

The diversity, community composition and seasonality of native and introduced ants (Hymenoptera: Formicidae) in northern New Zealand

Darren F. WARD



Abstract

Although there are only eleven native ant species in New Zealand, little is known about their biology. This paper examines the diversity, community composition and seasonality of native and introduced ants at seven native forest sites in northern New Zealand using leaf litter sampling, pitfall trap sampling and foliage beating. A total of seven native, and five introduced ant species were caught in this study. Litter sampling yielded an average of 5.1 ants and 1.6 species per 1×1 m quadrat. Fifty five percent of quadrats had only one species and 88% of quadrats had two species. Pitfall sampling also caught few species, with a catch rate of only 0.215 ants per pitfall trap per day. The composition of ant species was similar throughout the year and also across sites. A simple seasonal pattern (i.e., based on day length) explained much of the variation in abundance ($R^2 = 83\%$) and species richness ($R^2 = 77\%$) of ants. In both litter and pitfall sampling, three species contributed $> 90\%$ of the abundance of all ants. The two most common ant species are predators, *Heteroponera brounii* (FOREL, 1892) and *Pachycondyla castaneicolor* (DALLA TORRE, 1893). Only five ant specimens were collected from foliage beating samples from twelve monthly samples of 40 plants. The lack of a diverse and abundant ant fauna could have significantly influenced the evolution of the New Zealand biota, but this remains to be investigated.

Key words: Leaf litter, pitfall, dominance, Formicidae, New Zealand.

Myrmecol. News 12: 195-200 (online 8 June 2009)

ISSN 1994-4136 (print), ISSN 1997-3500 (online)

Received 19 November 2008; revision received 6 March 2009; accepted 6 March 2009

Dr. Darren F. Ward, Landcare Research, Private Bag 92170, Auckland, New Zealand.

E-mail: wardda@landcareresearch.co.nz

Introduction

Ants play major roles in natural ecosystems and characterising ant communities is a key step in understanding evolutionary and biodiversity patterns (AGOSTI & al. 2000). DUNN & al. (2007) have recently highlighted the lack of global analyses of ecological communities and the importance of examining general patterns for biogeography and macroecology. However, generalised patterns can also be used retrospectively to examine specific regional patterns. For example, are there "departures" from expected patterns in certain regions, and what are the ecological and evolutionary reasons and consequences for such departures?

ANDERSEN (1997) compared expected Australian patterns of diversity and dominance with North American ant communities. Although biogeographic patterns of functional groups were broadly similar across the two continents, Australian ant communities had considerably higher species richness and were almost always dominated by dolichoderines (ANDERSEN 1997). Ecological consequences of a poor representation of dolichoderines for North America included a lower diversity of hot climate specialist ant species, greater dominance by formicines in cool-temperate habitats and a greater susceptibility to invasion by behaviourally dominant introduced species such as *Solenopsis invicta* BUREN, 1972 and *Linepithema humile* (MAYR, 1868) (see ANDERSEN 1997). Ecological patterns of ant communities can also be compared across habitats. For example, ANDERSEN (1986a) has shown that the community structure and organization of Australian ant communities changes across

habitats, with opportunist species (*Rhytidoponera*) most abundant in woodlands, cool-climate (*Prolasius*) and cryptic species (*Solenopsis*) comprising the majority of ants in wet forests, and in arid ecosystems ant communities were dominated by dolichoderines (*Iridomyrmex*). Consequences of this affect ant community organization, where the importance of interspecific competition is more important in arid ant communities than in mesic regions (ANDERSEN 1986a).

However, while ant communities in North America and Australia are comparatively well known (DUNN & al. 2007), ant communities in other regions have been less studied. New Zealand is known for its depauperate social insect fauna (WHEELER 1935, BROWN 1958, DON 2007). There are no native eusocial wasps or bees, only three endemic termite species and eleven endemic ant species (WARD 2005, DON 2007). WHEELER (1935) included New Zealand in his checklist of the ants of Oceania to demonstrate the "meagerness and oceanic character of its ant fauna" (p. 3). Very little is known about the basic biology of the native ant fauna, including information on their diversity, abundance and seasonality in natural habitats. A number of introduced ant species have become established in New Zealand (WARD 2005, HARRIS & BARKER 2007, WARD 2007), and more has been published on these introduced species than on the native ant fauna.

