180	42.6	75.8	85.8	1, 2, 3, 7, 12	10
Pheidole rugosula	58	52.0	77.8	86.1	1, 2, 3, 5, 10, 14, 16	9
Technomyrmex albipes	122	40.3	73.7	84.5	1, 2, 3, 4, 12	16
Tetramorium grassii	94	81.9	98.4	99.4	1, 4, 12, 16	7

[1] annual mean temperature [1], mean monthly temperature range [2], isothermality [3], temperature seasonality [4], maximum temperature of warmest month [5], temperature annual range [7], mean temperature of warmest quarter [10], annual precipitation [12], precipitation of driest month [14], precipitation of wettest quarter [16].

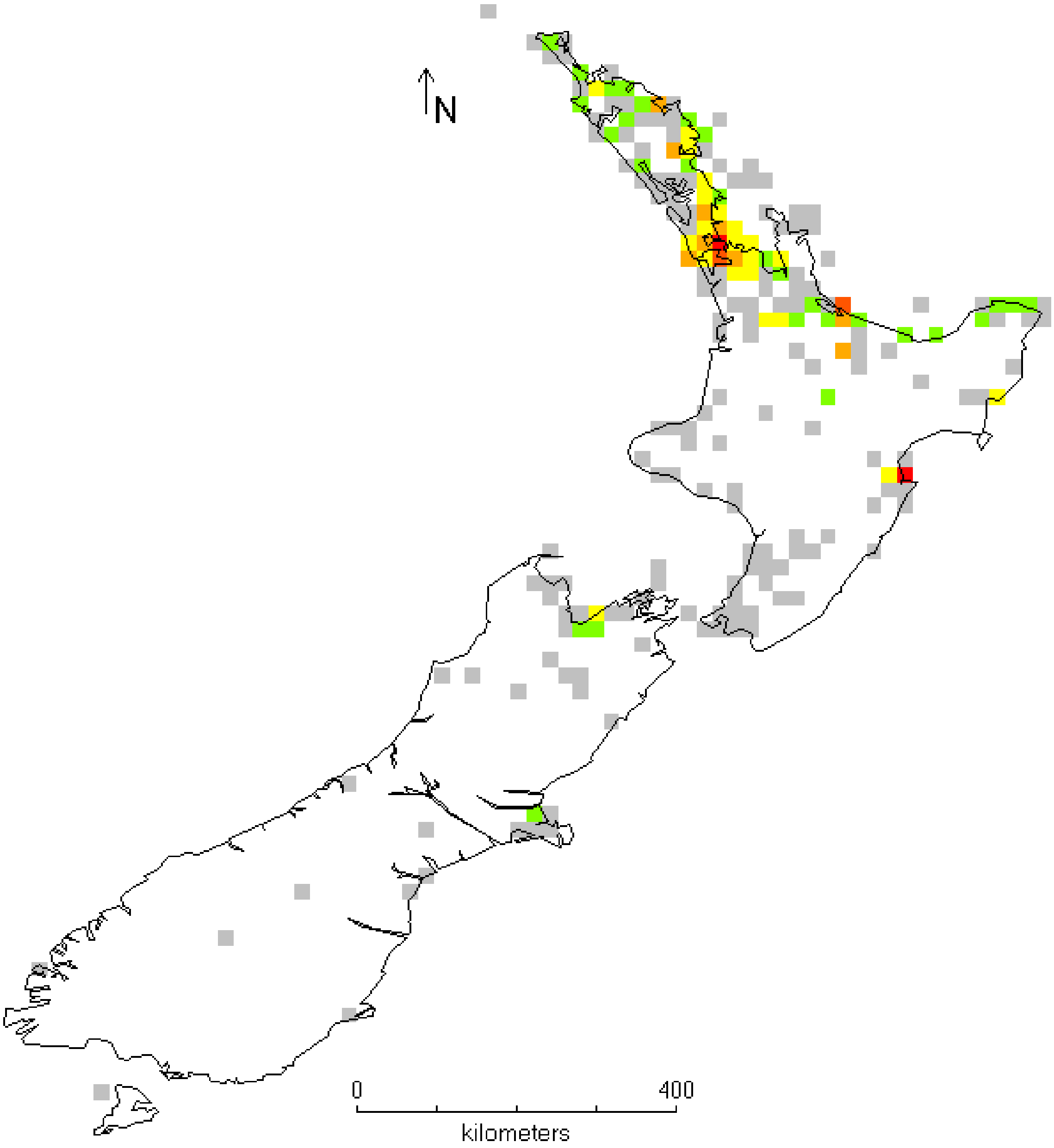

Figure 7.1 The current distribution of invasive species in New Zealand (mapped on 20 x 20 km scale). Colours refer to the number of invasive species recorded: white = 0, grey = 1 - 3, grey = 4 - 6, yellow = 7 - 9, orange = 10 - 12, red = 13 - 18. Points off the main islands represent small offshore islands.

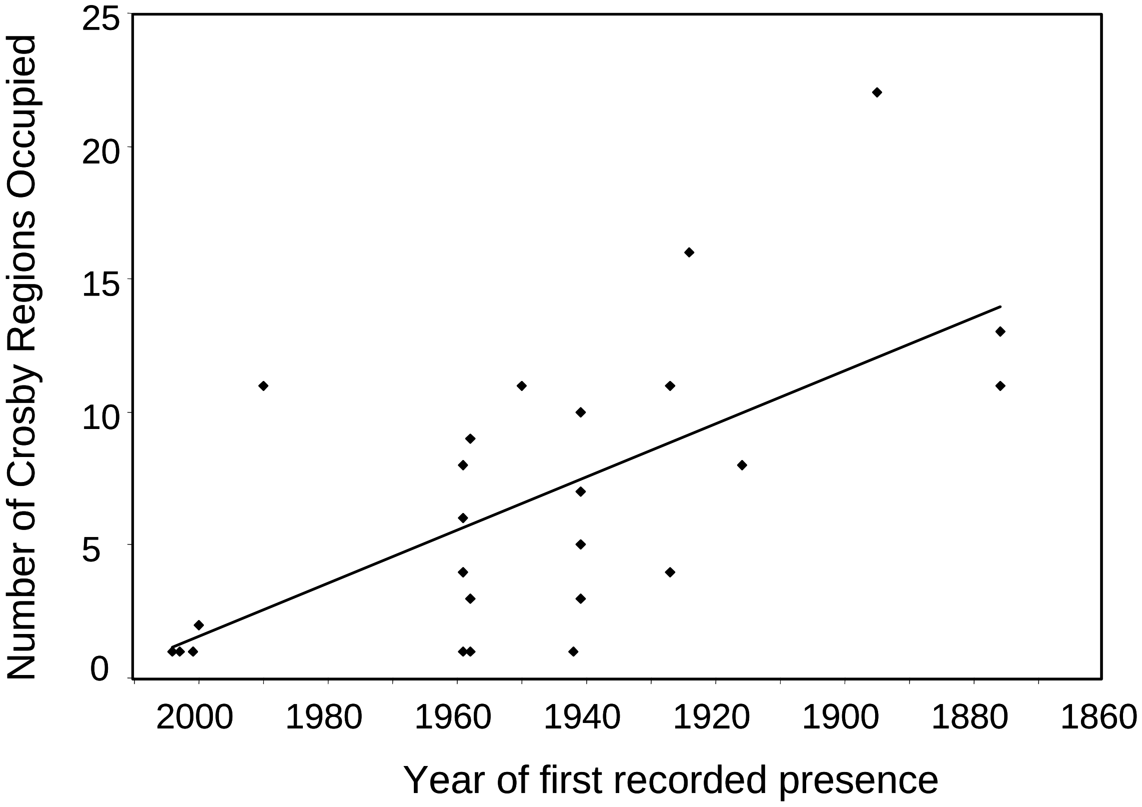

Figure 7.2 Relationship between the length of time an invasive species has been present in New Zealand and its current distribution (measured by the number of Crosby regions (Crosby et al. 1998); each point represents one species, $y = -0.1x + 201.66$, $r^2 = 0.436$, $p < 0.01$).

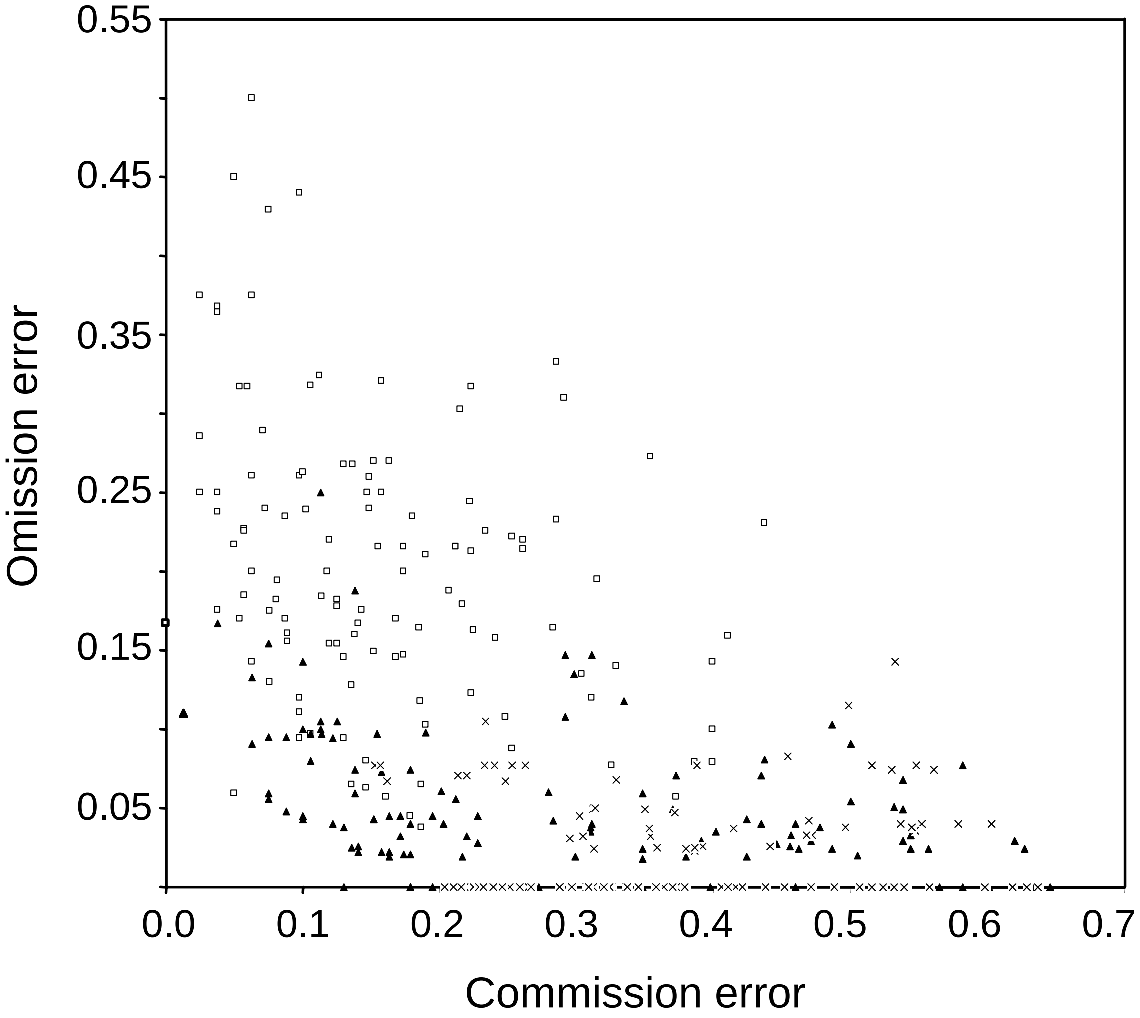

Figure 7.3 Omission versus commission error for modeling methods. Climate variable options (all vs select) are not distinguished. Points represent a single model: square = BIOCLIM, triangle = DOMAIN, cross = MAXENT.

