Invasion patterns of non-native ants in natural ecosystems in warm, temperate New Zealand

Article *in* New Zealand Journal of Ecology · February 2020

DOI: 10.20417/nzjecol.44.6

5 authors, including:

Anna Probert
Université de Fribourg
7 PUBLICATIONS **19** CITATIONS
SEE PROFILE

Darren Ward
Manaaki Whenua - Landcare Research
96 PUBLICATIONS **1,811** CITATIONS
SEE PROFILE

Jacqueline Beggs
University of Auckland
137 PUBLICATIONS **2,420** CITATIONS
SEE PROFILE

Margaret C Stanley
University of Auckland
68 PUBLICATIONS **853** CITATIONS
SEE PROFILE

NEW ZEALAND JOURNAL OF ECOLOGY

RESEARCH

Invasion patterns of non-native ants in natural ecosystems in warm, temperate New Zealand

Anna F. Probert[1,3]*, Darren F. Ward[1,2], Jacqueline R. Beggs[1], Willow Allison-Maxwell[1] and Margaret C. Stanley[1]

[1]Centre for Biodiversity & Biosecurity, School of Biological Sciences, University of Auckland, Private Bag 92019, Auckland 1142, New Zealand
[2]Manaaki Whenua Landcare Research, Auckland, Private Bag 92170, New Zealand
[3]University of Fribourg, Department of Biology, Ch. Du Musée, CH-1700 Fribourg, Switzerland
*Author for Correspondence (Email: anna.probert@unifr.ch)

Published online: 7 February 2020

Abstract: Non-native species have the ability to negatively impact ecosystems, and the recipient biodiversity they may invade. However, they must first go through a series of abiotic and biotic filters that limit their ability to spread once established, which ultimately influences their distribution across different habitats. By understanding which habitats are most vulnerable to invasion, pest managers can prioritise their surveillance areas to focus on those most at risk. We assessed temporal and spatial invasion by ants within forested and non-forested ecosystems using a replicated sample design based on data collected in 2005 and by repeating the sampling 10 years later. We predicted that forested ecosystems would be more resistant than non-forested ecosystems to invasion, likely due to unfavourable habitat factors that limit ant establishment and spread, even after a 10-year period. In both sampling years, non-forested ecosystems were more susceptible to invasion by non-native ants, with ants being found at both the edge and in the interior of these habitats. Conversely, in forested ecosystems, non-native ants were concentrated on the forest edges. Although there was invasion of non-native ant species further into some non-forested ecosystems over the 10-year period, spread did not penetrate beyond the edge in forest ecosystems suggesting that habitat characteristics are important in determining non-native ant spread. We recommend prioritising surveillance and management of pest ants in non-forested ecosystems rather than forested ecosystems in New Zealand. Our findings highlight the need for future work on the mechanisms of spread of non-native ants in non-forested ecosystems.

Keywords: Invasive species, edge effect, Formicidae, spatial, temporal

Introduction

Understanding what influences the distribution patterns of non-native species is a central focus of invasion biology (Richardson & Pyšek 2012). Complex interactions between ecosystem invasibility and species invasiveness may facilitate or impede the establishment of non-native species (Hunt et al. 2017; Lewis et al. 2017). The attributes of an ecosystem can influence non-native species invasion potential and distribution via abiotic factors (e.g. microclimate) and biotic factors (e.g. mediation of biotic resistance) (Pyšek et al. 2010), acting as filters that limit invasion success throughout the invasion process. Abiotic factors are fundamental to a species ability to colonise and establish outside of its native range, whereas biotic factors are thought to be more important at a local scale (McGill 2010; Theoharides & Dukes 2007; Zefferman et al. 2015).

Over 240 species of ants (Hymenoptera: Formicidae) have been transported outside of their native ranges and many are considered highly invasive (Bertelsmeier et al. 2017). For most ant species, human-mediated dispersal facilitates their introduction outside of their native ranges. Although subsequent invasion success often relates to key life history and behavioural traits, such as polygyny and superior competitive ability (Lester 2005; McGlynn 1999; Rabitsch 2011), characteristics relating to the suitability of the physical environment appear to be more critical for facilitating or inhibiting spread than biotic factors (Hoffmann & Saul 2010; Holway et al. 2002; Menke et al. 2007). Strong associations between habitat characteristics and the establishment and patterns of spread for non-native ants have been observed elsewhere, with disturbed, open habitats often comparably more invaded than their closed, more stable counterparts (Berman et al. 2013; King & Tschinkel 2016; Ward & Harris 2005). Open habitats—experiencing higher solar radiation—appear to provide ants with good opportunities for colony development, which is associated with minimum soil moisture and temperature requirements (Abril et al. 2010; Kadochová & Frouz 2014). Whether or not ants then spread from these disturbed or open environments into tall vegetation stature habitats is thus likely to depend on the ability of the ant

DOI: https://dx.doi.org/10.20417/nzjecol.44.6

species to reproduce within these environments. For instance, although Argentine ants can disperse > 150 m per year (Suarez et al. 2001), in New Zealand, their spread appears to be limited to open habitats with low-density canopies and high light levels; their lack of spread into native forest is presumed to be limited by the ant's habitat requirements (Ward & Harris 2005). Generally, it appears to be rare for non-native ants to invade temperate forest habitats (but see Guénard & Dunn 2010), although patterns of spread across multiple time points is not often studied.

