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Coexistence, habitat patterns and the assembly of ant communities in the Yasawa islands, Fiji

Darren Ward[*,1], *Jacqueline Beggs*

Tamaki Campus, School of Biological Sciences, University of Auckland, Private Bag 92019, Auckland, New Zealand

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ABSTRACT

Community assembly rules are important to help understand the dynamics of biological invasions. The coexistence of native and invasive ant species was examined by litter sampling on six remote islands within the Fijian archipelago, in the Pacific Ocean. The composition of ant assemblages of 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 island]) and on two null model data sets (co-occurrence and body size), showed that 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 (i.e. harsh environments), 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 a very similar set of invasive species to the Yasawa islands are ubiquitous throughout the region. Thus, similar patterns of competition, co-occurrence and community organisation that exist in the Yasawa islands could be manifested throughout the Pacific Ocean region.

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 and 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 and Levins, 1967; Diamond, 1975; Gotelli and 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 utilization is reduced. Thus, there is a limit to

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[*] *Corresponding author*. Tel.: +64 9 5744223; fax: +64 9 5744101.
E-mail address: wardda@landcareresearch.co.nz (D. Ward).

[1] Present address: Landcare Research, Private Bag 92170, Auckland, New Zealand.

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the similarity of species that can coexist in a community (MacArthur and Levins, 1967; Szabó and 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 and 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 and Ellison, 2002). Although abiotic factors, habitat requirements, and dispersal abilities are among several factors that can interact to shape ant communities (Cole, 1983; Savolainen and 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 and 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 and 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 paper we examine the structure of ant communities on an island archipelago from Fiji, in the Pacific Ocean. We examine how dominance and competition affect the coexistence of ant species at both local and regional scales. In particular, we examine the influence of habitat and the presence of invasive species on the structure of the native ant community.

2. Methods

2.1. The Yasawa islands

Fiji lies in the central Pacific Ocean between 12 and 21° South and between 175° West and 177° East longitudes (Evenhuis and Bichel, 2005; Fig. 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 (Fig. 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) have a warm, humid tropical maritime climate with mean monthly temperatures from 22 °C in July to 26 °C in January (Evenhuis and 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 and 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).

2.2. Sampling

Sampling took place on six islands in the Yasawa group (Kuata, Waya, Naviti, Matacawalevu, Tavewa, and Nanuya lailai) from the 5th to 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 1:50,000, 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 exotic species in Fiji, and is considered a weed 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