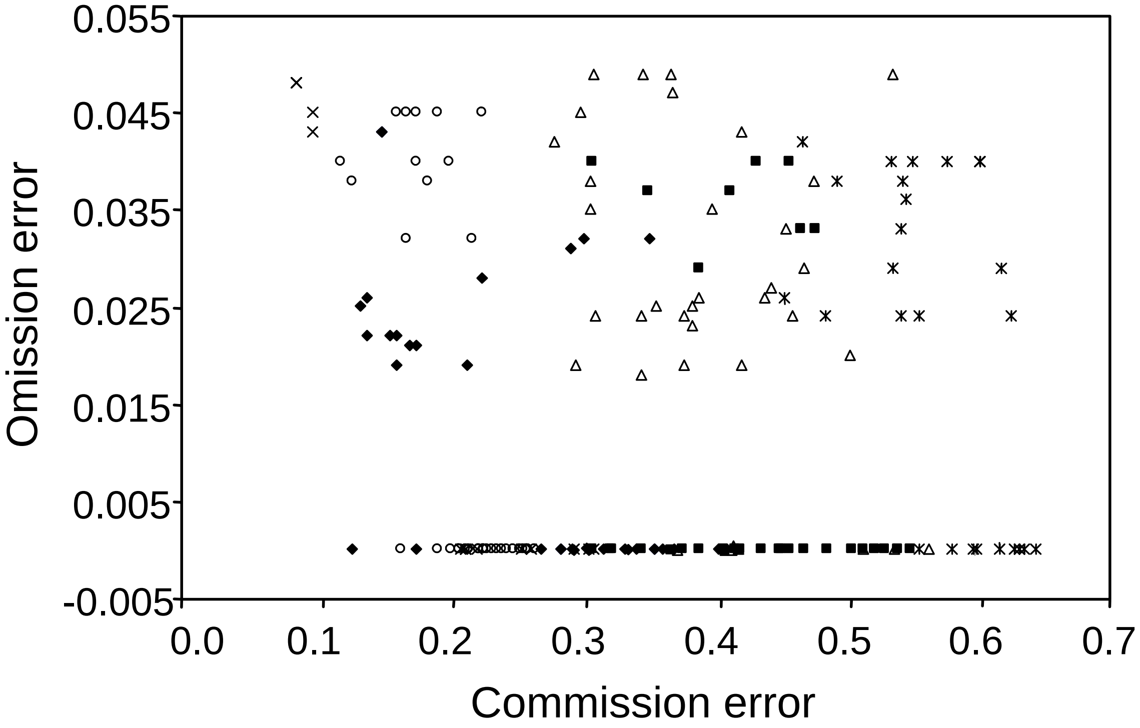

Figure 7.4 The range of commission error for each species from optimal models (omission error < 0.05). Points represent a single model: single cross = *Pheidole rugosula*, circle = *Tetramorium grassii*, diamond = *Iridomyrmex* sp., triangle = *Paratrechina* spp., square = *Ochetellus glaber*, double cross = *Technomyrmex albipes*.

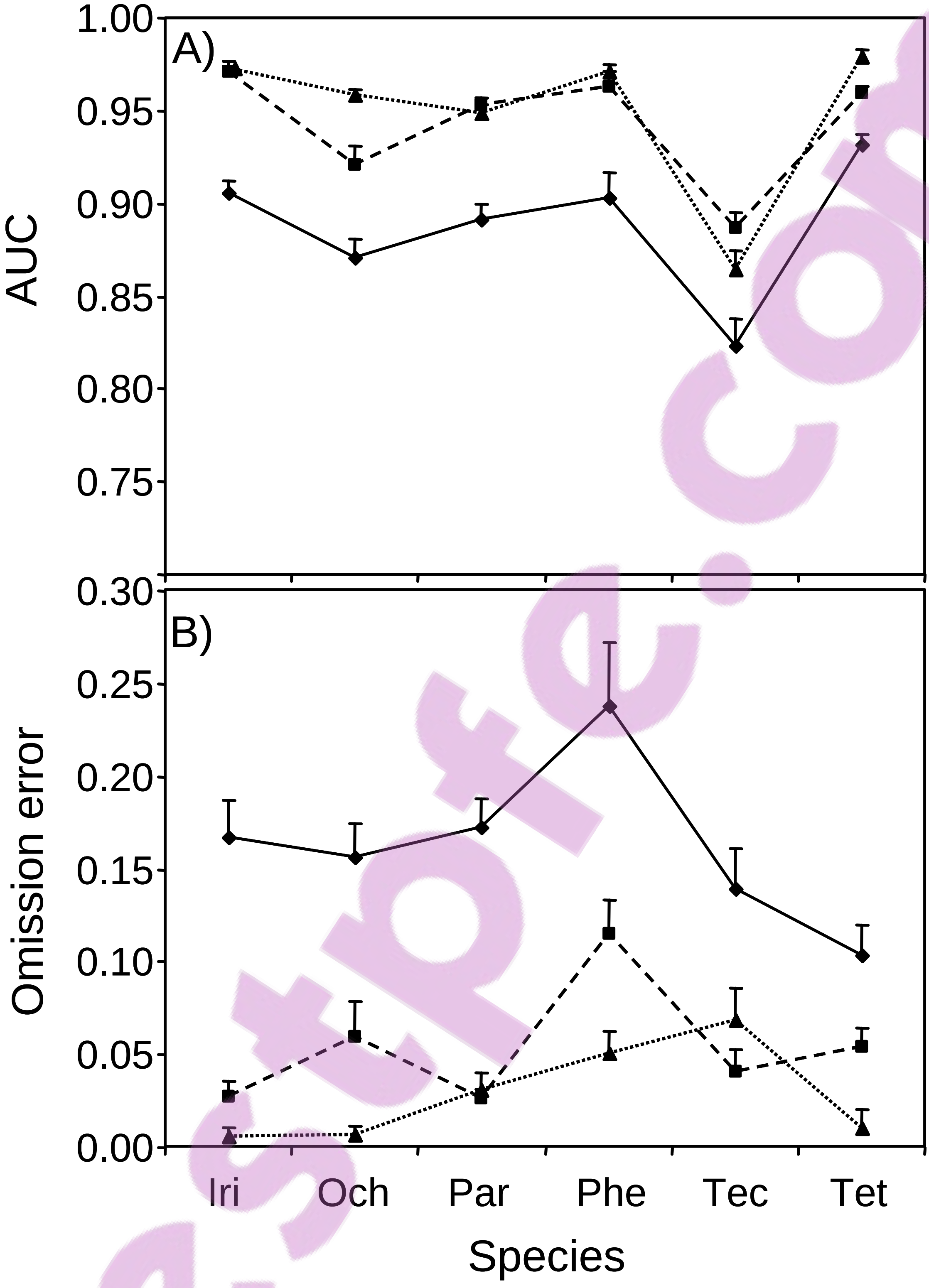

Figure 7.5 a) Average AUC values (± SD) and b) average omission error (± SD) for each species and modeling method: solid line = BIOCLIM, dashed line = DOMAIN, dotted line = MAXENT. Codes for species are: Iri = *Iridomyrmex* sp., Och = *Ochetellus glaber*, Par = *Paratrechina* spp., Phe = *Pheidole rugosula*, Tec = *Technomyrmex albipes*, Tet = *Tetramorium grassii*.

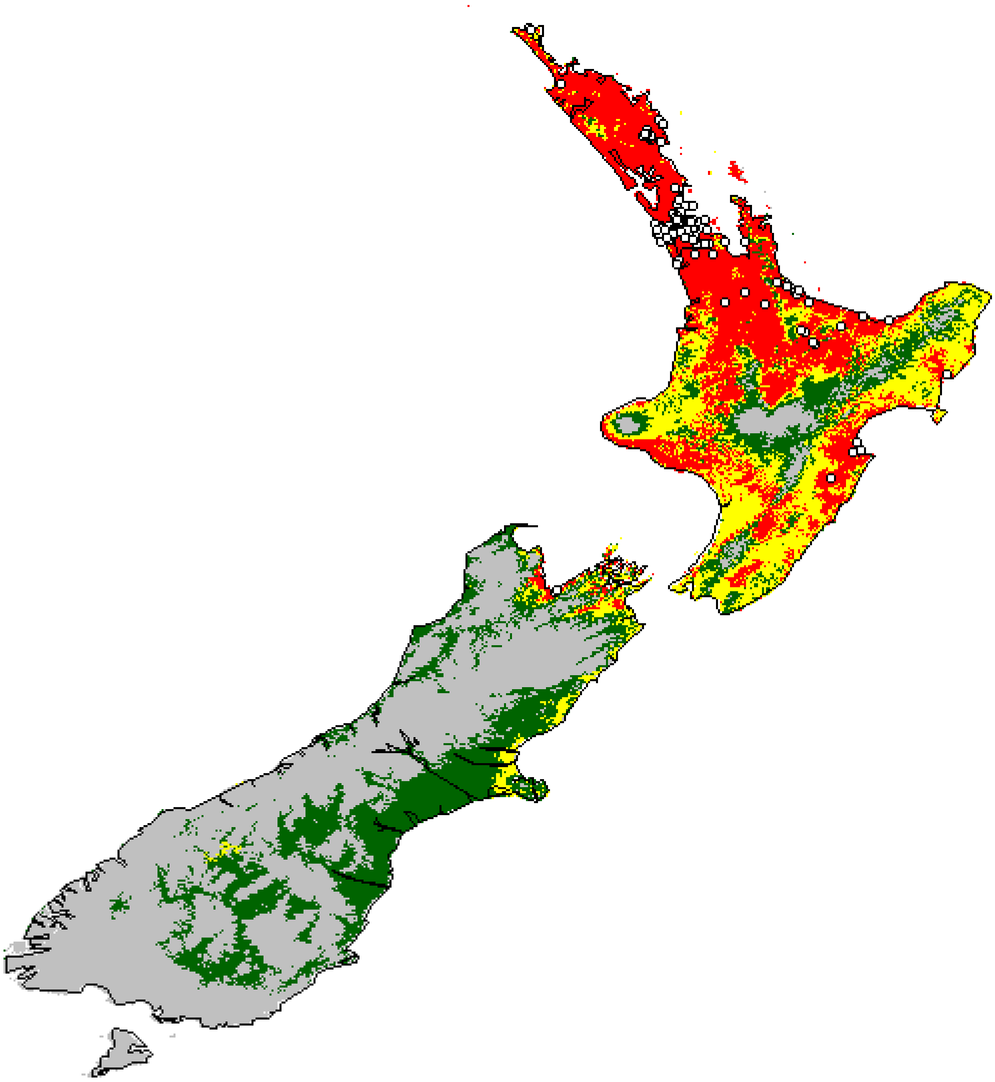

Figure 7.6 The potential geographic distribution of *Iridomyrmex* sp. in New Zealand, based on a DOMAIN model and score: grey = unsuitable, green = unlikely, yellow = possible, red = probable. Species presence points are marked by white dots.