The temporal patterns of spread by invasive ants into natural ecosystems are rarely documented due to the lack of long-term data sets. Predicting patterns of spread after establishment is difficult due to delays, which will be context dependent (Crooks 2005). Once established, species may proliferate and maintain numerical dominance, or in some cases, exhibit boom-bust trends; where after an initial period of rapid population growth, a significant decline is apparent (Simberloff & Gibbons 2004). Understanding temporal dynamics, and how they relate to particular environmental characteristics, can help to identify what facilitates the spread of particular non-native ant species, and potentially tease apart different driving factors. From a pest manager's perspective, identifying spatial and temporal patterns can help to prioritise surveillance and management for site-based biodiversity protection.

The aim of this study was to understand the invasibility of two different ecosystem types by non-native ants, using data collection with a 10-year time interval between sampling. Specifically, we were interested in (1) the differences in invasion patterns of already established non-native species from the edge into habitat fragments broadly classified as forested or non-forested, and (2) how this changed over a 10-year period. We undertook the study in the Auckland region of Aotearoa New Zealand. Auckland is a port city that represents a high-risk area for new non-native ant species incursions (Craddock & Mattson 2014). While Aotearoa New Zealand has a depauperate native ant fauna (11 species), almost three times as many non-native species have become established, with c. 40 species occurring in total (Don 2007). The majority of established non-native ant species originate from lower latitudinal areas with climates that are at least as warm as Auckland, if not warmer (tropical climates), with more than 60% being Australian in origin (Don 2007; Ward et al. 2006). Several of the non-native ants in New Zealand have little or no record of being introduced elsewhere; thus, the potential impact of these species on native biodiversity and ecosystems is poorly understood. Determining the ecosystems most at risk to invasion by non-native ants is, therefore, an important step that facilitates the future prioritisation of surveillance by pest managers.

We first predicted that 'non-forested' ecosystems (i.e. short stature vegetation without a continuous tree canopy) would facilitate the establishment of non-native species, offering a suitable habitat for reproduction (demographic increase), and subsequent spread (geographic increase). Increased solar radiation reaching the soil in short stature ecosystems (Davies-Colley et al. 2000) will facilitate colony development in ant species from warmer climates. We expected non-native ant occurrence to be generally ubiquitous from the edge to the interior of the ecosystem. In contrast, we predicted that 'forested' ecosystems (i.e. native forest with an established tree canopy) would impede the spread of non-native ants, which would exhibit a clustered distribution towards the edge of these habitats (Ward & Harris 2005; Ivanov & Keiper 2010), with abiotic factors associated with distance from the edge (e.g. lower solar radiation) affecting their ability to spread towards the interior. Lastly, we predicted we would observe patterns of spread over time in non-forested ecosystems, whereby species that appeared only at the edges in 2005, would be observed to penetrate the interior of non-forested ecosystems, but would remain at the edge in forested ecosystems.

Methods

Study sites

Eleven sites were selected in the wider Auckland region (Fig. 1), to represent natural ecosystems. The Auckland region experiences a mild climate with few extremes, with a mean annual temperature of c. 15°C (max: 34°C, min: −5°C) and c. 1200 mm of rainfall year^{-1} (Chappell 2013). A slight gradient occurs across the central isthmus, with eastern areas generally being warmer and drier, although the Hūnua Ranges to the south east are more similar to the west coast of Auckland (Chappell 2013). We selected sites based on similar topography, ability to gain permits, and representativeness of different ecosystem types in the region. We deliberately selected some forested and non-forested sites as we were interested in determining differences in invasion patterns between these ecosystem types given the strong environmental differences in forested and non-forested sites. Thus, sites (Table 1) were broadly categorised as 'non-forested ecosystems' (n = 6; native short stature vegetation without a continuous tree canopy) and 'forested ecosystems' (n = 5; native forest with an established tree canopy).

Sampling

Sampling occurred during the austral summer between December 2004 and February 2005 and was repeated 10 years

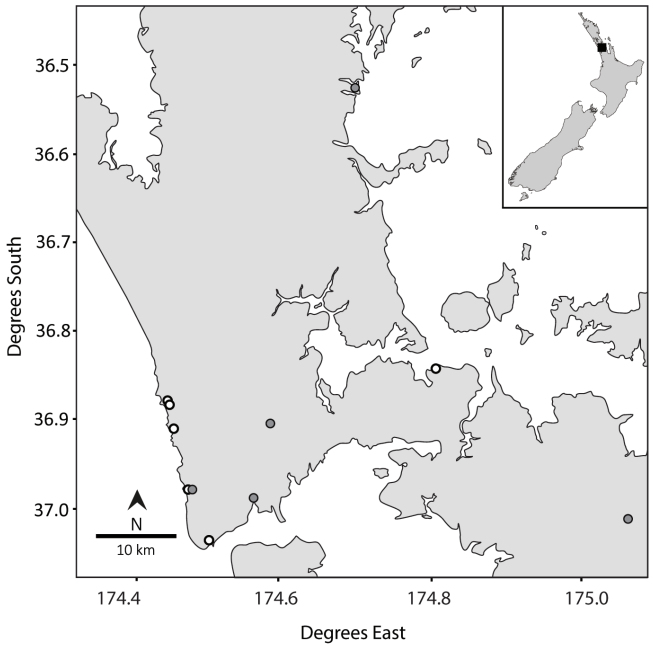

Figure 1. Map of sampling sites across the greater Auckland region in New Zealand. Insert indicates sampling region within New Zealand. White dots indicate non-forested ecosystem sampling sites and grey dots indicate forested ecosystem sampling sites.

Table 1. Sampling sites from the greater Auckland area, including information on canopy classification, ecosystem vegetation characterisation (Wardle 2002) and the distance that each ecosystem was sampled into from the edge.