This paper characterises the diversity, abundance, community composition and seasonality of the ant fauna at native forest sites in northern New Zealand. It is expected that

these wet cool temperate forests will be dominated by cool-climate specialists with relatively low species richness. Such data is a useful first step in understanding the role of native ants in natural ecosystems in New Zealand.

Methods

The sampling in the study is split into two parts, but all study sites are in a sub-tropical climate zone, having warm humid summers and mild winters (NIWA 2006). Maximum summer temperatures range from 22°C to 26°C, and maximum winter temperatures from 12°C to 17°C. Annual sunshine averages 2000 hours, and average rainfall is approximately 100 mm per month (NIWA 2006).

Seven study sites were used, all in the western range of the Auckland city region (North Island). 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). The seven study sites are representative of the historical vegetation. Huapai is a 15 ha reserve (36° 47.64' S, 174° 29.83' E), with several very large kauri trees at > 30 m tall, nikau palms (*Rhopalostylis sapida*) and silver tree ferns (*Cyathea dealbata*). The Oratia (36° 54.99' S, 174° 36.30' E), Swanson (36° 52.62' S, 174° 33.76' E) and Huia sites (36° 59.8' S, 174° 33.8' E) are also kauri forest, but are regenerating after milling in the late 1800s and are dominated by young kauri (rickers) and silver tree ferns. Karekare (36° 59.19' S, 174° 28.96' E) is a coastal forest consisting of pohutakawa (*Metrosideros excelsa*) and scrub vegetation of mahoe (*Melicactus ramiflorus*), kanuka (*Kunzea ericoides*) and *Coprosma* species. Poleline track (36° 56.23' S, 174° 30.21' E) in the Waitakere Ranges consisted of coastal scrub vegetation of mahoe and kanuka. Shona reserve is a forest remnant in urban Auckland (36° 53.30' S, 174° 36.99' E) and consists of podocarp and broad-leaved forest with stands of rimu (*Dacrydium cupressinum*), kahikatea (*Dacrydium dacrydioides*), and several species of tree fern.

Ant sampling: At five of the study sites (Oratia, Huapai, Poleline, Huia, and Karekare) a 180 m transect was randomly placed in a north-south direction and a 1 m × 1 m quadrat leaf litter was collected every 10 m. Litter was scooped by hand into a litter-sifter (1 cm mesh), allowing fine litter to fall to bottom where it was collected, tied into a cloth pillow case and transported to the lab. Large debris was broken apart into the sifter. Sampling took place in December 2004 and January 2005. Litter was either placed into a Winkler sack or a Berlese funnel (light 15 watts), both left to operate for 48 hrs. The volume of litter collected was measured, and litter weight (wet and dry) was taken (dry weight at 50°C for 72 hrs). This gave 20 quadrats per site and a total of 94 quadrats (three sites were reduced to 18 quadrats because of limitations in availability of Winkler and Berlese funnels). At each quadrat, the following environmental measurements were taken: litter depth, % of ground cover (bare, litter, stone/rock, plant, other), plant height and % canopy cover using a densiometer.

At four of the study sites (Oratia, Huapai, Swanson, and Shona Reserve) sampling was undertaken once a month over a twelve month period using pitfall traps and foliage beating. At each site 12 pitfall traps were set in a 6 × 2 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 ethanol / 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 dates were, in 2005, 23 February - 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, and in 2006, 17 - 24 January. Each month, at each site, the foliage of ten plants was beaten with a wooden stick five times to dislodge ants onto a white calico collecting sheet (110 × 75 cm). Ants were collected with an aspirator and placed into 75% ethanol. Plants were haphazardly chosen across the site for beating each month.

Upon collection all specimens were stored in vials of 75% ethanol. Ants were identified by using reference material in the New Zealand Arthropod Collection (NZAC) and an online key (LANDCARE RESEARCH 2005). All specimens are held at the NZAC in ethanol.