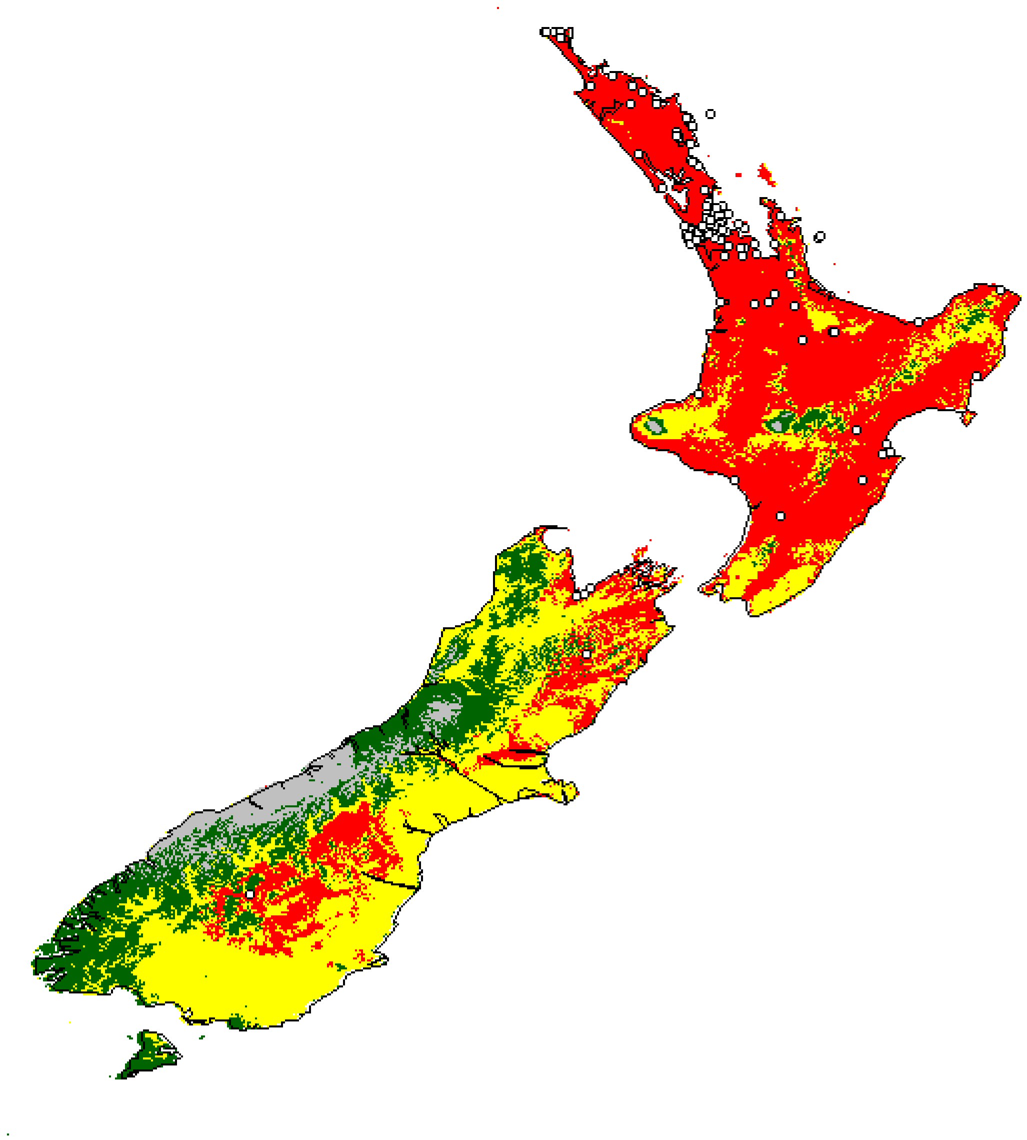

Figure 7.7 The potential geographic distribution of *Ochetellus glaber* in New Zealand, based on a DOMAIN model and score: grey = unsuitable, green = unlikely, yellow = possible, red = probable. Species presence points are marked by white dots.

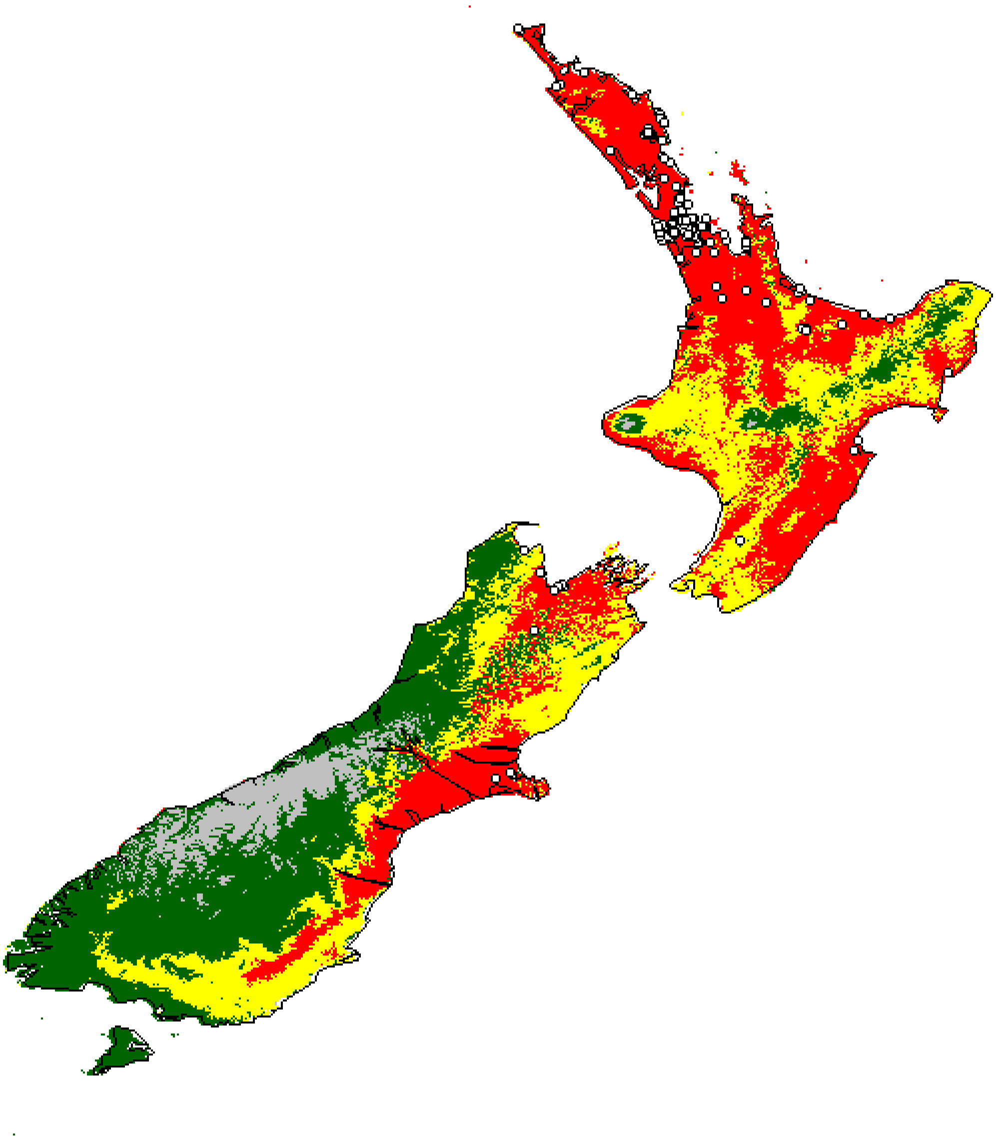

Figure 7.8 The potential geographic distribution of *Paratrechina* spp., in New Zealand, based on a DOMAIN model and score: grey = unsuitable, green = unlikely, yellow = possible, red = probable. Species presence points are marked by white dots.

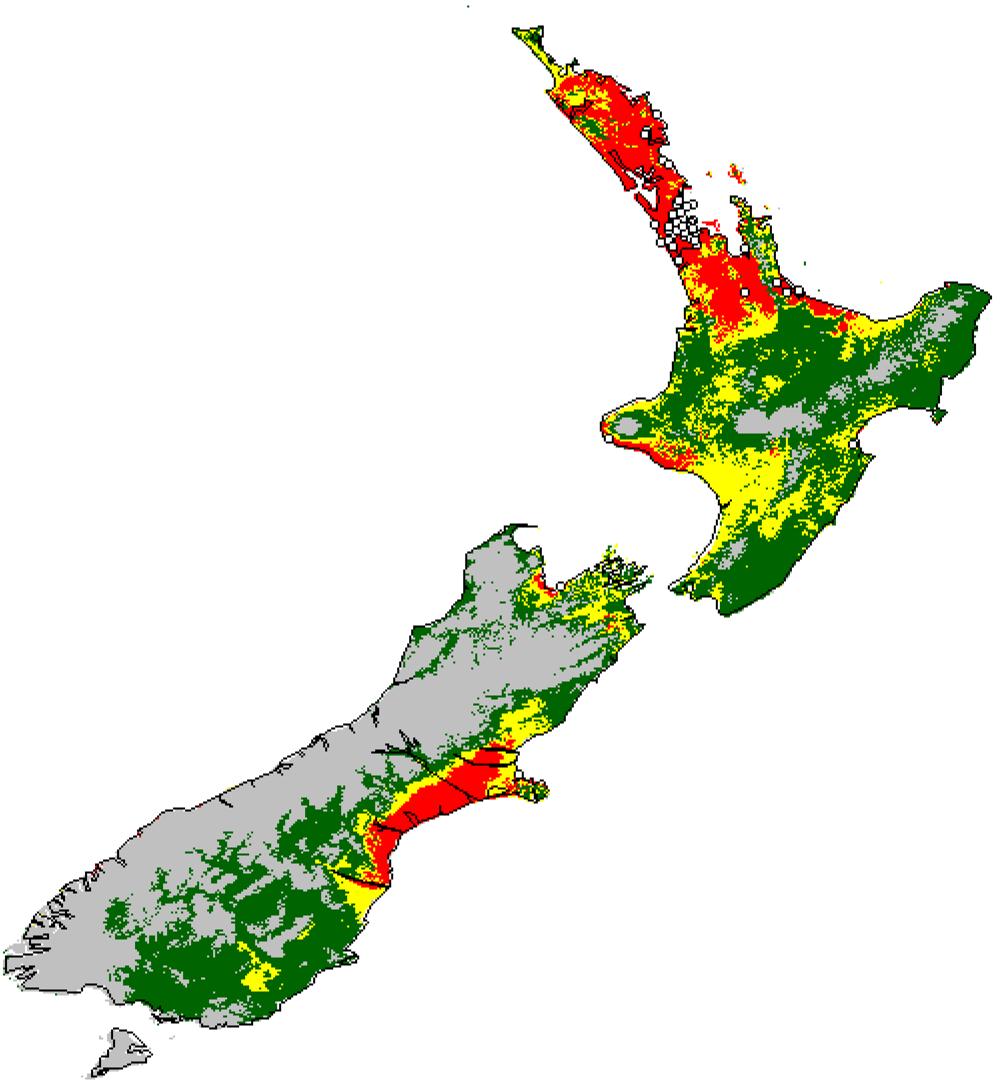

Figure 7.9 The potential geographic distribution of *Pheidole rugosula* in New Zealand, based on a DOMAIN model and score: grey = unsuitable, green = unlikely, yellow = possible, red = probable. Species presence points are marked by white dots.

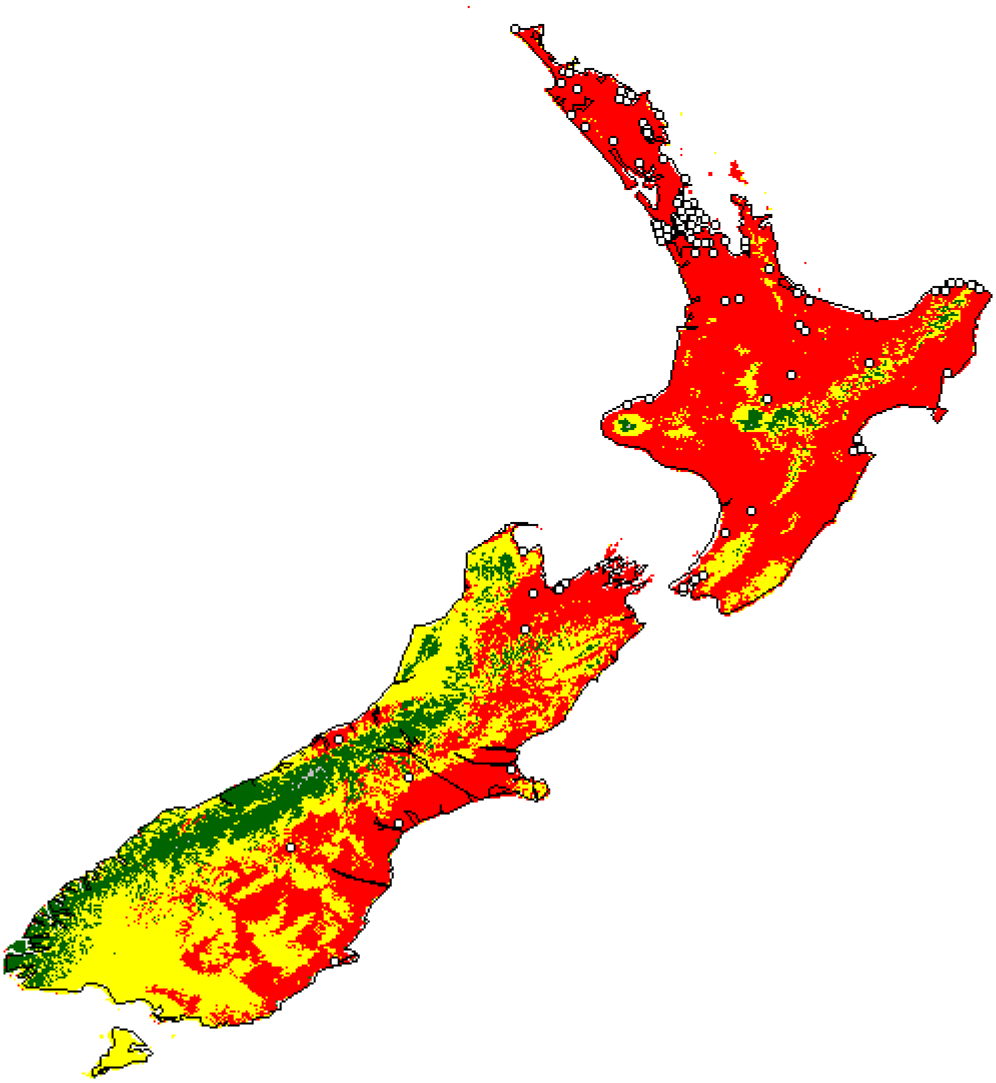

Figure 7.10 The potential geographic distribution of *Technomyrmex albipes* in New Zealand, based on a DOMAIN model and score: grey = unsuitable, green = unlikely, yellow = possible, red = probable. Species presence points are marked by white dots.