Site	Canopy Classification	Ecosystem Type	Distance Sampled (m)*
Huia	Forested	Kauri-podocarp-broadleaved forest	180
Hūnua	Forested	Mixed conifer-broadleaf forest	140
Karakare	Forested	Pōhutukawa-broadleaved forest	180
Oratia	Forested	Kauri-podocarp-broadleaved forest	140
Wenderholm	Forested	Pōhutukawa-broadleaved forest	160
Anawhata	Non-forested	Coastal scrub	200
Bastion Point	Non-forested	Restoration planting/scrub	140
Karakare	Non-forested	Coastal scrub	140
Te Henga	Non-forested	Sand dunes	160
Te Henga	Non-forested	Wetland	160
Whatipu	Non-forested	Wetland	100

* Distance varies because topography influenced the ability to sample consistently between sites.

later between January 2015 and March 2015 (hereafter referred to as the 2005 and 2015 sampling years). All sampling was conducted in fine weather between 1000 h and 1500 h. At each site, a transect of up to 200 m was established, running from the edge of the habitat (−20 m and 0 m) into the interior (Table 1). Transect length was determined by the topography at each site. Ant sampling was undertaken using bait stations that were positioned at 20 m intervals along the transect.

Food preferences vary within and between ant species (Hooper-bùi et al. 2002; Nyamukondiwa & Addison 2014); therefore, bait stations were baited with different food types to maximise their attractiveness to different ant species. Five bait types were used: peanut butter (one teaspoon [tsp]), tuna (in spring water; one tsp), non-toxic XstinguishTM (protein + lipid + carbohydrate; Bait Technology Ltd, New Zealand; 5 g), soybean oil (in cotton wool; 5 ml), and sugar-water (1:4 ratio, in cotton wool; 5 ml). Each bait was placed in separate 35 ml plastic vials, positioned in a circular arrangement (15 cm diameter) with the lids removed. Bait stations were left unattended for 1–2 h before collection. To offset limitations associated with bait sampling, additional hand collection of ants via direct visual surveying of the area surrounding baiting stations was conducted at each station for three minutes when baits were being collected. A description of the immediate microhabitat and environment was recorded at each bait station including vegetation type, canopy cover (%) and litter cover (%). All specimens were kept in 75% ethanol and later identified to species level using a taxonomic keys to New Zealand ant species (Don 2007).

Statistical analyses

All analyses were conducted in R version 3.4.4 (R Core Team 2018). Significance was assessed at the $P < 0.05$ level. All reported values are mean ± SE.

Species occurrence

Ant species occurrence (i.e. presence) was used in all analyses rather than species abundance (i.e. number of individuals collected), due to biases related to the variation of recruitment strategies among species (Holway 1999).

To examine the differences in non-native and native ant species occurrence, we performed logistic regression using generalised linear mixed effect models with a Poisson distribution using the 'glmmTMB' package (Brooks et al. 2015). Two models were used with non-native ant species and native ant species occurrences at baiting stations as the response variables. For both models, the explanatory variables were distance from the edge, ecosystem type (non-forested versus forest), canopy cover, litter cover and year, with site as a random effect. We used a zero-inflated Poisson model for non-native ant occurrence in forest ecosystems. We used the DHARMa package (Hartig 2019) to validate all the models.

Our models found that for non-native ant species, there was a significant interaction between the ecosystem type and distance from edge ($z = 3.0$, $P = 0.003$). Several species were frequently found in bait stations at −20, 0, and 20 m for forest ecosystems, but did not occur further into the interior of the site. For this reason, we analysed non-native ant data for forest and non-forest ecosystems separately.

Ant community composition

To assess the variation in ant communities between forest and non-forest ecosystems, we performed (1) permutational multivariate analysis of variance (PERMANOVA; Anderson 2001), (2) permutational analysis of multivariate dispersions (PERMDISP; Anderson 2006) and (3) similarity percentage (SIMPER) analysis (Clarke 1993) using the vegan package in R (Oksanen et al. 2018).

We were most interested in assessing the presence of an edge effect to understand whether forest ecosystems were acting as a filter to non-native ant invasion. Therefore, we initially grouped data into two categories: (1) 'edge', which consisted of ant sampling data at the −20 m, 0 m, and 20 m sampling distances, and (2) 'interior', which consisted of ant sampling from 40 m onwards. The distance determined for 'edge' was based on other research which identified the most pronounced edge-effects on ants to be in the first 25 m (Ivanov & Keiper 2010; Ward et al. 2006). Before testing differences, we made sampling distance a fixed factor based on distance from habitat edge, with three levels (edge: −20–20 m; middle: 40–100 m; interior: 120–200 m), which allowed us to analyse variation at a finer-scale. PERMANOVA was used to test if ant community composition differed between forest and non-forest, using 999 permutations. We included an interaction term between ecosystem type (forest and non-forest), sampling distance and year, as well as canopy height, canopy cover, and litter cover as fixed effects, with site as a random effect. There was a significant interaction between

ecosystem type and sampling distance so we used pairwise comparisons between different sampling groups for non-forest and forest ecosystems (Martinez Arbizu 2017).

To assess the differences in the variability (i.e. dispersion) of ant communities between forest and non-forest we undertook PERMDISP analyses to compare the mean dispersion between groups based on 999 permutations. Finally, we used SIMPER analysis to identify the species contributing most to the differences in ant community composition.

Results

In total, we captured 19 ant species from 15 genera (12 non-native and 7 endemic species), with 17 species captured in 2005 (12 non-native, 7 endemic), and 16 species captured in 2015 (9 non-native, 6 endemic; Table 2).