Analysis: Pearson correlations were used to examine the relationship between litter volume and the abundance and species richness of ants. A generalised linear model with log link and negative binomial distribution was used to examine ant abundance and species richness for each quadrat against measured environmental variables in R 2.5.1 (R DEVELOPMENT CORE TEAM 2006).

Estimates of species richness and accumulation in pitfall traps 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 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 was compared across sites (or seasons) using non-metric multidimensional scaling (nMDS) ordination in PRIMER v5.0 software, using a Bray-Curtis similarity matrix (4th root transformation) from 50 restarts (CLARKE & WARWICK 2005). An ordination groups sites (or seasons) based on the similarity of the composition of species and their abundance. Sites which are most similar are grouped more closely together. One-way analysis of similarities (ANOSIM) was used to analyse differences between sites, and between seasons separately. ANOSIM creates an overall test statistic (R) that indicates if differences between treatments exist. R values range from -1 to 1 and as R approaches 1, there is more dissimilarity. CLARKE & WARWICK (2005) give categories of R values as: well separated > 0.75, clearly different > 0.5, and barely separable < 0.25.

Nine climate variables were examined representing climate information for the 1971-2000 period for Auckland (NIWA 2006); mean monthly air temperature (°C; MMAT), mean daily maximum air temperature (°C; MDMAT), mean 10 cm earth temperature (°C; MET), mean monthly sunshine (hours; MMS), mean monthly rainfall (mm; MMR), mean daily global radiation (megajoules / square metre; MDGR), mean relative humidity (%; MRH), mean number of days of ground frost (MNDGF), mean daily minimum air temperature (°C; MDMAT). To explore the association between seasonality and the abundance and species richness of ants in pitfall samples, a simple sinusoidal

Tab. 1: The abundance of ant species from pitfall traps and litter quadrats (all months combined), biostatus (N = native, I = introduced), with observed / estimated species richness for pitfall trapping.

Site	Biostatus	Pitfall				Litter				
		Shona Reserve	Oratia	Swanson	Huapai	Oratia	Huapai	Poleline	Huia	Karekare
<i>Amblyopone saundersi</i> FOREL, 1892	N	1	1	0	1	0	0	0	0	0
<i>Discothyrea antarctica</i> EMERY, 1895	N	2	0	3	0	3	3	4	2	1
<i>Heteroponera brounii</i> (FOREL, 1892)	N	55	61	170	97	30	46	31	79	17
<i>Monomorium antarcticum</i> (Fr. SMITH, 1858)	N	28	4	8	1	1	8	2	9	42
<i>Huberia brounii</i> FOREL, 1895	N	0	0	0	0	0	0	2	0	0
<i>Pachycondyla castaneicolor</i> (DALLA TORRE, 1893)	N	232	9	99	3	7	6	27	35	0
<i>Prolasius advenus</i> (Fr. SMITH, 1862)	N	20	7	3	39	2	5	0	0	2
<i>Amblyopone australis</i> ERICHSON, 1842	I	1	4	13	1	0	1	0	0	1
<i>Paratrechina</i> sp.	I	2	0	0	1	0	0	0	0	0
<i>Pheidole rugosula</i> FOREL, 1902	I	0	1	0	0	0	0	0	0	0
<i>Technomyrmex jocosus</i> (Fr. SMITH, 1910)	I	0	0	0	1	0	0	1	0	0
<i>Tetramorium grassii</i> EMERY, 1895	I	1	0	1	0	0	0	0	0	0
Total abundance of ants		342	87	297	144	43	69	67	125	63
Observed species richness		9.0	7.0	7.0	8.0					
Estimated richness (Chao 2)		9.9	7.4	7.0	17.1					
% Efficiency		90.7	93.8	100.0	46.5					

curve of day length was fitted (maximum in January, minimum in July). A single climate variable was then compared to this curve. The sinusoidal curve models a general seasonal pattern; thus, if the climate variable has a low p-value, it means that there is evidence that this climate variable has a non-sinusoidal component that additionally affects ant abundance or richness.