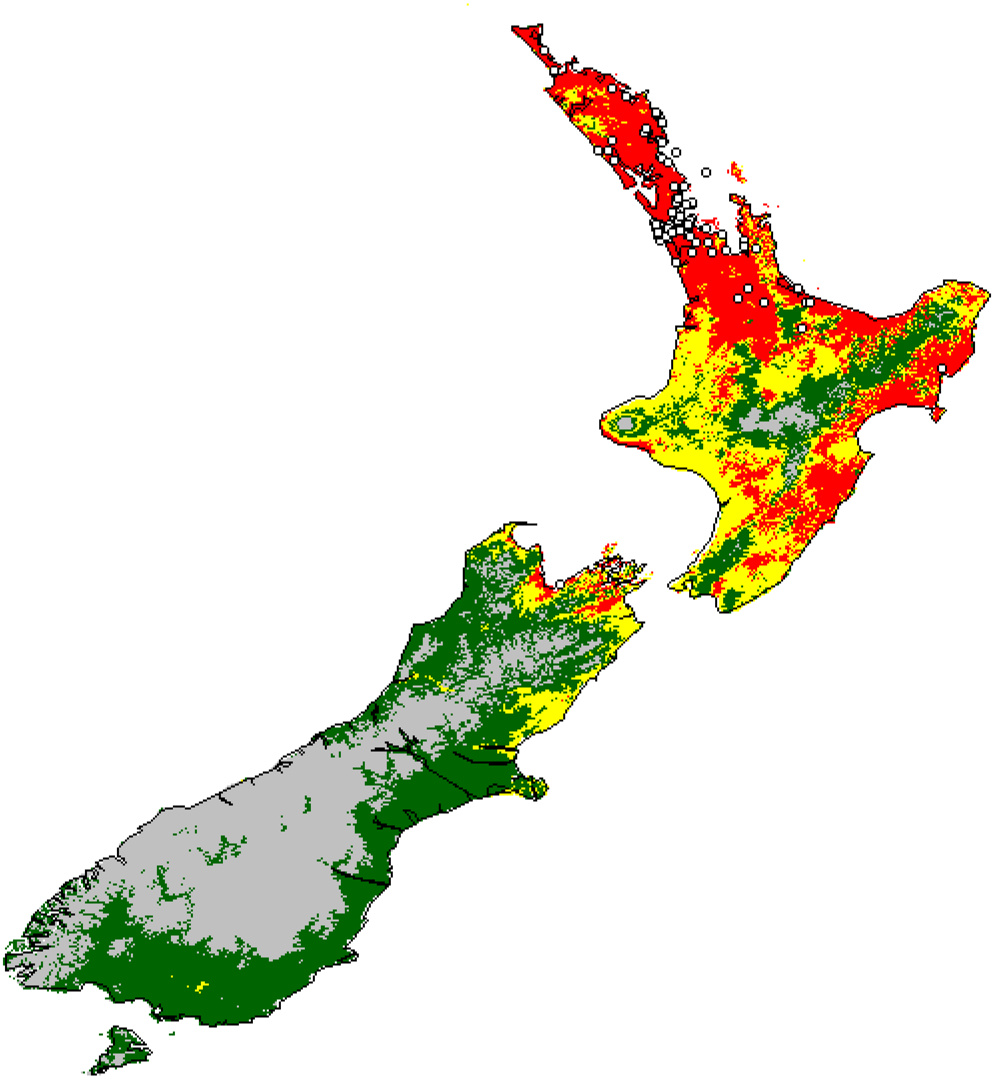

Figure 7.11 The potential geographic distribution of *Tetramorium grassii* in New Zealand, based on a DOMAIN model and score: grey = unsuitable, green = unlikely, yellow = possible, red = probable. Species presence points are marked by white dots.

The Diversity and Origin of Exotic Ants Arriving in New Zealand via Human-Mediated Dispersal

8

Abstract

The number of exotic ant species being dispersed to new regions by human transportation and the trade pathways responsible for this are poorly understood. In this study, the taxonomic diversity, trade pathways and origin of exotic ants intercepted at the New Zealand border were examined for the period 1955-2005. Overall, there were a total 4355 interception records, with 115 species from 52 genera. The ten most frequently intercepted genera, and the twenty most frequently intercepted species contributed >90% of all records. Many of the species frequently intercepted are regarded as invasive species, and several are established in New Zealand. The most intercepted species was *Pheidole megacephala*. Despite a relatively low trade relationship, a high proportion (>64%) of the exotic ants which were intercepted, originated from the Pacific region. However, the majority of species intercepted from the Pacific are themselves invasive in the region (71%), or to a lesser extent, wide ranging native Pacific species. No endemic species from the Pacific were intercepted. The effectiveness of detecting exotic ant species at the New Zealand border ranged from 48-78% for different trade pathways, indicating a number of species remain undetected. Trade routes associated with specific geographic regions represent a major filter for the arrival of exotic ant species. Despite limitations associated with historical border records, they represent a valuable resource to provide practical information on the dispersal of exotic species and to prioritise trade pathways and commodities for the detection of unwanted organisms.

8.1 Introduction

It is well recognised that biological invasions occur along an invasion pathway, typically divided into initial dispersal, establishment and spread (Vermeij 1996; Heger & Trepl 2003). Initial dispersal is the fundamental stage upon which all other stages are reliant. Only those species which successfully pass through the initial dispersal filter proceed along the invasion pathway. However, there is relatively little information on this critical stage, with most of the knowledge regarding biological invasions relating to the establishment and spread stages (Kolar & Lodge 2001; Puth & Post 2005).

Global trade and transportation by humans has greatly extended the capacity of many species to become established in regions outside their natural range (Drake et al. 1989; Mooney & Drake 1989; Williams 1994; Sandland et al. 1999; Floerl & Inglis 2004). Trade routes essentially represent pathways for invasion, with transport hubs (shipping ports, airports, mail centres) acting as important foci for the arrival and spread of exotic species (Ricciardi & Rasmussen 1998; Floerl & Inglis 2004). The likelihood that a new region will receive exotic species is largely influenced by the presence of, or proximity to, a major port of entry (Mack et al. 2000). Accurate estimates of arrival rates of exotic species are required to develop risk assessments for specific trade pathways and species. However, there have been few opportunities to quantify arrival rates of exotic species (Work et al. 2005).

Two recent international examples serve to show the number and diversity of insects being transported by human trade. Stanaway et al. (2001) surveyed the floors of empty sea containers arriving in Brisbane, Australia, over a six month period. They demonstrated that containers were regularly exposed to timber, agricultural and nuisance arthropod pests. Thirty-nine percent of containers were found to be contaminated with arthropods. In a much larger study, Work et al. (2005) examined several types of cargo entering the USA; refrigerated and non-refrigerated marine cargo, air cargo, and cargo across the USA-Mexico border. During 1997-2001, they estimated a new insect species was intercepted every 54 inspections. However, projected estimates suggested that inspectors only detected 19-28% (non-refrigerated marine cargo) and 30-50% (USA-Mexico border) of insects. Work et al. (2005) also found that the number of insect species detected from maritime cargo (refrigerated) entering the USA was poor, compared to other cargo pathways.

Invasive ant species are currently receiving considerable attention from around the globe, with increasing evidence of economic and agricultural impacts, health effects on humans, displacement of native species, and disruption to natural ecosystems (Williams 1994; Christian 2001; Holway et al. 2002; O'Dowd et al. 2003). Previous estimates suggest at least 150 species of ants have arrived at new regions accidentally through global trade (McGlynn 1999). There is also increasing evidence that human transportation is the major explanation for the range expansion within a region of established invasive ant species (Suarez et al. 2001; Ward et al. 2005). However, few regions have undertaken a comprehensive assessment of exotic ant species and the mechanisms behind their arrival and establishment (Deyrup et al. 2000; Harris et al. 2005). Recently, Suarez et al. (2005) examined historical records of human transportation and the interception of exotic ant species in the United States. This is one of the few examples for any taxonomic group that provides information on the number, diversity and type of species that have had the opportunity to overcome the initial barrier to invasion. Such data are important in predicting why some species become successful biological invaders while other species do not (Lester 2005; Suarez et al. 2005).

New Zealand has a very small endemic ant fauna (11 species). This is probably because of its long (>80 million years) geographic isolation from Australia, which has presented an extreme limitation to the natural dispersal of ants (distance of >2500km). However, through human trade 28 exotic ant species have become established and are invasive. Ants are the second most common family of insects intercepted at the New Zealand border (Keall 1980, after armoured scale insects, Homoptera: Diaspididae). The recent arrival of the Argentine ant, *Linepithema humile*, has led to considerable attention towards the risk and potential impacts posed by invasive ant species to New Zealand (Lester et al. 2003; Hartley & Lester 2003; Harris et al. 2005; Ward et al. 2005; Ward & Harris 2005).

In a major review of biological invasions, Mooney and Drake (1989) posed several fundamental questions relevant to the initial dispersal stage of biological invasions; who are the invaders, how do they get there, and where do there come from? Reducing the threat of new invasions requires a focus on the ways humans facilitate the transport of species to new areas (Hayes 2003; Floerl & Inglis 2004). The aim of this chapter is to provide statistics on the taxonomic diversity, trade pathways and origins of exotic ant species being unintentionally transported by humans at the New Zealand border. Additionally, estimates of the number of species and the effectiveness of detecting exotic ant species in border inspections are evaluated. An understanding of the pathways used by exotic ants to arrive in New Zealand, and the origins of the exotic species, will be of major practical benefit to biosecurity authorities in New Zealand, but patterns within the data may also be relevant to other geographic regions.

8.2 Methods

The New Zealand Ministry of Agriculture and Forestry Quarantine Service (MQS) is part of the Ministry of Agriculture and Forestry (MAF), and is responsible for examining cargo, goods and mail which are imported, and people that arrive, into New Zealand. MQS personnel sample cargo in shipments that arrive via maritime vessels or air transport. Because New Zealand is a island nation, shipments via land vehicles crossing the border are not relevant.

Products transported through different cargo pathways vary significantly in their quantity, size and shape, and therefore, the sampling units used for MQS inspections also vary. In general, the sampling unit from air cargo represents the collection of items described by the accompanying manifest for a given shipment. At airports, approximately 9000 people per day arrived in New Zealand (Hayden & White 2003). For the period 1993-1999, approximately 11.4 - 15.7% of passengers declared risk items and 1.5 - 2.3% (detected rate) did not declare such items (Hayden & White 2003).