Ant species occurrence in forest versus non-forested ecosystems

Overall species richness was low, reflective of the New Zealand ant fauna. No differences were found in the number of non-native and native ant species between ecosystem types or sampling years. In non-forested ecosystems, we found 3.8 ± 0.7 non-native species per site in 2005 compared to 2.8 ± 0.4 in 2015. We found a similar number of non-native species per site in forest ecosystems with 3.4 ± 1.0 in 2005 and 2.2 ± 0.6 in 2015. In the non-forested sites, we found 1.8 ± 0.5 native ant species in 2005 and 1.0 ± 0.3 in 2015. In forest sites we found 2.4 ± 0.2 native ant species in 2005 and 1.4 ± 0.6 in 2015. Species richness varied with distance from the edge to the interior for both ecosystem types and between sampling years (Fig. 2).

In forest ecosystems there was a significant negative relationship between non-native ant occurrence and distance from edge ($z = -3.400$, $P < 0.001$), and although litter cover ($z = -0.012$, $P = 0.024$) and canopy cover were found to be significant predictors, the sampling year was not ($z = -1.370$, $P = 0.170$). In non-forested ecosystems, the occurrence of non-native ant species at baiting stations did not correlate with distance from edge ($z = 0.432$, $P = 0.666$), year ($z = -0.894$, $P = 0.371$), percentage litter cover ($z = 0.415$, $P = 0.678$), or percentage canopy cover ($z = -1.294$, $P = 0.196$). For native ant species, there were no differences between ecosystem type ($z = 0.524$, $P = 0.600$), distance from edge ($z = 1.232$, $P = 0.218$), percentage canopy cover ($z = 0.708$, $P = 0.479$), percentage litter cover ($z = 0.100$, $P = 0.920$), although their occurrence differed between sampling years ($z = -2.40$, $P = 0.017$).

When comparing ant community composition between forest and non-forest, PERMANOVA analysis revealed a significant interaction between ecosystem type and distance from edge ($F_{1,136} = 2.0$, $P = 0.022$), as well as a significant difference in percentage canopy cover ($F_{1,136} = 5.0$, $P = 0.004$).

Further, pairwise tests demonstrated that in forest ecosystems, the ant communities at the edge and interior were significantly different (Table 3). However, no differences were found in ant community composition between any of the distance groups for non-forested ecosystems. PERMDISP revealed no differences in the dispersion within ant communities

Table 2. Percentage of baiting stations at which ant species were detected for non-forested and forest ecosystems for the 2005 and 2015 sampling years (n = 57 and n = 50 baiting stations for non-forested and forest ecosystems, respectively, for each year of sampling).

Species	Biostatus	% bait stations detected			
		Non-forested		Forest	
		2005	2015	2005	2015
Amblyoponinae					
Amblyopone australis	Non-native	0	0	2	0
Dolichoderinae					
Iridomyrmex suchieri	Non-native	5	10	0	2
Linepithema humile	Non-native	2	0	0	2
Ochetellus glaber	Non-native	19	26	2	2
Technomyrmex jocosus	Non-native	12	0	10	0
Ectatomminae					
Rhytidoponera chalybaea	Non-native	2	2	0	0
Rhytidoponera metallica	Non-native	4	0	0	0
Formicinae					
Nylanderia sp.	Non-native	12	19	12	14
Heteroponerinae					
Heteroponera brouni	Native	2	2	12	0
Myrmicinae					
Huberia brounii	Native	0	0	0	2
Huberia striata	Native	4	5	2	2
Mayriella abstinens	Non-native	0	2	26	16
Monomorium antarcticum	Native	25	16	10	6
Monomorium antipodum	Native	7	0	12	4
Pheidole rugulosa	Non-native	2	2	6	6
Tetramorium grassii	Non-native	28	12	12	0
Ponerinae					
Austroponera castanea	Native	2	0	8	4
Austroponera castaneicolor	Native	0	0	2	0
Hypoponera eduardi	Non-native	2	0	0	0