Results

Leaf litter sampling: A total of 367 ants from eight species were caught from 72 quadrats (24% of the 94 quadrats had no ants), representing an average of 5.1 ants and 1.6 species per quadrat. Most (55%) quadrats had only 1 species, 88% of quadrats had only two species, and the maximum number of species was four (occurring in 2 quadrats). Six native and two introduced species were caught across the four sites (Tab. 1).

The volume of litter was significantly correlated with ant abundance ($R^2 = 0.097$, $p = 0.006$) and species richness ($R^2 = 0.200$, $p < 0.01$), but R^2 values were low, limiting pre-

dictive power. With increased canopy cover there were significantly fewer ants in quadrats ($p = 0.010$). Litter depth and plant cover also influenced ant abundance, but there was no overall significant trend, and their effect was inconsistent between sites. No environmental variable was significant in explaining species richness.

Foliage beating: Only five ants were collected from foliage beating samples; *Monomorium antarcticum* (1; see Table 1 for taxon authorities of all species sampled), *Prolasius advenus* (3), and *Technomyrmex jocosus* (1), from 12 monthly samples of 40 plants.

Pitfall sampling: A total of 4032 pitfall trap days caught 870 ants from 11 species over the twelve month period (Tab. 1). This equates to a catch rate of 0.215 ants per pitfall trap per day (12 months, 12 traps / site, 7 days duration, 4 sites). Estimates of species richness (using the Chao 2 estimator) showed that sampling was highly successful (> 90%) in capturing ant species at three of the four sites (Tab. 1). The low species richness estimate at Huapai (46%) was due to the fact that five of the eight species caught were singletons, therefore inflating estimates.

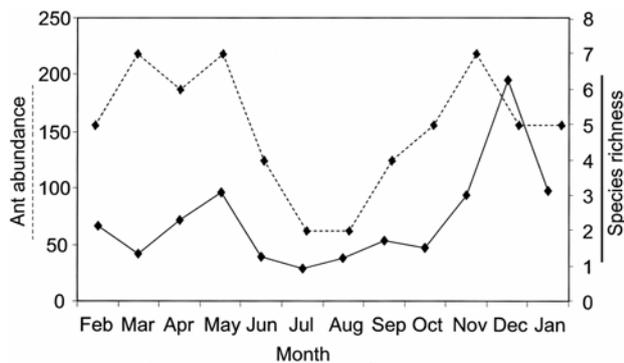


Fig. 1: Total abundance (solid line) and species richness (dashed line) of ants (all species combined) at all sites. Months indicated by a three letter code.

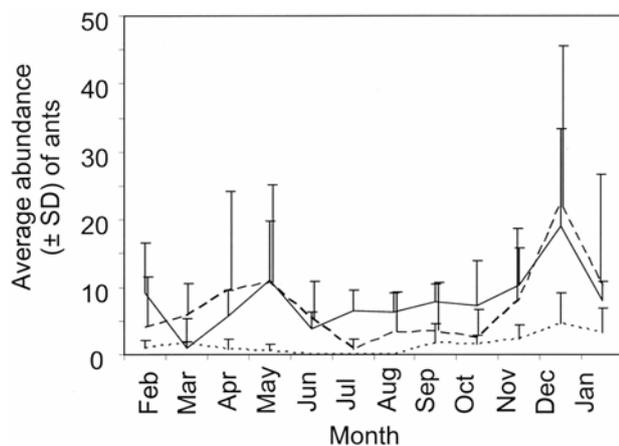


Fig. 2: The average abundance (\pm SD) of the three most common ant species throughout the year. *Heteroponera brounii* (solid line), *Pachycondyla castaneicolor* (dashed line), *Prolasius advenus* (dotted line).

In pitfalls, the three most abundant species (across all sites) contributed 91.3% of all ants caught; *Heteroponera brounii* (44.0%), *Pachycondyla castaneicolor* (39.4%) and *Prolasius advenus* (7.9%). Sites were also largely dominated by few species (Tab. 1); on average, one species contributed 65% of all ant abundance, and two species contributed 87% at sites.