For maritime cargo, sampling unit are containers (6m and 12m lengths). Three sampling approaches are taken to detect exotic species; 1) cargo with high risk packing are selected for inspection, 2) cargo which is certified as free from contamination is verified by randomly sampling 10% of the cargo, and 3) a proportion of cargo is inspected on the basis of estimated risk; 100% of very high risk goods are examined, with low risk goods examined less (to as low as 5%). Examples of high risk goods include: soil, wood, hay, sea containers, nursery stock, and vehicles. Low risk goods include: mail, personal items, treated building material. Prior to 2004, approximately 20% of maritime containers were inspected by MQS personnel that arrived annually into New Zealand. For example, in 1999-2000, over 350 000 maritime containers arrived in New Zealand, of which 27.8% were inspected and of those, 24.8% were contaminated and required quarantine action (Hayden & White 2003). In 2003, over 550 000 sea containers arrived into New Zealand (MAF unpub. data). However, since 2004, all sea containers entering New Zealand are now examined. High risk commodities are still examined by

MQS personnel, but low risk goods are examined by trained inspectors at transitional facilities (an approved facility for the purpose of storage, treatment, quarantine or destruction of uncleared goods away from ports of entry).

Details of positive detections of exotic ant species are recorded in a MAF database of interception records. Two sets of border interception records were obtained from MAF to determine the exotic ants arriving into New Zealand.

8.2.1 Historical port of entry (POE) records

Previously published MAF records for the period 1955-2003 were used to provide a historical background on the exotic ant species which have been intercepted at the New Zealand border. Published records were obtained for five time periods: for 1955-1965 from Manson and Ward (1968), 1966-1972 from Richardson (1979), 1973-1978 from Keall (1981), 1979-1982 from Townsend (1984), and unpublished records of 1983-2003 from MAF. The validity of species names were checked using Bolton (1995), and subfamily nomenclature follows Bolton (2003). For historical records, ants detected on fresh produce, nursery stock and plant products were required to be identified at the National Plant Pest Reference Laboratories (NPPRL) of MAF. Other pathways were at the discretion of the quarantine officer as to whether the ants are submitted for identification.

8.2.2 All ants, all pathways records

During the period December 2004 to June 2005 (inclusive), MQS undertook an assessment of ‘all ants, all pathways’ (AAAP). The aim of this assessment was to characterise all the exotic ant species entering New Zealand. During the AAAP period *all* ants from *all* pathways which were detected were required to be submitted for identification.

The major difference between the AAAP period and Historical POE records is that analysis and interpretation of data based on Historical POE records need much greater caution, and are less useful for statistical analyses. With the historical POE records there is far greater uncertainty of 1) what ant species were detected during quarantine sampling but *not* sent for identification and subsequent databasing, 2) the sampling procedures varied over such a long time period (50 years), and were less stringent than compared with present-day procedures, and 3) only since 2004 have all low risk goods from maritime containers been examined. Thus the AAAP assessment represents the best dataset to fully characterise the efficiency of detection of exotic ant species entering New Zealand.

AAAP records were obtained from MAF, and re-classified into four trade pathways: air cargo, air passengers, maritime cargo, and total cargo. Country information from POE records was re-classified into a region of origin: Australia, Pacific, Europe, Asia, the Americas, and Africa/Middle East. Commodity information was also re-classified into larger subsets of information: containers (air/maritime), timber, fresh produce, vehicle (cars, equipment, and machinery), personal effects (including mail).

To evaluate the effectiveness of inspections at detecting exotic ant species during the AAAP time period, the number of species arriving through four trade pathways (maritime cargo, air cargo, air passengers, and total cargo) was estimated, using sample-based rarefaction procedures in EstimateS software v.7.5 (Colwell 2005). In these analyses, specimens identified only to genus were treated as a unique species. For example, if there were 3 records of "*Camponotus*", these records are treated as one species but kept separate from other named *Camponotus*. This approach avoids overestimating effectiveness (by not ignoring unidentified species) and also avoids over-inflating rarefaction curves (by not treating each unidentified records as a species). Abundance data were not used, because such data are not always accurately recorded in border interceptions, where the emphasis is on detecting the presence or absence of a species (Venette et al. 2002). Additionally, the number of worker ants is not an accurate measure of abundance, because the fundamental unit of ants is the colony (Hölldobler & Wilson 1990). Therefore, AAAP records were coded as binary data.

Three sets of rarefaction curves were used to estimate the number of exotic ant species within a trade pathway (see Work et al. 2005). The observed number of exotic ant species detected through MQS interceptions (AAAP records) was defined as the 'best-case' scenario. In this scenario, the observed rarefaction curves only represent the 'best-case' scenario if they reach an asymptote. If an asymptote is not reached, it indicates that sampling has underestimated the number of species arriving in each trade pathway. In trade pathways where no asymptote is reached, a 'probable' and 'worst-case' scenario were calculated using the Chao 2 estimator of species richness (Colwell 2005). A 'probable' scenario was assessed using the Chao 2 estimator. A 'worst-case' scenario was assessed using the Chao 2 +1 standard deviation, which can be considered the upper limit of the total number of species (both detected and undetected).

The Chao 2 estimator is particularly useful for datasets which have many rare specie, as it up-weights the importance of singletons and doubletons (species with a score of one and two respectively). (Colwell & Coddington 1994; Colwell 2005). This effect accelerates the rarefaction curve towards an asymptote, and thus an estimate of the number of species that would have been detected given increased sampling effort (Colwell & Coddington 1994). Datasets with high numbers of singletons and doubletons indicate sampling is incomplete. The default parameters in EstimateS were used, with 50 runs, and the classic formula for the Chao 2. The efficiency of detecting exotic ant species within each trade pathway was evaluated using the number of observed species divided by the Chao 2 estimate of species richness.

8.3 Results

8.3.1 Historical port of entry records

From 1955 to 2003 there were 4355 POE records of ants intercepted at the New Zealand border. Of these, 1036 records (23.8%) were identified to genus, and 3213 (73.8%) were identified to species level. Within such a large dataset some taxonomic issues relating to species-level identification will arise. Nevertheless, I am confident that the identified species are representative of the actual species arriving at the border because if species-level identification could not be made, or was doubtful, specimens were only identified to genera.

A total of 110 species were intercepted from 51 genera (Appendix 8.1). Forty four species have only one record (singletons), and 12 species have only two records (doubletons). Nine subfamilies were represented in the POE records, although species from Myrmicinae, Formicinae and Dolichoderinae were the most frequently intercepted (Table 8.1). Species from POE records differed significantly from ants in general with respect to taxonomic composition at the level of the subfamily ($X^2 = 26.28$, d.f. = 4, $P < 0.01$, Table 8.1), with proportionally fewer Myrmicinae but more Dolichoderinae in POE records.

Additionally, there was a significance difference between the proportion of species in POE records versus all established exotic species in New Zealand ($X^2 = 9.83$, d.f. = 4, $P < 0.05$, Table 8.1). There are currently 28 exotic species of exotic ants established in New Zealand (Ward 2005), of which 15 were recorded in the POE records (Appendix 8.1).

The most intercepted genus was *Pheidole* (34.7% of total), and the ten most frequently intercepted genera contributed 90.1% of all records (Table 8.2). The most intercepted species was *Pheidole megacephala* (27.7% of all records), and this was also the most frequently recorded species in each time period (range for time periods 14.4 - 32.4%). Overall the 20 most frequently intercepted species contributed >90% of all records (range for time periods 83.3 - 95.7%).

8.3.2 All ants, all pathways records

During this period (December 2004 - June 2005), there were 344 detection records of exotic ants from 319 positive inspections. Thirty species were identified and 18 generic-level identifications were made. Five taxa were recorded in this period that had previously not been identified in POE records (Appendix 8.1).

There was strong overlap between the historical POE records and AAAP records. For example, 18 of the 20 most frequently intercepted species were present in both sets of records absent from AAAP records were *Camponotus pennsylvanicus* and *Monomorium monomorium*. In the AAAP records *Monomorium pharaonis* was the most recorded species (54 records), whereas *Pheidole megacephala* was second (47 records).

Maritime cargo made up the largest proportion of AAAP records (42.6%), but air passengers (34.4%) were also a significant source, with air cargo (16.0%), and mail (4.6%) making smaller contributions. Worker ants made up the majority of the life stages of ants that were intercepted (75.9%). However, reproductive castes, including queens, males, alates, and combinations of these reproductive stages with workers, contributed 24.1% of intercepts.

The majority of the AAAP records (64.4%) originate from countries in the Pacific region. Fiji, Tonga and Samoa contribute >70% of Pacific records, but ant species were intercepted from a total of 12 Pacific nations. Countries in Asia contribute 22.2% and Australia 8.8% of AAAP records. These data also parallel POE records from 1983-2003, which show a high proportion (>65%) of POE records originate from countries in the Pacific region. Fiji, Tonga and Samoa also contribute >85% of all records from 1983-2003. Overall, 21 species were intercepted from the Pacific (Appendix 8.1). Fifteen (71.4%) of these are invasive in the Pacific islands; the remaining six species (28.6%) are wide ranging species native to the Pacific. No endemic species from the Pacific were intercepted.

The main commodity on which ant species arrived was fresh produce (46.7%; Table 8.3). The number of species detected from each commodity type was very strongly correlated with the number of AAAP records ($y = 0.0995x + 10.755$, $R^2 = 0.98$). There was some variation in the importance of different commodities and origins for each specific trade pathway (Table 8.4). For example, fresh produce was an important source of exotic species from air cargo and air passengers, which arrived predominantly from the Pacific (Table 8.4). For maritime cargo, containers and used vehicles were the major source of exotic species, predominantly from Asia.

For each trade pathway the number of exotic ant species detected increased as the number of records increased, but, asymptotes were never reached (Figure 8.1). This indicates that a number of other species remained undetected in these pathways. Projected estimates of the total number of exotic species for the ‘probable-case’ scenario, suggested that species asymptotes were reached for air cargo, air passengers and total cargo (Figure 8.1). Efficiency of detection was 78% for air passengers, 73% for air cargo, 66% for total cargo, but only 48% for maritime cargo. However, a species asymptote was not reached for any scenario (Figure 8.1) for maritime cargo, so this estimate needs to be treated with caution.

8.4 Discussion

8.4.1 Diversity of species, commodities and origins

Over a 50 year period (1955-2005), at least 114 species of ants from 52 genera and nine subfamilies were intercepted at the New Zealand border. McGlynn (1999) listed 147 species of ants which had been transported to new regions around the globe, but only 45% of the species in this study were also recorded by McGlynn (1999). Suarez et al. (2005) also documented the ant species entering the United States through human trade. Their results showed that over a 60 year period, 232 species (58 genera) were intercepted from 394 samples. Taken together, these studies illustrate the remarkable diversity of ant species that have been, and are being, transported by global trade.

The data also show that there can be considerable diversity of exotic species arriving at the borders of a relatively small trading country. For example, the land area of the United States is 35x larger, the population 75x larger, and the imported goods into the United States is 750x larger than New Zealand (Anon 2005). The exotic ant datasets of both countries are based on border authorities collecting information on positive interceptions of species, yet almost the same number of genera, and half the number of species were intercepted from New Zealand in comparison to the United States (Suarez et al. 2005). Furthermore, the United States samples generally contained many species with few records (e.g. a high number of singletons, 68%), while interceptions into New Zealand were dominated by a few species with many records (e.g. 20 species contributed >90% of all records).

I am unsure why such a high number of taxa has been recorded from New Zealand (or a low number from the United States). New Zealand is regarded as having very strict border control procedures which may have meant that a higher proportion of species has been detected. However, the number of POE records/samples may also account for part of the ‘disported comparison’ between the New Zealand (>4000) and the United States (394). If more records were available from the United States, the number of taxa recorded there would probably increase. However, this would only substantially add to the already high diversity of ant species being transported around the globe.

Suarez et al. (2005) found that the exotic ant species intercepted in the United States most commonly originated from the Neotropics. However, these data are in stark contrast to our study where the majority of exotic ant species were intercepted on commodities originating from the Pacific islands. Trade volumes do not account for the relationship between the Pacific and New Zealand. Trade and immigration of people from the Pacific into New Zealand represents an extremely small proportion of New Zealand’s overall trade and immigration (total imported cargo NZ$ million is <1%; human immigration ~3.5% from the Pacific; Anon 2002). Furthermore, imported goods into New Zealand from South and Central America (Neotropics) are two to three times larger than between New Zealand and the Pacific (Anon 2002). In addition, many of the species being transported to New Zealand from the Pacific are invasive species (McGlynn 1999; Holway et al. 2002). McGlynn (1999) has previously shown that while the majority (>55%) of intercepted exotic ant species originate from Neotropical and oriental regions, the Pacific region is the recipient of most of these species.