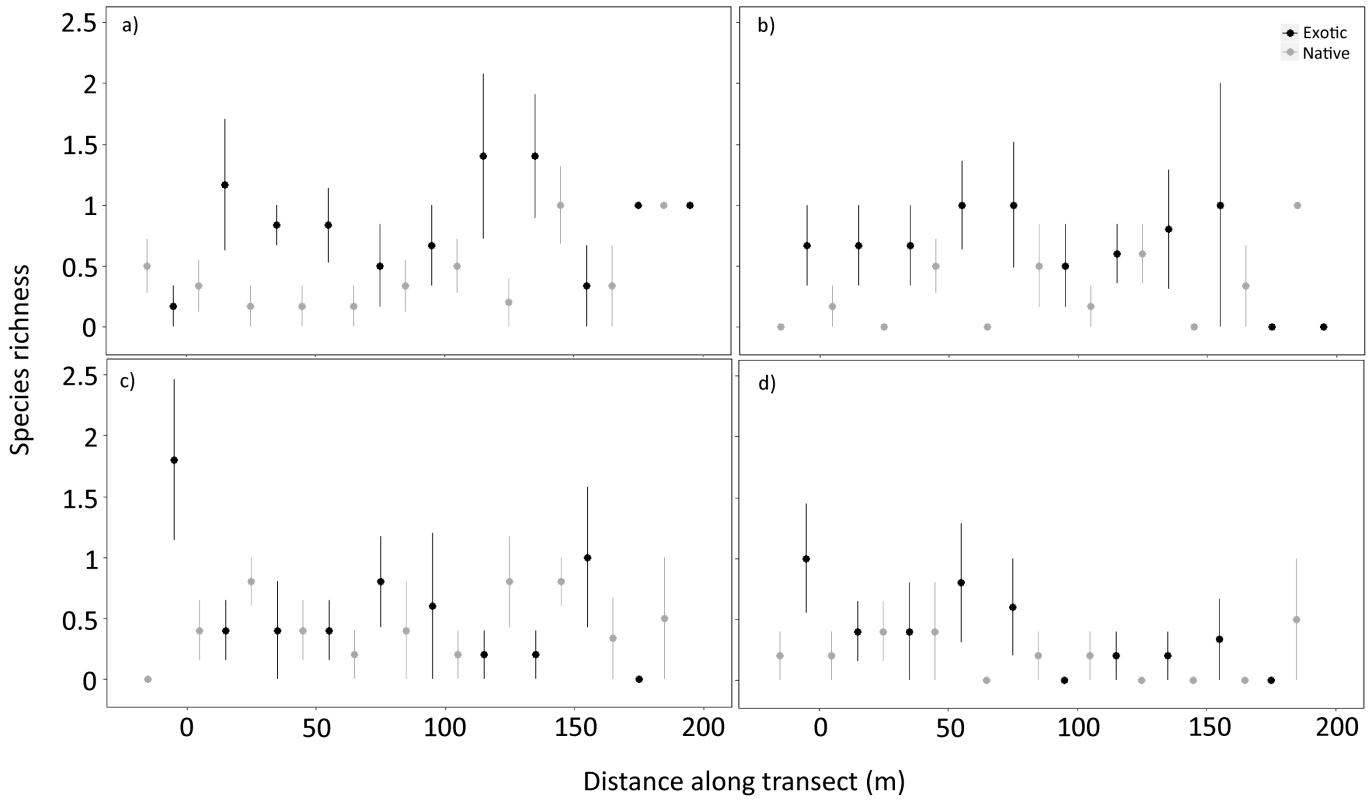

Figure 2. Mean number of non-native and native ant species at bait stations along an edge (−20 m) to interior (200 m) transect at 20 m intervals in a) non-forested ecosystems in 2005, b) non-forested ecosystems in 2015, c) forested ecosystems in 2005 and d) forested ecosystems in 2015. Error bars represent standard error of the mean. Black represents non-native species and grey represent native species.

Table 3. Results of pairwise tests among the distance groups for both non-forested and forest ecosystems. Tests were conducted using the 'pairwise adonis' function in R (Martinex Arbizu 2017), using a Benjamini-Hochberg correction. Pair names refer to the following sampling distances: edge (−20–20 m), middle (40–100 m), interior (120–200 m).

Pairs	Non-forested	Forest
Edge v. middle	$P = 0.911$	$P = 0.051$
Edge v. interior	$P = 0.168$	$P = 0.006$
Middle v. interior	$P = 0.276$	$P = 0.891$

between forest and non-forest, so whilst the ant communities in the two ecosystem types were compositionally distinct, they had similar dispersion.

SIMPER analysis revealed differences in ant community composition to be driven by five key species, of which four were non-native, with *Monomorium antarcticum* Smith (native), *Nylanderia* sp., *Mayriella abstinens* Forel, *Ochetellus glaber* Mayr, and *Tetramorium grassii* Emery contributing to more than 60% of the total difference when comparing forest and non-forest ecosystems.

Temporal differences

PERMANOVA analysis revealed significant differences in ant community composition between sampling years ($F_{1,136} = 5.20$, $P = 0.001$). Variation in ant community composition between sampling years was driven by five key species, as revealed by SIMPER analysis, of which four were non-native, with *M. antarcticum* (native), *Nylanderia* sp., *T. grassii*, *O. glaber*, *M. abstinens*, and *Technomyrmex jocosus* Forel contributing to more than 65% of the total difference.

None of the non-native ant species detected at the edges of forests in 2005 (up to 40 m from forest edges), had penetrated forest interiors further in 2015. In contrast, non-native species that were only detected towards the edges of two non-forested ecosystems in 2005, had penetrated further in 2015: *O. glaber*, *Nylanderia* sp. (up to 80 m), and *Iridomyrmex suchieri* Forel (up to 120 m) in the Te Henga sand dune; and *O. glaber*, *Nylanderia* sp., and *T. grassii* (all up to 160 m) in the Te Henga wetland site (Fig. 1).

Non-native ant species occurrence at baiting stations was lower in 2015 than 2005 ($z = -2.24$, $P = 0.025$). This was largely driven by the differences in the occurrence of *T. grassii*, *M. abstinens*, and *T. jocosus* which were more frequently detected in 2005 than 2015 (Table 2).

There were fewer native species occurrences in 2015 compared to sampling in 2005 ($z = -3.17$, $P = 0.002$). This difference was mainly driven by *Heteroponera brouni* Forel and *M. antarcticum* (Table 2).

Discussion

Our study reveals habitat-associated variation in non-native ant species distributions within natural ecosystems. In agreement with our predictions, we found distinct differences in ant species occurrences between forested and non-forested habitats. Generally, non-native species occurrences were uniform

across transects in non-forested ecosystems, and restricted to the edges of forest ecosystems. Finally, we found temporal differences between 2005 and 2015, although there was no evidence for spatial spread of non-native species further into forest ecosystems over the 10-year period. Together, our results suggest that non-forested ecosystems enable invasion by non-native ant species; conversely, forest ecosystems appear to impede ant spread from the edge.