Overall, the total abundance of ants across all sites was relatively consistent across the year, but with a large catch of *P. castaneicolor* and *H. brounii* in December (Fig. 1). The three most common species were present throughout the year, with no apparent species-specific foraging cycle (Fig. 2). In terms of species richness, the summer period had approximately 2 - 3 times more species than the winter period (Fig. 1).

A simple seasonal pattern (i.e., based on day length) explained much of the variation in abundance ($R^2 = 83\%$) and species richness ($R^2 = 77\%$) of all ants. However, there was evidence that humidity, the number of ground frost days and the temperature variables had a non-sinusoidal component that additionally affected abundance (Tab. 2). There was no evidence that any climate variable had an additional effect on species richness other than a seasonal sinusoidal curve (Tab. 2).

Composition of ant species was similar across the four sites (Fig. 3), as data points for a site are intermixed and

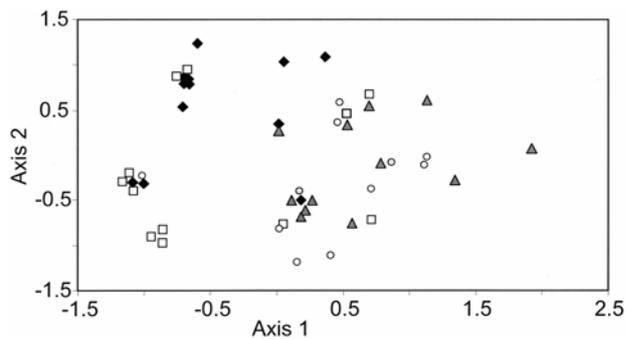


Fig. 3: The composition of ant species for each site associated with pitfall trap sampling (nMDS ordination). Shona reserve (grey triangle), Swanson (white circle), Huapai (black diamond) and Oratia (white square). Some point jittered for clarity. Ordination two dimensional stress value 0.16.

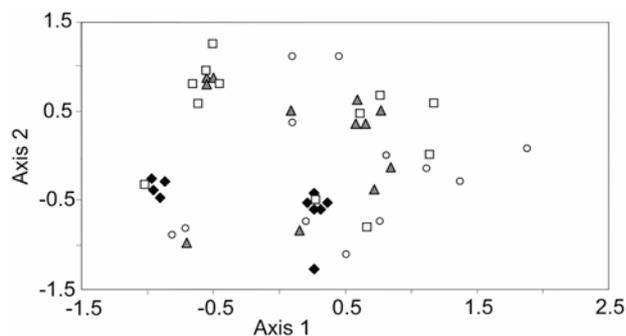


Fig. 4: The composition of ant species for each season of pitfall trap sampling, showing the overlap of ant composition between seasons (nMDS ordination). Summer (December - February, grey triangle), autumn (March - May, white circle), winter (June - August, black diamond) and spring (September - November, white square). The layout of sites is the same as in Figure 3. Ordination two dimensional stress value 0.16.

overlapping with other sites (ANOSIM $R = 0.369$). The composition of ant species was also very similar between seasons (Fig. 4, ANOSIM $R = 0.128$), although there was some clumping of winter samples, possibly reflecting the lower abundance of ants.

Discussion

Overall, the dominant finding was of very low ant abundance and richness in these northern New Zealand forests. The low number of species in New Zealand is essentially explained by its geological history; separating from Gondwana and becoming increasingly oceanic at a time when ant diversification was occurring (MOREAU & al. 2006). However, the very low abundance of worker ants in the environment is remarkable, and more difficult to explain. The catch rate of ants in pitfalls was very low with only 0.215 ants per pitfall trap per day. Also surprisingly, extremely few ants were collected from foliage beating (only 5 ants from 12 monthly samples of 40 plants). Although ants can be collected on trees (D.F. Ward, unpubl.), it seems these habitats could be an under-utilised niche in New Zealand. I suggest that these results are an accurate reflection of the abundance and diversity of ants in these forests. It is unlikely that additional methods of searching for ants would have resulted in different results (i.e., higher species rich-

Tab. 2: Association between climate variables and a general seasonal pattern for the abundance or species richness of ants. A significant p-value indicates a climate variable affects ant abundance or richness (degrees of freedom for each variable is 84). * significance at $p < 0.05$.