Another major difference between the present study and Suarez et al. (2005) is in the taxonomic composition of species at the subfamily level. While POE records from Suarez et al. (2005) represented a subset of global ants and established species were also a subset of POE records, this was not the case for New Zealand. POE records from New Zealand had proportionally more species of Dolichoderinae but fewer Myrmicinae than expected based on the taxonomic composition of global ants. However, fewer Formicinae species but more Myrmicinae have become established in New Zealand. A number of factors will combine to influence the taxonomic composition of POE records. One of the most important is the regional pool of species. For example, several subfamilies of ants are not present in the Pacific (Ward & Wetterer 2006) and so would not be expected in POE records from that region. Sampling procedures at the border may also bias detection and records, for example, in the New Zealand data a number of species may be hidden within genera only records.

8.4.2 Recommendations for quarantine authorities

Although valuable, historical POE records provide imperfect information and need careful interpretation. There is often a multitude of information collected from trade related activities at the border of a country, mostly for economic reasons. However, for biosecurity purposes this information is often inadequate, inconsistent and difficult to utilise for the purposes of generating comparable statistical data. For example, quantifying the effort put into detecting exotic ant species from the POE records in New Zealand is not possible, and how this effort changes over long periods of time is uncertain (e.g. because of government policies). The ability to quantify sampling and detection procedures to estimate arrival rates of exotic species and to develop risk assessments remains a key challenge. However, greater interaction between quarantine authorities and researchers would greatly assist in defining the information needed to obtain such data.

Results from the AAAP pilot study showed that current levels of border inspection in New Zealand remain inadequate to detect all exotic ant species. The effectiveness of detecting exotic ant species at the New Zealand border was estimated at 66-78% for different trade pathways, indicating a number of species remain undetected. For maritime cargo, a species asymptote was not reached, indicating that detection of exotic ant species from this pathway was the least effective.

Detection rates of ant species will vary depending on an array of factors, including the trade pathways and commodities that border authorities focus on, the traits of the taxa (e.g. cryptic behaviour, nesting habit, body size), and importantly, the sampling protocols in place for detecting species (Venette et al*.* 2002). Despite strict quarantine standards in New Zealand, exotic ants species remain undetected from several trade pathways. Although these undetected species undoubtedly occur in low numbers or are of a low occurrence, several authors have shown that exotic ant species can establish with either no, or very few POE records (Lester 2005; Suarez et al. 2005). Thus, there is a clear need for post-border monitoring to at least document and quantify these occurrences.

The unintentional dispersal of insect taxa by humans remains largely understudied (Kolar & Lodge 2001; Suarez et al. 2005; Work et al. 2005). However, trade pathways represent a major filter for the arrival of exotic species. Trade which is associated with specific geographic regions will limit the available pool of species which can be dispersed. Identification of potential donor regions and dispersal pathways is a key step in predicting future invasive species and mitigating their effects

(Ricciardi & Rasmussen 1998). Despite limitations associated with historical records, they represent a valuable resource (Suarez et al. 2005), not only to test hypotheses concerning biological invasions, but to also provide practical information on the dispersal of exotic species and to prioritise trade pathways and commodities for the detection of unwanted organisms.

8.5 References

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Table 8.1 The number of species from different subfamilies intercepted at the New Zealand border (POE records 1955 – 2003), and the number of exotic species established in New Zealand (as of 2005). Global ant species data from Bolton (1995). *Includes records of ants from the recently separated subfamilies Ponerinae, Ectatomminae, and Amblyoponinae (Bolton 2003).

Subfamily	**POE records (%)**	**Established (%)**	**Global ant species (%)**
Myrmicinae	40 (36.4)	15 (53.6)	4377 (48.4)
Formicinae	33 (30.0)	2 (7.1)	2458 (27.2)
Dolichoderinae	19 (17.3)	5 (17.9)	554 (6.1)
Ponerimorphs*	14 (12.7)	6 (21.4)	1299 (14.4)
Myrmeciinae	2 (1.8)	0	89 (1.0)
Pseudomyrmecinae	1 (0.9)	0	197 (2.2)
Dorylinae	1 (0.9)	0	61 (0.7)

Table 8.2 The ten most frequently recorded ant genera intercepted at the New Zealand border (POE records 1955-2003).

Genera	**Total Records**	**% of total**	**Records to genus only**
Pheidole	1470	34.6	327
Paratrechina	584	13.7	149
Monomorium	391	9.2	51
Tetramorium	337	7.9	24
Camponotus	308	7.2	195
Tapinoma	238	5.6	26
Technomyrmex	188	4.4	15
Solenopsis	114	2.7	20
Iridomyrmex	110	2.6	68
Anoplolepis	91	2.1	1
All other genera	418	9.6	160

Table 8.3 The number of records and number of exotic ant species intercepted from different commodities (AAAP records 2004-2005).

Commodity	**Number of records**	**% records**	**Number of species**
Fresh produce	156	46.7	26
Air/maritime containers	75	22.4	18
Personal items	53	15.8	17
Vehicle	37	11.1	15
Timber	13	3.9	11

Table 8.4 The number of records, observed number of exotic ant species, proportion of records that originate from the Pacific, and predominant countries and commodities for different trade pathways (AAAP records 2004-2005).

Trade Pathway	Number of records	Number of species	% Pacific records	Predominant country % of total records	Number of countries	Predominant commodities % of total records
Air cargo	49	19	89.1	Fiji 67.3%	8	Fresh produce 89.1%; personal items 5.4%
Air passenger	110	23	64.4	Samoa 25.4%	20	Fresh produce 26.3%; personal items 22.0%
Maritime cargo	137	36	47.3	Japan 14.4%	26	Container 43.8%; used vehicles 19.2%
Total cargo	319	48	64.4	Fiji 22.2%	36	Fresh produce 46.7%; Container 22.4%

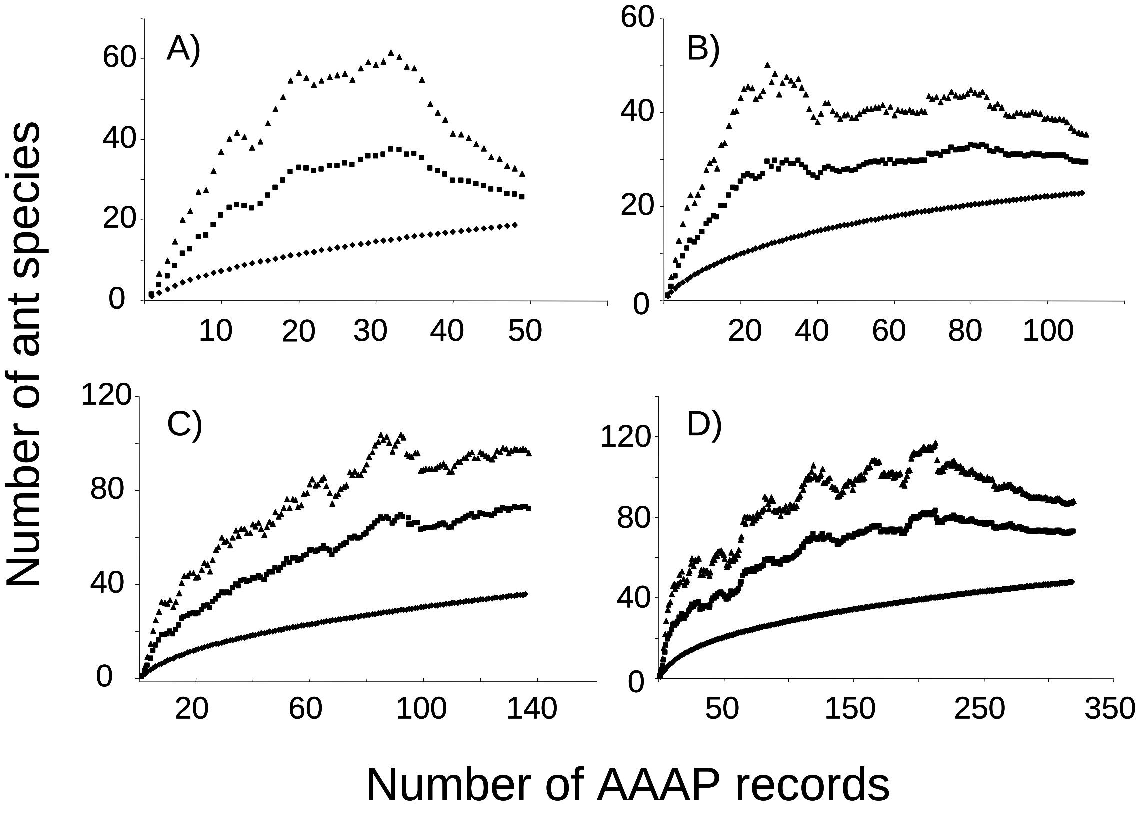

Figure 8.1 Observed rarefaction curves (‘best-case’ scenario, bottom curve), ‘probable case’ estimates (Chao 2 estimator, middle curve) and ‘worst case’ estimates (Chao 2 estimator ±1SD, top curve) of the total number of exotic ant species arriving into New Zealand (December 2004 - June 2005) by a) air cargo, b) air passenger, c) maritime cargo, and d) total AAAP records. Note changes in scales.

Appendix 8.1 List of species intercepted and the number of records for the period 1955-2005. * denotes the species is established in New Zealand. Interceptions from the Pacific (AAAP records) are indicated as: PE = invasive species in the Pacific, PN = native species in the Pacific.

Top twenty species (by number of records): *Pheidole megacephala**^{PE} (Fabricius) (890), *Paratrechina longicornis*^{PE} (Latreille) (294), *Pheidole fervens*^{PE} Roger (235), *Tapinoma melanocephalum*^{PE} (Fabricius) (211), *Tetramorium bicarinatum**^{PE} (Nylander) (196), *Technomyrmex albipes**^{PN} (Smith) (173), *Monomorium pharaonis**^{PE} (Linnaeus) (170), *Paratrechina vaga*^{PE} (Forel) (94), *Anoplolepis gracilipes*^{PE} (F. Smith) (90), *Camponotus pennsylvanicus* (De Geer) (73), *Solenopsis geminata*^{PE} (Fabricius) (67), *Monomorium floricole*^{PE} (Jerdon) (64), *Monomorium destructor*^{PE} (Jerdon) (59), *Ochetellus glaber** (Mayr) (54), *Tetramorium pacificum*^{PN} Mayr (51), *Monomorium monomorium* Bolton (45), *Linepithema humile** (Mayr) (42), *Paratrechina bourbonica*^{PE} (Forel) (37), *Tetramorium simillimum*^{PE} (Smith) (32), *Iridomyrmex anceps* (Roger) (31).

Species with >5 records: *Camponotus chloroticus* Emery, *Camponotus herculeanus* (Linnaeus), *Camponotus irritans* (Smith), *Cardiocondyla emeryi* Forel, *Hypoponera eduardi** (Forel), *Hypoponera punctatissima** (Roger), *Iridomyrmex purpureus* (Smith), *Iridomyrmex rufoniger* (Lowne), *Lasius niger* (Linnaeus), *Notoncus ectatommoides* (Forel), *Ochetellus itoi* (Forel), *Odontomachus simillimus* Smith, *Oecophylla smaragdina* (Fabricius), *Paratrechina minutula* (Forel), *Pheidole oceanica*^{PN} Mayr, *Pheidole umbonata* Mayr, *Plagiolepis alluaudi* Emery, *Polyrhachis femorata* Smith, *Rhytidoponera aspera* (Roger), *Rhytidoponera chalybaea** Emery, *Rhytidoponera metallica** (Smith), *Rogeria sublevinodis* Emery, *Solenopsis invicta* Buren, *Solenopsis papuana* Emery, *Strumigenys godeffroyi* Mayr, *Strumigenys rogeri* Emery, *Tetramorium grassii** Emery, *Tetramorium lanuginosum* Mayr, *Tetramorium tonganum*^{PN} Mayr.