Non-native ant species were dominant, in terms of species richness, in both non-forested and forest ecosystems for both sampling years. This is unsurprising given the low diversity of the New Zealand native ant fauna (Don 2007). While we did not conduct abundance analyses due to biases related to recruitment strategies, non-native ant species were numerically dominant and visually conspicuous at baiting stations in nearly all ecosystems compared to their native counterparts (AFP, pers. obs.). This is congruent with small colony sizes and densities recorded for most New Zealand ants.

We found differences in both ant species occurrence and community composition between forested and non-forested sites. In non-forested ecosystems, the occurrence of non-native ant species was generally ubiquitous across the sampled area, yet restricted to edges for forest ecosystems. This difference is likely explained, in part, by the environmental preferences of non-native ants. Temperature, and in particular soil temperature, is often an important factor associated with ant distribution, with species richness and colony size positively associated with increasing temperature (Kaspari et al. 2004; Kwon 2016; Sanders et al. 2007; Warren & Chick 2013). The majority of non-native ant species present in New Zealand originate from warmer regions (Don 2007; Lester 2005; Ward et al. 2006), and therefore, are predicted to be more restricted by thermal tolerances relating to a 'temperature-humidity envelope' (Hölldobler & Wilson 1990). Non-forested sites were associated with sparse canopy cover and presumably higher solar insolation and soil temperature when compared to forest sites (Davies-Colley et al. 2000). Although soil moisture is an important factor driving distribution for some ant species, effects are most pronounced in water-stressed environments (Menke & Holway 2006). We suggest soil moisture is unlikely to be a limiting factor for non-native ants in Auckland where average annual rainfall is c. 1200 mm (Chappell 2013). Although we have not directly tested the effects of soil variable on ant distribution, we consider temperate forests in New Zealand may be restricting the invasion of non-native ants through habitat filters, given physiological limits of ant reproduction. Future work should attempt to quantify microclimatic conditions between habitat types to determine if these abiotic factors are limiting non-native ant species at a micro-scale.

The microclimatic differences driving variation in community composition and non-native ant species occurrences between forested and non-forested sites are likely to cause the observed 'edge effect' in the ant communities in forested sites. The strength and direction of a species' response to the presence of edges depends on its size and mobility, with smaller species generally more sensitive to edges at a finer spatial scale (Lidicker Jr 1999; Vasconcelos & Bruna 2012; Wiens et al. 1985). The edge effect we report is slightly stronger than other ant community studies, which report the most pronounced effects to be within 25–50 m of the habitat interior (Ivanov & Keiper 2010). We found significant differences in ant species occurrence when comparing the edge, the middle, and interior of forested sites; with our data showing a distinct ant community present in the forest edge habitat. As previous sampling has demonstrated that, within Auckland forests, Argentine ants are limited to 20 m from the edge (Ward & Harris 2005), it suggests that these habitats are largely inhospitable to at least some non-native ant species.

We show temporal variation at the community-level for non-native ant species occurrence in forest ecosystems and for native ant species overall. We found no evidence that non-native species occurring at the edge of the forest ecosystems in 2005 were invading towards the interior in 2015. This supports our prediction that distribution limitations are determined for non-native ants via a habitat filter rather than a potential delayed effect. In contrast, some non-native species spread in some non-forested ecosystems, with *T. grassii*, *I. suchieri*, *O. glaber*, and *Nylanderia* sp. expanding their distribution from the edge to the interior over the ten-year period. Species richness was lower in the 2015 sampling year for both ecosystem types, and there were fewer non-native species occurrences compared to 2005. This disparity may reflect different climatic conditions between the sampling years as the 2015 summer was associated with below average rainfall and above average temperatures (NIWA 2018). Some ant species exhibit a positive response to increasing rainfall (Heller et al. 2008; Sanders et al. 2003), and this may explain the reduced diversity and occurrence, particularly for native ant species which may be more sensitive to extreme climate variation. Alternatively, or in addition, these differences could be related to competitive interactions and nesting behaviours. For instance, competition by non-native ants has been found to drive variation in community composition (Lester et al. 2009), and competitive advantages may lead to the suppression of other species that would occur in the absence of particular species (Holway 2005). Furthermore, although ant nests may be maintained for many years, some species exhibit ephemeral nest sites, relocating nests regularly for various reasons (McGlynn 2012). The ant species driving differences between forested and non-forested sites and sampling years were, unsurprisingly, the species that represented the highest number of species occurrences overall. Several of these are generalists that dominate urban ant communities within New Zealand (Stringer et al. 2009). *Mayriella abstinens* was almost exclusively found within forest ecosystems, whereas *O. glaber* was found throughout non-forested ecosystems, but restricted to the edges of forest sites. The *Nylanderia* sp. followed a similar pattern to *O. glaber*, in non-forested ecosystems.

Our study demonstrates ecosystem type is an important factor in determining the distribution of non-native ants, highlighting non-forested ecosystems as more likely to be invaded. In contrast, forest ecosystems appear to impede non-native ant spread, constraining their distribution to the edges of habitats, even after a ten-year period. This suggests a habitat filter is important in determining the distribution of non-native ants in natural ecosystems. However, since this is a correlative study, further research is required to understand the exact mechanism. Occasionally, non-native ant species become invasive in temperate forest ecosystems, (Guénard & Dunn 2010; Warren et al. 2015) so although our findings reveal restricted spread patterns for the current non-native ant community in New Zealand, the future arrival of species adapted to these habitats poses high risk to native forest ecosystems.