Variable	Abbreviation	*Abundance		*Richness	
		F-value	p-value	F-value	p-value
Monthly air temperature	MMAT	3.92	0.05 *	0.80	0.37
Maximum air temperature	MDMAT	4.36	0.04 *	0.87	0.35
Minimum air temperature	MDMAT	4.05	0.05 *	0.62	0.43
Earth temperature	MET	4.36	0.04 *	0.64	0.43
Monthly sunshine	MMS	0.58	0.45	0.24	0.63
Monthly rainfall	MMR	0.06	0.81	0.08	0.80
Global radiation	MDGR	2.39	0.13	0.02	0.89
Relative humidity	MRH	6.01	0.02 *	0.73	0.40
Ground frost	MNDGF	4.43	0.04 *	3.25	0.08

Tab. 3: Comparison of the number of ant species and abundance of ant workers from leaf litter samples. Data from Australia, Canada and the USA from Table 8.1 in WARD (2000). New Zealand data from this study. All sites are between latitudes 36° and 46° for comparison.

	Number of species			Number of workers			Sample size
	Mean	Standard deviation	Range	Mean	Standard deviation	Range	
Australia	15.5	7.5	5-21	241.3	122.1	65-332	4
Canada	5.0	3.6	1-8	36.3	26.3	2-64	4
USA	3.1	2.0	0-7	21.6	26.2	0-99	16
New Zealand	1.2	0.9	0-4	3.9	5.7	0-38	94

ness or abundance), as results from pitfall and litter sampling (and personal collecting) are in agreement, and as these are standard techniques for measuring ant diversity.

These results are striking when comparable international data is examined. For comparable data I used leaf litter data from P. WARD (2000), taking sites between latitudes of 36° to 46° (latitudes of New Zealand) to increase comparability (Tab. 3). The richness and abundance of ants in New Zealand data is lower compared to that of Canada and the USA, but is an order of magnitude lower than that of comparable samples in Australia.

Also surprising was that for both leaf litter and pitfall sampling, sites were dominated (occurrence and abundance) by only one or two species; *Heteroponera brownii*, an assumed predator, which probably nests in logs and is a cold climate specialist (BROWN 2000), and *Pachycondyla castaneicolor*, a large solitary predator (BROWN 2000). Typically ant communities are a mosaic of different functional groups, and species which are most common and abundant are Dominant Dolichoderinae, Opportunists and Generalized Myrmicinae (ANDERSEN 1997). Having a solitary predator and a predatory cold climate specialist as dominant species is very unusual.

These predatory groups are also thought to be removed

from competitive interactions with other ants because of their specialized diets and low population densities (ANDERSEN 1997). This, in combination with results showing there are (I) many samples without ants (the number of litter quadrats without ants was 24%), (II) relatively few species in these forests, and (III) a low abundance of ants, suggests that interactions between ant species may be relatively uncommon and that inter-specific competition does not play a major role in structuring native ant communities in northern New Zealand forests.

Seasonality was evident in these ant communities with a seasonal trend of lower abundance and species richness in cooler months, which is probably characteristic of ants being less active in winter, and then increased foraging and biomass in spring / summer (ANDERSEN 1986b, HÖLLDOBLER & WILSON 1990). Statistically, a simple seasonal pattern (based on day length) explained much of the variation in abundance ($R^2 = 83\%$) and species richness ($R^2 = 77\%$) of ants. There was also a lack of species-specific foraging cycles throughout the year and the composition of ant species was similar throughout the year. There are often, but not always, species-specific foraging cycles in ants over an annual period, allowing the coexistence of species (ANDERSEN 1986b).