Species with 2 records: *Brachymyrmex obscurior* Forel, *Camponotus chromaiodes* Bolton, Camponotus *tortuganus* Emery, *Camponotus variegatus* (F. Smith), *Cardiocondyla nuda*^{PN} (Mayr), *Dolichoderus thoracicus* (Smith), *Iridomyrmex emeryi* Crawley, *Lasius flavus* (Fabricius), *Myrmica rubra* (Linnaeus), *Polyrhachis ammon* (Fabricius), *Pristomyrmex pungens* Mayr, *Wasmannia auropunctata*^{PE} (Roger).

Species with 1 record: *Amblyopone australis** Erichson, *Anonychomyrma itinerans* (Lowne), *Camponotus compressus* (Fabricius), *Camponotus nearcticus* Emery, *Camponotus novaehollandiae* Mayr, *Camponotus maculatus* (Fabricius), *Camponotus truncatus* (Spinola), *Cardiocondyla minutior** Forel, *Diacamma rugosum* (Le Guillou), *Doleromyrma darwiniana* (Forel), *Formica fusca* Linnaeus, *Hypoponera confinis* (Roger), *Hypoponera opaciceps* (Mayr), *Iridomyrmex chasei* Forel, *Leptomyrmex wiburdi* Wheeler, *Liometopum microcephalum* (Panzer), *Mayriella spinosior* Wheeler, *Melophorus hirsutus* Forel, *Meranoplus bicolor* (Guérin-Méneville), *Monomorium australicum* Forel, *Monomorium sechellense* Emery, *Myrmica ruginodis* Nylander, *Myrmecia gulosa* (Fabricius), *Myrmecia nigrocincta* Smith, *Orectognathus antennatus* Smith, *Pachycondyla stigma* (Fabricius), *Pheidole indica* Mayr, *Pheidole rugosula** Forel, *Pheidole sexspinosa* Mayr, *Platythyrea parallela* (Smith), *Polyrchachis atropos* Smith, *Polyrhachis erato* Forel, *Polyrhachis hector* Smith, *Polyrhachis semiaurata* Mayr, *Polyrhachis trapezoidea* Mayr, *Ponera swezeyi* (Wheeler), *Prenolepis imparis* (Say), *Prionopelta kraepelini* Forel, *Rogeria exsulans* Wilson & Taylor, *Solenopsis aurea* Wheeler, *Solenopsis molesta* (Say), *Strumigenys perplexa** (Smith), *Tapinoma minutum*^{PN} Mayr, *Tetraponera rufonigra* (Jerdon).

Genera with only 1 record: *Azteca*, *Dorylus*, *Lepisiota*, *Pheidologeton*, *Prolasius*.

Additional taxa recorded from AAAP sampling: *Camponotus nigroaeneus* (Smith), *Cardiocondyla wroughtonii*^{PN} (Forel), *Iridomyrmex cyaneus* Wheeler, and *Tapinoma sessile* (Say), *Heteroponera* spp.

General Discussion

9

The focus of this thesis is the spatial distribution of invasive ant species. However, within this, three broad questions are addressed which have previously received relatively little attention for invasive ants. These questions are: 1) how the distribution of ant species is influenced by interactions between the invader(s) and the abiotic and biotic components of the recipient community, 2) can the distribution of invasive ant species be predicted using modeling techniques, and 3) what are the geographic origins and diversity of invasive ant species arriving in new regions, using New Zealand as a case study.

9.1 Community interactions and distribution

Interactions between the invading species and abiotic and biotic components of the recipient environment were an important component of this thesis. Although invasive ants have been relatively well studied in terms of their interactions with native ants (Human & Gordon 1997; Holway 1999; Thomas & Holway 2005; Rowles & O'Dowd 2007), the majority of research is limited to just two invasive species; the Argentine ant (*L. humile*) and the red-imported fire ant, *S. invicta* (Holway et al. 2002). Other invasive species have received relatively little attention (Holway et al. 2002). Furthermore, there are relatively few cases were invasion has been where there are for multiple invaders (Sakai et al. 2001), although see Morrison (1996) for an example of invasive ants in French Polynesia.

An aim of this thesis was to examine species which have had little or no previous research, but also to explore the idea of studying multiple invasive ant species and their interactions with the recipient environment. Emphasis was on the Pacific region which is known to have a disproportionately high number of invasive ant species but where information is very limited (McGlynn 1999).

Chapter Two essentially provides an overview to the invasive ant species present in Fiji and the Pacific region. Fiji has often been at the margins of ant research in the Pacific, and as a result, there has not been a comprehensive review of the Fijian ant fauna since Mann (1921). I undertook to create a checklist of the Fijian ant fauna because previous lists of ant species from Fiji were outdated as a result of numerous changes in nomenclature and many new species descriptions. During a survey of the main island of Viti Levu, I collected 67% of invasive ant species previously recorded, many of which were frequently collected. I also discovered four additional invasive species not previously recorded from the literature.

Lists of invasive ant species from different island groups in the Pacific were included to highlight the number of invasive species present, but also the widespread nature of many species. A total of 67 invasive ant species have become established in the Pacific region, and undoubtedly many others have been transported to the region but have not established (see McGlynn 1999). Interestingly, there appears to be a ‘core’ assemblage of about 15 invasive ant species which are very common (>10 island groups) across the Pacific region. Thus, conservation impacts and problems resulting from these species are likely to be manifest throughout the wider Pacific region.

9.1.1 Habitat and inter-specific competition

Habitat structure and inter-specific competition are important in determining the distribution and coexistence of ant species. Behaviourally or numerically dominant ant species can affect the spatial occurrence of other species, thus structuring the ant community and creating mosaic-like patterns of species co-occurrence (Room 1975; Savolainen & Vepsäläinen 1989). The mosaic-like patterns can also be mediated by habitat differences. For example, Morrison (1996) showed that habitat primarily determined the distribution of several invasive ant species in French Polynesia.

Chapter Three examines the role of habitat structure and inter-specific competition in determining the distribution of ant species on the Yasawa Islands, a remote island archipelago in Fiji. There was no evidence that habitat type affected the composition of ant assemblages on these islands. Furthermore, there was little evidence that ant assemblages were structured by inter-specific competition – despite analyses at two different spatial scales and on two data sets. However, there was some evidence that habitat did influence the coexistence of species; with inter-specific competition (segregation patterns) for forest, but not for scrub or coconut palm habitats. Both scrub and coconut habitats consist of vegetation which is invasive to these islands, and are also subjected to frequent disturbance through human activities (e.g. stock grazing, fire wood collecting). Therefore, it is possible that disturbance has acted to influence the assembly of the ant fauna in scrub and coconut habitats.

I also suggested an additional explanation for the random patterns of species co-occurrence in the Yasawa Islands, based on several recent studies on invasive ants (Holway 1999; Gotelli & Arnett 2000; Sanders et al. 2003). It is possible that two invasive species, *Pheidole megacephala* and *Anoplolepis gracilipes* may have ‘disassembled’ the native ant fauna, resulting in random patterns of species co-occurrence. I showed that these species had broken a competitive trade-off in the discovery and domination of resources. This trade-off has been identified as an underlying factor in the invasion success of Argentine ants in California (Holway 1999).

However, this theory requires further research in the Yasawa Islands to disentangle the causes the random patterns. Interestingly, a number of behaviourally or numerically dominant ant species which are commonly found elsewhere in Fiji (e.g. *Solenopsis geminata, Pheidole fervens*) are not present in the Yasawa Islands, or were rarely collected (*Paratrechina longicornis*). By following the establishment and spread of these species, further information could be gained to help separate the effects of habitat and competition, and better understand the assembly of ant communities on these islands. Furthermore, I speculate that there is a succession of ‘community replacement’ occurring on these islands, where the native ant community is largely being replaced with a community of invasive species. These should be given future attention because it has implications across the Pacific region where there is a similar set of ‘core’ invasive species.

9.1.2 Habitat templets and niche opportunity

Several recent studies have illustrated how the physical environment shapes ant communities (Yanoviak & Kaspari 2000; Gotelli & Ellison 2002; Ratchford et al. 2005). For example, studies have shown a major contrast between the canopy and the ground litter, and have demonstrated how the physical conditions of these two habitat templets consequently form distinct ant communities (Yanoviak & Kaspari 2000).

Chapter Four examines the ecological partitioning of ant species in canopy and litter habitats at Colo-i-Suva Park, in Fiji, with two aims. The first aim was to examine if canopy and litter habitats differentially shape the ant fauna in Fiji, and secondly, to determine if niche opportunities exist for exploitation by invasive ant species. There was good evidence that canopy and litter habitats had a different composition of ants, with a relatively low species overlap between the habitats. Diversity was also higher in the canopy as expected.

In terms of invasive ant species, there was no difference in the number of invasive species between the canopy and litter. However, the most common species, *P. vaga*, was significantly less abundant and less frequently collected in the canopy. The body size of invasive species was significantly smaller than native species in the canopy, but not in the litter. This was the result of a shift in the body size of native species in the canopy (larger), an expected result of the canopy-litter templet. Furthermore, there was a significantly lower average resource overlap between invasive and native species in the canopy, compared to the litter. A reduction in niche overlap with native species provides a niche opportunity for exploitation by an invasive ant species. Taxonomic disharmony is often regarded as an important factor in the success of invasive species in areas without similar native species. The ant fauna in Fiji is taxonomically unbalanced, particularly in the canopy where many genera, commonly found elsewhere, are missing. This may provide an opportunity for invasion, although, other factors such as habitat characteristics and body size also appear to be important in shaping niche opportunities for invasive ant species at Colo-i-suva Park.

9.1.3 Ant communities in New Zealand

Chapter Five investigates the composition and structure of ant communities in different habitats in New Zealand. Emphasis was placed on the interactions among ant species and how species are spatially and temporally partitioned in the environment. There was a significant effect of habitat partitioning, and as a consequence, two distinct ant communities are evident; one of native ant species in forest, and the other of invasive ant species in scrub. Although abundance and species richness of ants declined in the cooler winter months, species composition was consistent throughout the year. Hence, there was no evidence of temporal partitioning by ant species over an annual scale. Furthermore, there was no evidence that inter-specific competition structured the invasive ant community at either regional or local scales. Of interest to the study of invasive ants in New Zealand is why environments remain largely unsaturated in terms of ants; despite being effectively unoccupied by native ant species – and thus presumably with little biotic resistance. In general terms, there were relatively few ants in the environment; on average only 56% of baits were occupied, and at half of the sites there were three or fewer ant species. Also unexpected was that the ability to discover, and also to numerically and behaviourally dominate baits, was quite similar for many of the species detected.

9.2 Modeling the distribution of invading species

Predicting the potential distribution of invasive ant species through ecological modeling was a major theme of the thesis. Emphasis was particularly placed on comparing different modeling methods and techniques for determining distribution. Model comparison has recently been recognised as a major issue for species distribution modeling, and is of major importance to improve the future utility of distribution models for practical purposes (Guisan & Zimmermann 2000; Anderson et al. 2003; Segurado & Araújo 2004; Guisan & Thuiller 2005; Araújo & Guisan 2006; Elith et al. 2006). In particular, issues regarding the optimal use of different modeling approaches and evaluation statistics, using more than one species, and selecting the variables to use, have all been raised. The analysis of large-scale distribution patterns for invasive ant species has historically received relatively little attention. Although there have been a number of very recent publications on this topic (Hartley & Lester 2003; Morrison et al. 2003; Roura-Pascual et al. 2004, 2006; Sutherst & Maywald 2005; Hartley et al. 2006; Fitzpatrick et al. 2007), these are all focused on only two species; *L. humile* or *S. invicta*. Furthermore, there has been relatively little examination of methodological issues associated with distribution modeling using ants.