These findings have implications for potential surveillance and management of pest ant species. Understanding ecosystems most at risk to potential invasion of species allows pest

managers to narrow their field of surveillance and prioritise management. We therefore recommend increased focus towards non-forested ecosystems when considering the current ant community. Some non-forested ecosystems are naturally rare in New Zealand (Williams et al. 2007), and some of these are endangered (Holdaway et al. 2012). This steps away from a solely species-trait based method of risk assessment and towards a more integrated system; we suggest that an integrated system that combines species traits and ecosystem attributes will provide an improved basis for risk assessment (Probert et al. In Press). Future work is required to determine the impact of non-native ants in New Zealand, as to date, there is little understanding of how these species are interacting with native biodiversity and their environments.

Acknowledgements

We thank Ngāti Whātua-o-Ōrākei and Auckland Council for permission to conduct this study. This study was funded by the Ministry for Primary Industries and University of Auckland Partnership Postgraduate Scholarship and Kate Edger Educational Charitable Trust awarded to AFP. All authors were supported by the University of Auckland. We would also like to thank Phil Lester, Lori Lach, Peter Bellingham and anonymous reviewers for their helpful comments on earlier versions of the manuscript.

References

Abril S, Oliveras J, Gómez C 2010. Effect of temperature on the development and survival of the Argentine ant, *Linepithema humile*. Journal of Insect Science 10: 1–13.

Anderson MJ 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecology 26: 32–46.

Anderson MJ 2006. Distance-based tests for homogeneity of multivariate dispersions. Biometrics 62: 245–253.

Brooks ME, Kristensen K, van Benthem KJ, Magnusson A, Berg CW, Nielsen A, Skaug HJ, Maechler M, Bolker BM 2017. glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. The R Journal, 9(2), 378-400.

Berman M, Andersen AN, Hély C, Gaucherel C 2013. Overview of the distribution, habitat association and impact of exotic ants on native ant communities in New Caledonia. PLoS ONE 8: e67245.

Bertelsmeier C, Ollier S, Liebhold A, Keller L 2017. Recent human history governs global ant invasion dynamics. Nature Ecology & Evolution 1: 0184.

Chappell PR 2013. The climate and weather of Auckland. NIWA Science and technology series. Wellington, NIWA. 40 p.

Clarke KR 1993. Non-parametric multivariate analyses of changes in community structure. Australian Journal of Ecology 18: 117–143.

Craddock P, Mattson L 2014. National invasive ant surveillance programme annual report: 2014. MPI Technical Paper 2014/35. Wellington, Ministry for Primary Industries. 55 p.

Crooks JA 2005. Lag times and exotic species: The ecology and management of biological invasions in slow-motion. Ecoscience 12: 316–329.

Davies-Colley RJ, Payne GW, Elswijk MV 2000. Microclimate gradients across a forest edge. New Zealand Journal of Ecology 24 111–122.

Don W 2007. Ants of New Zealand. Dunedin, Otago University Press. 240 p.

Guénard B, Dunn RR 2010. A new (old), invasive ant in the hardwood forests of eastern North America and its potentially widespread impacts. PLoS ONE 5: e11614.

Hartig F 2019. DHARMa: Residual diagnostics for hierarchical (multi-level / mixed) regression models. R package version 0.2.4.

Heller NE, Sanders NJ, Shors JW, Gordon DM 2008. Rainfall facilitates the spread, and time alters the impact, of the invasive Argentine ant. Oecologia 155: 385–395.

Hoffmann BD, Saul W-C 2010. Yellow crazy ant (*Anoplolepis gracilipes*) invasions within undisturbed mainland Australian habitats: no support for biotic resistance hypothesis. Biological Invasions 12: 3093–3108.

Holdaway RJ, Wiser SK, Williams PA 2012. Status assessment of New Zealand's naturally uncommon ecosystems. Conservation Biology 26:619–629.

Hölldobler B, Wilson EO 1990. The Ants. Cambridge, Harvard University Press. 746 p.

Holway DA 1999. Competitive mechanisms underlying the displacement of native ants by the invasive Argentine ant. Ecology 80: 238–251.

Holway DA 2005. Edge effects of an invasive species across a natural ecological boundary. Biological Conservation 121: 561–567.

Holway DA, Suarez AV, Case TJ 2002. Role of abiotic factors in governing susceptibility to invasion: A test with Argentine ants. Ecology 83: 1610–1619.

Hooper-bùi LM, Appel AG, Rust MK 2002. Preference of food particle size among several urban ant species. Journal of Economic Entomology 95: 1222–1228.

Hunt S, Galatowitsch ML, McIntosh AR 2017. Interactive effects of land use, temperature, and predators determine native and invasive mosquito distributions. Freshwater Biology 62: 1564–1577.

Ivanov K, Keiper J 2010. Ant (Hymenoptera: Formicidae) diversity and community composition along sharp urban forest edges. Biodiversity and Conservation 19: 3917–3933.

Kadochová Š, Frouz J 2014. Thermoregulation strategies in ants in comparison to other social insects, with a focus on red wood ants (*Formica rufa* group). F1000Research 2: 280.

Kaspari M, Ward PS, Yuan M 2004. Energy gradients and the geographic distribution of local ant diversity. Oecologia 140: 407–413.

King JR, Tschinkel WR 2016. Experimental evidence that dispersal drives ant community assembly in human-altered ecosystems. Ecology 97: 236–249.

Kwon T-S 2016. What is important for ant assemblages in temperate forest soils? Journal of Asia-Pacific Biodiversity 9: 138–143.

Lester PJ 2005. Determinants for the successful establishment of exotic ants in New Zealand: Predicting invasive ant species. Diversity and Distributions 11: 279–288.