In comparison to "expected patterns", it appears that ant communities in native forests in northern New Zealand are characterised by very low species richness, abundance and functional groups diversity. Future work on native ants in New Zealand could focus on determining if the patterns of diversity and dominance indicated in this paper are consistent in other forest ecosystems throughout the country. There is anecdotal evidence that the abundance of ants may be greater in South Island beech forest (*Nothofagus*) where these forests have extremely high carbohydrate (honeydew) production (BEGGS 2001). However, this needs to be determined. Also, understanding the evolutionary response of New Zealand's flora and fauna to the lack of a diverse and abundant ant fauna, as typically occurs elsewhere in the world, would also be of great interest (WILSON 1996).

Acknowledgements

Thanks to Margaret Stanley and Jacqueline Beggs for comments on an earlier version of this manuscript, to Alan Andersen and Phil Lester for additional comments which have improved the manuscript, and Greg Arnold for statistical advice and analyses. This work was supported by the Entomological Society of New Zealand (21st Anniversary Fund), Landcare Research (OBI - Defining New Zealand's Land Biota, FRST C09X0507), the University of Auckland, and a FRST doctoral scholarship to DW.

Zusammenfassung

Wenngleich Neuseeland nur elf heimische Ameisenarten beherbergt, ist über deren Biologie wenig bekannt. Diese Arbeit untersucht die Diversität, Gemeinschaftszusammensetzung und Saisonalität der heimischen und exotischen Ameisen an sieben heimischen Waldstandorten im nördlichen Neuseeland, mittels Laubstreuuntersuchungen, Barberfallen und Vegetationsklopfschirm. Insgesamt wurden sieben heimische und fünf exotische Ameisenarten erfasst. Laubstreuuntersuchungen ergaben durchschnittlich 5,1 Ameisenindividuen und 1,6 Ameisenarten je 1 × 1 m Quadrat. In 55 % der Quadrate wurde nur eine Art festgestellt und in 88 % zwei Arten. Auch der Einsatz von Barberfallen erbrachte wenige Arten, bei einer durchschnittlichen Fangrate von nur 0,215 Ameisen pro Barberfalle und Tag. Die Artenzusammensetzung war im Jahresverlauf und zwischen den Untersuchungsflächen ähnlich. Ein einfacher Aspekt von Saisonalität, nämlich die Tageslänge, erklärte einen großen Teil der Variation von Abundanz ($R^2 = 83\%$) und Zahl der festgestellten Arten ($R^2 = 77\%$). Sowohl bei den Laubstreu- als auch bei den Barberfallenfängen trugen drei Arten mit über 90 % zur Gesamtabundanz der Ameisen bei. Die zwei häufigsten Arten waren Räuber: *Heteroponera brounii* (FOREL, 1892) und *Pachycondyla castaneicolor* (DALLA TORRE, 1893). Nur fünf Ameisenindividuen wurden mittels Klopfschirm gesammelt, bei einmal monatlicher Besammlung von je 40 Pflanzen über zwölf Monate hinweg. Das Fehlen einer an Arten und Individuen reichen Ameisenfauna könnte die Evolution der neuseeländischen Biota wesentlich beeinflusst haben; weiterreichende Untersuchungen dazu sind aber noch ausständig.

References

AGOSTI, D., MAJER, J.D., ALONSO, L.E. & SCHULTZ, T.R. (Eds.) 2000: Ants. Standard methods for measuring and monitoring biodiversity. – Smithsonian Institution Press, Washington, DC, 280 pp.