Chapter Six examines the geographical transferability of distribution models. Model transferability has generated attention because of the recent niche conservation debate, that is, whether species retain ancestral ecological characteristics (Wiens & Graham, 2005). If a species niche is conserved, then invasive species should only be able to invade regions that have similar niche conditions to that of their native range (Wiens & Graham, 2005). In terms of species distribution modeling, it is assumed that a species' niche will be conserved, and therefore, models are transferable from one region to another. Recent research results have been variable, although niche conservation is generally not supported. Roura-Pascual et al. (2006), found that the ecological niche of the Argentine ant did not differ markedly between its native and invaded ranges; demonstrating evidence for conservatism. However, Randin et al. (2006) found model transferability varied widely for different plant species and was often asymmetrical between regions. In general transferability failed for 53-68% of species, and they urged caution when using niche-based models. Fitzpatrick et al. (2007) also found distribution models were generally not transferable, however, most importantly they showed that after the initial invasion, fire ants began to invade different environments to those that occurred in their native range;

evidence against the niche conservatism concept. Broennimann et al. (2007) have also recently found that models were better at predicting areas of initial introduction, but were less successful at predicting the full extent of the invaded distribution of spotted knapweed (*Centaurea maculosa*), a herbaceous weed introduced to western North America from Europe.

The results of Chapter Six also indicate that the niches of two invasive ant species were not conserved between their native and introduced ranges. The species used in the models are both important invasive ant species in the Pacific region (see Chapter Two). *A. gracilipes* is very widespread, and although *W. auropunctata* is limited to a few island archipelagos, it has the potential to spread much further. Consequently *W. auropunctata* has become a focus for Pacific biosecurity authorities, with regional planning aimed at minimising its spread and impacts. The results highlighted the importance of model methodology and how various modeling options could affect the interpretation of whether models were 'successfully transferred', thus having implications for predicting the distribution of these two species.

Chapter Seven models the potential distribution of six invasive ant species in New Zealand, with two main aims. The first aim was to predict the potential distribution of invasive ant species in New Zealand from a management perspective. Distribution maps, the result of modeling, provide biosecurity authorities in New Zealand (e.g. Biosecurity New Zealand, and local governments) with a tool to assist in the surveillance of invasive ant species. Results of this chapter show that many regions in New Zealand are predicted to be climatically suitable for the six species modeled, particularly coastal and lowland areas of both the North and South Islands. However, results also suggest that there is a considerable time lag with the spread of invasive ants. For example, it has taken many species several decades (40-60 years) to obtain a distribution of 17-25% of New Zealand regions. This is the first time such a time lag has been described for invasive ant species.

The second aim was to examine different modeling methods and options for determining a species distribution. By using a wide range of modeling techniques/approaches I was able to select optimal models and hence increase the confidence in the predicted distributions of these six invasive ant species in New Zealand.

9.3 Opportunity to invade: implications for New Zealand

The transfer of invasive species and the opportunity to invade was also a key theme of the thesis. It has recently been recognised that there is very little information on a key stage of the invasion process, that is, when organisms are transported to new regions (Kolar & Lodge 2001; Puth & Post 2005). Much of the information on biological invasions relates to the establishment and spread stages (Puth & Post 2005), yet initial dispersal is the fundamental stage upon which all other stages (establishment and spread) are reliant (Heger & Trepl 2003). This is a critical gap in our knowledge of the invasion process.

New Zealand is well known for its problems with invasive species. After only 200 years of European colonisation and subsequent introductions of various animal and plant species, New Zealand ranks among the most highly invaded areas on the planet (Williams & Timmins 2002). New Zealand has the greatest number of invasive mammals (n =34), the second highest number of invasive birds (n = 34), and there are also over 1 900 naturalised plant species (Williams & Timmins 2002). There are an estimated 2 200 species of naturalised or invasive invertebrates (Barlow & Goldson 2002).

However, in the past few decades the opportunity for species to be transported from their natural range to New Zealand has increased dramatically; the result of increased quantities of sea and air cargo, the removal of trade barriers, and a diversification of trading partners and products (Cook et al. 2002). As a result, the number of border interceptions and post-border incursions of insects has also increased (Cook et al. 2002). This, coupled with substantial media attention of several high profile incursions (e.g. the painted apple moth [*Teia anartoides*], the white-spotted tussock moth [*Orgyia thyellina*], the southern saltmarsh mosquito [*Ochlerotatus camptorhychus*], the Asian tiger mosquito [*Aedes albopictus*], and the honeybee mite [*Varroa jacobsoni*]), has continued to raise government and public awareness of ongoing biosecurity issues regarding invasive invertebrates.

Although ants are the second most common family of insects intercepted at the New Zealand border (Keall 1980), invasive ants have received very little attention in New Zealand. Information on them has essentially been limited to species lists compiled by various authors (Brown 1958; Cumber 1959, 1967; Taylor 1961; Keall 1980; Valentine & Walker 1991; Berry et al. 1997; Harris & Berry 2001; Ward 2005). The arrival of the Argentine ant, *Linepithema humile* (1990), and incursions (but not the establishment) of *Solenopsis invicta* (2001), has raised the profile of invasive ant species in New Zealand. Much of this recent attention has been focused towards the Argentine ant (Harris 2000, Lester et al. 2003; Hartley & Lester 2003; Ward et al. 2005; Ward & Harris 2005; Hartley et al. 2006; Corin et al. 2007), or the risk posed by invasive ant species not yet established in New Zealand (MAF Biosecurity Authority 2002; Harris et al. 2005). However, very little is known about the invasive ant fauna already established in New Zealand (excluding Argentine ants). Chapters Five and Seven examined several factors affecting the distribution of invasive ant species in New Zealand, while Chapter Eight examines exotic ant species arriving at the New Zealand border.

Chapter Eight summarises the diversity of exotic ant species arriving at the New Zealand border. The overall aim was to examine historical information to determine the extent to which other ant species could potentially establish in New Zealand. Several studies have shown the importance of using historical information and retrospective analysis to examine the establishment exotic ants (McGlynn 1999; Lester 2005; Suarez et al. 2005). McGlynn (1999) was one of the first to examine the extent to which exotic ant species were being transported by human activities. His review showed approximately 150 exotic species of ants had been introduced into new environments around the globe by humans. Suarez et al. (2005) has also examined the pathways, origins and establishment of exotic ant species entering the USA via human transport.

Chapter Eight summarises data from a fifty year period, where at least 115 ant species from 52 genera have been intercepted at the New Zealand border. The ten most frequently intercepted genera, and the twenty most frequently intercepted species contributed >90% of all records. Despite a very low trade relationship, a high proportion (>64%) of the exotic ants intercepted originated from the Pacific region. However, the majority (71%), of the species intercepted from the Pacific are themselves invasive species in the Pacific region.

Border control remains the major line of defence for preventing the establishment of exotic species (Hayden & White 2003). However, historical data had records for only 15 of the 28 invasive ant species already established in New Zealand. Furthermore, the effectiveness of detecting exotic ant species at the New Zealand border ranged from 48-78% for different trade pathways. This indicates that not all species have historically been, or are currently being, detected at the border. Thus, caution must be used when using historical information to analyse trends regarding the establishment of exotic species. Furthermore, it should not be unexpected to discover more exotic ant species becoming established in New Zealand in the future.

However, the origin of these future invaders is debatable. Despite the prevailing importance of the Pacific in terms of border interceptions, doubt remains over whether these ‘Pacific-intercepted’ ant species can actually establish and become invasive in New Zealand. Lester (2005) has recently modeled the establishment probability of exotic ant species in New Zealand using a range of historical, life-history and climatic factors. Lester’s (2005) list of exotic species that are most likely to establish in New Zealand include 19 of the 21 species intercepted from the Pacific in the historical border records used in Chapter Eight. However, only four of these intercepted species had a probability >0.5 of successful establishment, of which two have already established in New Zealand, *Technomyrmex albipes* and *Tetramorium bicarinatum*.

Should New Zealand biosecurity authorities continue to be concerned about exotic ants from tropical origins? I suggest that exotic ant species from Australia potentially represent a greater ecological risk than exotic species from the tropics, for several reasons. Australia represents a very large trading partner to New Zealand, it is geographically close, a large part of the flora and fauna of New Zealand shares a related evolutionary history - particularly from cool temperate forests - and Australia has an extremely large and diverse ant fauna (Majer et al. 2004). The majority (>60%) of the invasive ant species which are presently established in New Zealand are of Australian origin (see Table 5.2), including many of the ant species that have established most recently (Harris & Berry 2001; Stringer & Lester 2007). Furthermore, recent research indicates that Argentine ants also entered New Zealand via Australia (Corin et al. 2007). These factors indicate that trade pathways with Australia should be given increased scrutiny at the New Zealand border.

9.4 Ideas for further progress

9.4.1 Opportunities in the Pacific

One of the key problems of invasion biology is the inability to separate confounding effects and hold certain variables constant (Lodge 1993; Mack et al. 2000). The Pacific region presents a number of opportunities to address this problem, particularly for the study of invasive ants: 1) many of these islands, although geographically widespread, have very similar abiotic, biotic and historical conditions, and therefore, can act as replicates for comparison; 2) the diversity of the endemic and native ant fauna is not logistically overwhelming; and 3) there appears to be a ‘core’ assemblage of about 15 invasive ant species which are very common across the region. Thus, it is possible to study a similar set of invasive species across a number of similar environments. Recently, in the Pacific region there have been several studies addressing invasive ants (Morrison 1996; Abbott et al. 2006; see Chapter Three and Four in this thesis), but there has been no co-ordinated effort to exploit this opportunity – something which could be given future attention.

9.4.2 Getting more specific: invasion in the context of regions and trade

Given the ability of ants to be transported by humans and their high arrival rates, it seems paradoxical that they have received very little attention in this regard (McGlynn 1999; Lester 2005; Suarez et al. 2005; Ward et al. 2006). There are several important issues that need to be examined to further progress understanding of this early stage of invasion.

Trade routes associated with specific geographic regions represent a major filter for the arrival of exotic ant species to a new region. There is a need to better link the arrival of exotic ant species with specific trade pathways and from specific geographic regions (i.e. donor regions). Ricciardi & Rasmussen (1998) have previously stressed the importance of putting invasion in the context of donor regions and dispersal pathways for identifying future invaders. However, there appear to be few examples for invasive ants, although, Ormsby (2003) has recently linked exotic ants coming from the South Pacific via a specific pathway (sawn timber) to New Zealand. Examining the risk of species from specific geographic regions is highly relevant to New Zealand, where I suggest it is questionable to place emphasis on the Pacific region (see the previous section 9.3).

Historical information and retrospective analysis associated with border interception records are useful to examine certain patterns and numbers. However, care needs to be taken with these data, as information which has not been recorded is also important part of understanding biological invasions. The recent pre-border risk assessment of invasive ants for New Zealand by Harris et al. (2005) connects taxa with trade regions, pathways, commodities and ports of entry into New Zealand. Such specific information allows assessments to be made for areas within a new region, and may also help develop better surveillance strategies and the detection tools to target certain taxa. However, such assessments should not be seen as ‘one-off documents’, rather they must be dynamic and ‘living documents'. Future risk assessments must have the ability to be automatically updated as part of a national biosecurity strategy, as changes to trading partners, pathways, and modes of transport occur.

9.4.3 Complementary approaches to understanding invasion

This thesis has taken a multi-species, community approach (i.e. synecological approach) to examining invasive ants. Essentially, I have examined factors which have an affect on the broader scale distribution of invasive ant species, that is, a top-down approach. However, colony, population and species level studies (i.e. autecology) are also useful complementary approaches to studying biological invasions. Previous research on ant species has shown the importance of autecological studies for understanding the composition of communities. For example, a number of studies have shown that fine scale microhabitat variation, species-specific thermal tolerances, and food and nesting preferences play an important role in the coexistence and distribution of ant species Cerdá et al. 1997; Gotelli & Ellison 2002; Ratchford et al. 2005; Thomas & Holway 2005).

Species-specific differences in dispersal and colonisation also play a role in ant communities (Vepsalainen & Pisarski 1982; Andersen 2006). However, the importance of dispersal and colonisation in promoting the diversity and coexistence of species and structuring ant communities is only starting to be realised (Andersen 2006). If such factors are important in native ant communities, they should also be given far greater attention for invasive ants, and may provide a better understanding of how invasive ant species integrate into, and impact upon native biodiversity.

A better understanding of how climate variables directly and indirectly affect a species autecology is needed to improve the utility of species distribution modeling. Future work on the distribution of invasive ants should focus on how the physical environment affects colony growth, persistence, density, and dispersal, and how these factors scale up to affect broader patterns of distribution.

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