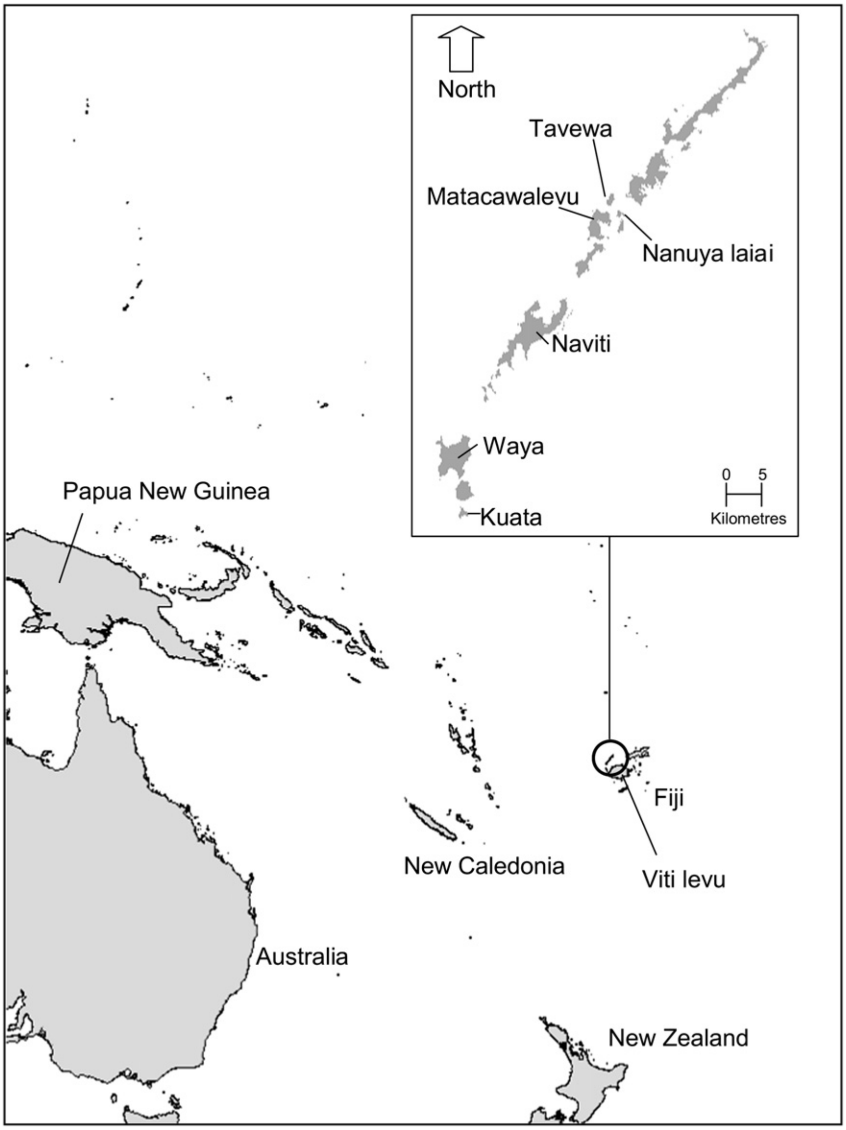

Fig. 1 – Fiji in relation to the western Pacific Ocean, the Yasawa island archipelago of Fiji and the six islands sampled (inset).

widely cultivated and many plantations have been abandoned, including those on the Yasawa islands.

To sample ants a 0.5 × 0.5 m quadrat was placed on the ground and litter within the quadrat was scooped into a white tray (30 × 40 × 10 cm). Litter was sifted through a 1 × 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 one time, between 1 and 4 trays were needed. However, a standardised time of 15 min 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 ($F = 10$, $S = 0$, $C = 20$).

2.3. *Food baiting experiment*

To determine what 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 × 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 × 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 min after the bait was placed out. Each station was examined for 20 s. 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: $1 \leq 5$ ants, $2 = 5$–9, $3 = 10$–19, $4 = 20$–50, $5 \geq 50$. 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 ×2), scrub (3 grids: Kuata ×2, Matacawalevu), coconut (2 grids: Matacawalevu, Tavewa), and grassland (grass < 0.5 m tall, used for stock grazing, 5 grids: Kuata, Waya, Naviti, Tavewa ×2).

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 and 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. Statistical analyses

3.1. *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 and Warwick, 2005). Pairwise tests of island and habitats were examined using Analysis of Similarities (ANOSIM) with 999 permutations.

3.2. *Coexistence in litter communities*

Co-occurrence of species was examined using EcoSim software (Gotelli and 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 3 separate matrices, 1 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 and 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 standardized effect size (SES) for the set of assemblages does not differ from zero. SES is generated in EcoSim, where $\text{SES} = (I_{\text{obs}} - I_{\text{sim}})/s_{\text{sim}}$ 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 and Wilson, 1990). Measurements were made on 10 specimens of each species where possible. Only the minor caste of polymorphic taxa was 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 bait at which they occurred). Interference competition was measured by (1) aggressive behaviour (defined as the number of times a species “attacked” or “w as 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 min baiting period). The time taken by a species to discover bait (proportion of occurrence at baits at 12 min) was also examined as a measure of exploitative competition.

4. Results

4.1. *Faunal composition*

Litter quadrats yielded 27 species, 17 species were native (including six endemic to Fiji), and 10 were invasive (Table 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 1). A further 10 species (a mix of invasive and native) were found on four or more islands. Six species were

Table 1 – The frequency of a species collected from the Yasawa islands; from each habitat type and from all litter quadrats

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	

Numbers in parentheses are the number of litter quadrats. # Islands refer to the number of islands where a species was found.

only detected on one island (Table 1). In general, Chao 2 estimates of species richness showed that sampling was highly successful in capturing ant species in the litter (Table 2). Species diversity was the lowest on the three islands that were numerically dominated by a single species (low $1/D$ ratio) (Table 2): Tavewa, which was dominated by *Pheidole megacephala*; and Naviti and Kuata, which were dominated by *Anoplolepis gracilipes*.