- ANDERSEN, A.N. 1986a: Patterns of ant community organization in mesic southeastern Australia. – *Australian Journal of Ecology* 11: 87-97.
- ANDERSEN, A.N. 1986b: Diversity, seasonality and community organization of ants in adjacent heath and woodland sites in South-Eastern Australia. – *Australian Journal of Zoology* 34: 53-64.
- ANDERSEN, A.N. 1997: Functional groups and patterns of organization in North American ant communities: a comparison with Australia. – *Journal of Biogeography* 24: 433-460.
- BEGGS, J. 2001: The ecological consequences of social wasps (*Vespula* spp.) invading an ecosystem that has an abundant carbohydrate resource. – *Biological Conservation* 99: 17-28.
- BROWN, W.L. 1958: A review of the ants of New Zealand. – *Acta Hymenopterologica* 1: 1-50.
- BROWN, W.L. 2000: Diversity of ants. In: AGOSTI, D., MAJER, J.D., ALONSO, L.E. & SCHULTZ, T.R. (Eds.): Ants. Standard methods for measuring and monitoring biodiversity. – Smithsonian Institution Press, Washington, DC, pp. 45-79.
- CLARKE, K.R. & WARWICK, R.M. 2005: Change in marine communities. An approach to statistical analysis and interpretation. 2nd Edition. – Plymouth Marine Laboratory, Plymouth, 161 pp.
- COLWELL, R.K. 2005: EstimateS: Statistical estimation of species richness and shared species from samples (version 7.5). – <<http://purl.oclc.org/estimates>>, retrieved on 27 November 2006.
- DON, A.W. 2007: The ants of New Zealand. – Otago University Press, Dunedin, 239 pp.
- DUNN, R.R., SANDERS, N.J., FITZPATRICK, M.C., LAURENT, E., LESSARD, J.-P., AGOSTI, D., ANDERSEN, A.N., BRUHL, C., CERDA, X., ELLISON, A.M., FISHER, B.L., GIBB, H., GOTELLI, N.J., GOVE, A., GUENARD, B., JANDA, M., KASPARI, M., LONGINO, J.T., MAJER, J., MCGLYNN, T.P., MENKE, S.B., PARR, C.L., PHILPOTT, S.M., PFEIFFER, M., RETANA, J., SUAREZ, A.V. & VASCONCELOS, H.L. 2007: Global ant (Hymenoptera: Formicidae) biodiversity and biogeography – a new database and its possibilities. – *Myrmecological News* 10: 77-83.
- HARRIS, R.J. & BARKER, G. 2007: Relative risk of invasive ants (Hymenoptera: Formicidae) establishing in New Zealand. – *New Zealand Journal of Zoology* 34: 161-178.
- HÖLLDOBLER, B. & WILSON, E.O. 1990: The ants. – Harvard University Press, Cambridge, MA, 732 pp.
- LANDCARE RESEARCH 2005: Key to the ants of New Zealand. – <<http://www.landcareresearch.co.nz/research/biocons/invertebrates/ants/key>>, retrieved on 10 January 2005.
- MOREAU, C.S., BELL, C.D., VILA, R., ARCHIBALD, S.B. & PIERCE, N.E. 2006: Phylogeny of the ants: diversification in the age of angiosperms. – *Science* 312: 101-104.
- NIWA 2006: Overview of New Zealand Climate. – <<http://www.niwa.govt.nz/education/resources/climate/overview>>, retrieved on 27 November 2006.
- R DEVELOPMENT CORE TEAM 2006: R: a language and environment for statistical computing. – R Foundation for Statistical Computing, Vienna, 1642 pp.
- THOMAS, G.M. & OGDEN, J. 1983: The scientific reserves of Auckland University. 1. General introduction to their history, vegetation, climate and soils. – *Tane* 5: 12-17.
- WARD, D.F. 2005: Changes to the classification of ants (Hymenoptera: Formicidae). – *The Weta* 30: 16-18.
- WARD, D.F. 2007: Modelling the potential geographic distribution of invasive ant species in New Zealand. – *Biological Invasions* 9: 723-735.
- WARD, P.S. 2000: Broad-scale patterns of diversity in leaf litter ant communities. In: AGOSTI, D., MAJER, J.D., ALONSO, L.E. & SCHULTZ, T.R. (Eds.): Ants. Standard methods for measuring and monitoring biodiversity. – Smithsonian Institution Press, Washington, DC, pp. 99-121.
- WHEELER, W.M. 1935: Check list of the ants of Oceania. – *Occasional Papers of the Bernice P. Bishop Museum* 11: 1-56.
- WILSON, E.O. 1996: Hawaii – a world without social insects. – *Occasional Papers of the Bernice P. Bishop Museum* 45: 3-7.