Lester PJ, Abbott KL, Sarty M, Burns K 2009. Competitive assembly of South Pacific invasive ant communities. BMC Ecology 9: 3.

Lewis JS, Farnsworth ML, Burdett CL, Theobald DM, Gray M, Miller RS 2017. Biotic and abiotic factors predicting the global distribution and population density of an invasive large mammal. Scientific Reports 7: 44152.

Lidicker Jr WZ 1999. Responses of mammals to habitat edges: an overview. Landscape Ecology 14: 333–343.

Martinez Arbizu P 2017. pairwiseAdonis: Pairwise multilevel comparison using adonis. R package version 0.3.
McGill BJ 2010. Matters of scale. Science 328: 575–576.
McGlynn TP 1999. The worldwide transfer of ants: geographical distribution and ecological invasions. Journal of Biogeography 26: 535–548.
McGlynn TP 2012. The ecology of nest movement in social insects. Annual Review of Entomology 57: 291–308.
Menke SB, fisher RN, Jetz W, Holway DA 2007. Biotic and abiotic controls of Argentine ant invasion success at local and landscape scales. Ecology 88: 3164–3173.
Menke SB, Holway DA 2006. Abiotic factors control invasion by Argentine ants at the community scale. Journal of Animal Ecology 75: 368–376.
NIWA 2018. CliFlo: NIWA's National Climate Database on the Web. http://cliflo.niwa.co.nz/ (Accessed 1 October 2016).
Nyamukondiwa C, Addison P 2014. Food preference and foraging activity of ants: Recommendations for field applications of low-toxicity baits. Journal of Insect Science 14: 1–13.
Oksanen J, Blanchet G, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHM, Szoecs E, Wagner H 2018. Vegan: Community Ecology Package. R package version 2.5–4.
Probert AF, Ward DF, Beggs JR, Lin S-L, Stanley MC In Press. Conceptual risk framework: Integrating ecological risk of introduced species with recipient ecosystems. BioScience: biz131.
Pyšek P, Chytrỳ M, Jarošík V 2010. Habitats and land-use as determinants of plant invasions in the temperate zone of Europe. Bioinvasions and globalization: ecology, economics, management and policy. Oxford, Oxford University Press. 267 p.
R Core Team 2017. R: A language and environment for statistical computing. https://www.R-project.org/.
Rabitsch W 2011. The hitchhiker's guide to alien ant invasions. BioControl 56: 551–572.
Richardson DM, Pyšek P 2012. Naturalization of introduced plants: ecological drivers of biogeographical patterns. New Phytologist 196: 383–396.
Sanders N, Moss J, Wagner D 2003. Patterns of ant species richness along elevational gradients in an arid ecosystem. Ecology and Biogeography 12: 93–102.
Sanders NJ, Lessard J-P, Fitzpatrick MC, Dunn RR 2007. Temperature, but not productivity or geometry, predicts elevational diversity gradients in ants across spatial grains. Global Ecology and Biogeography 16: 640–649.
Simberloff D, Gibbons L 2004. Now you see them, now you don't! Population crashes of established introduced species. Biological Invasions 6: 161–177.
Sobrinho TG, Schoereder JH 2007. Edge and shape effects on ant (Hymenoptera: Formicidae) species richness and composition in forest fragments. Biodiversity and Conservation 16: 1459–1470.
Stringer LD, Stephens AEA, Suckling DM, Charles JG 2009. Ant dominance in urban areas. Urban Ecosystems 12: 503–514.
Suarez AV, Holway DA, Case TJ 2001. Patterns of spread in biological invasions dominated by long-distance jump dispersal: Insights from Argentine ants. Proceedings of the National Academy of Sciences 98: 1095–1100.
Theoharides KA, Dukes JS 2007. Plant invasion across space and time: factors affecting nonindigenous species success during four stages of invasion. New Phytologist 176: 256–273.
Vasconcelos HL, Bruna EM 2012. Arthropod responses to the experimental isolation of Amazonian forest fragments. Zoologia 29: 515–530.
Ward DF, Harris RJ 2005. Invasibility of native habitats by Argentine ants, *Linepithema humile*, in New Zealand. New Zealand Journal of Ecology 29: 215–219.
Ward DF, Beggs JR, Clout MN, Harris RJ, O'Connor S 2006. The diversity and origin of exotic ants arriving in New Zealand via human-mediated dispersal. Diversity and Distributions 12: 601–609.
Warren RJ, Chick L 2013. Upward ant distribution shift corresponds with minimum, not maximum, temperature tolerance. Global Change Biology 19: 2082–2088.
Warren RJ, McMillan A, King J R, Chick L, Bradford MA 2015. Forest invader replaces predation but not dispersal services by a keystone species. Biological Invasions 17: 3153–3162.
Wiens JA, Clifford CS, Gosz JR 1985. Boundary dynamics: a conceptual framework for studying landscape ecosystems. Oikos 45: 421–427.
Williams PA, Wiser S, Clarkson B, Stanley MC 2007. New Zealand's historically rare terrestrial ecosystems set in a physical and physiognomic framework. New Zealand Journal of Ecology 31:119–128.
Zefferman E, Stevens JT, Charles GK, Dunbar-Irwin M, Emam T, Fick S, Morales LV, Wolf KM, Young DJN, Young TP 2015. Plant communities in harsh sites are less invaded: a summary of observations and proposed explanations. AoB PLANTS 7: 056.

Received 7 September 2019; accepted 29 September 2019
Editorial board member: Peter Bellingham