Pairwise comparisons from ANOSIM showed that the overall ant composition of islands were very similar (Table 3). The differences (defined as $R > 0.5$, Clarke and 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. *A. 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 2), indicating that other species are present in the litter, but was not detected using the litter quadrats. The coconut habitat had the lowest species diversity, and was numerically dominated either by *Tapinoma minutum* or *P. megacephala*. Pairwise comparisons also showed that the ant composition of different habitats (across all islands) was barely separable (defined as $R < 0.25$, Clarke and Warwick, 2005); forest–scrub, $R = 0.135$; forest–coconut, $R = 0.252$; and scrub–coconut, $R = 0.217$.

4.2. *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 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 5). Body sizes in ant communities from scrub and coconut were randomly assembled (Table 5).

Eleven species were recorded during the baiting experiment (Table 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 above four species also showed a high level of ability to monopolise baits (Table 6). There was a positive correlation ($p = 0.165$) between species ranked by discovery and dominance (interference) abilities (Fig. 2).

5. 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.

Table 2 – Estimates of species richness and sampling efficacy for different islands and habitats from litter quadrats

Number of Species

Island/habitat	Observed	Chao 2 Sampling		Singletons	Doubletons	H'	$1/D$
		Estimate	Efficacy %				
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

A higher Shannon Diversity (H') and Simpson ($1/D$) index means the community is more diverse.

Table 3 – Pairwise comparisons between islands (R test statistic) of faunal composition for all habitats and within each habitat

Pairwise comparison	All	Forest	Scrub	Coconut
Stress	0.13	0.20	0.14	0.08
Kuata, Waya	0.434	0.446	**0.696**	
Kuata, Naviti	0.378	0.435	0.397	
Kuata, Matacawalevu	0.292		0.030	
Kuata, Tavewa	**0.626**	**0.614**		
Kuata, Nanuya lailai	0.245	0.237		
Waya, Naviti	0.292	0.372	0.044	
Waya, Matacawalevu	0.219		0.383	
Waya, Tavewa	0.438	0.381		
Waya, Nanuya lailai	0.060	0.450		
Naviti, Matacawalevu	0.064		0.141	
Naviti, Tavewa	**0.607**	**0.794**		
Naviti, Nanuya lailai	0.228	0.455		
Matacawalevu, Tavewa	**0.504**			**0.845**
Matacawalevu, Nanuya lailai	0.150			0.299
Tavewa, Nanuya lailai	0.253	0.342		**0.661**

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.

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.

Table 4 – Meta-analysis of effect sizes for co-occurrence patterns at the local scale for each habitat

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}

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 Section 2 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 at $p = 0.05/3 = 0.016$).

Table 5 – Meta-analysis of effect sizes for body size overlap patterns at the local scale

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}

Data organised as in Table 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 $p = 0.05/3 = 0.016$).

However, there is evidence to show that 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 introduced (non-native) vegetation 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 assembly rules 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 and 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 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 and Gordon, 1999; Holway et al., 2002). Thus, we 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 (Table 3) and both species also excel at exploiting and monopolising resources (Table 6, Fig. 2). 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

Table 6 – Dominance measures of species for the food baiting experiment

Species (+species code)	Numerical dominance			Interference competition		Exploitative competition
	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

See Section 2 for definitions of each dominance measure. Species are sorted in decreasing order of monopoly. No behavioural interactions were observed for *Pheidole megacephala*.

competition that promotes coexistence in ant communities (Davidson, 1998). In the Yasawa islands there was a positive correlation between 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).

6. 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 Ocean islands show that a very similar set of invasive species are ubiquitous throughout the region (Morrison, 1996; Wetterer, 2002; Abbott et al., 2006; Ward and Wetterer, 2006). Thus, similar patterns of competition, co-occurrence and community organisation that exist in the Yasawa islands could be manifested throughout the Pacific Ocean region.

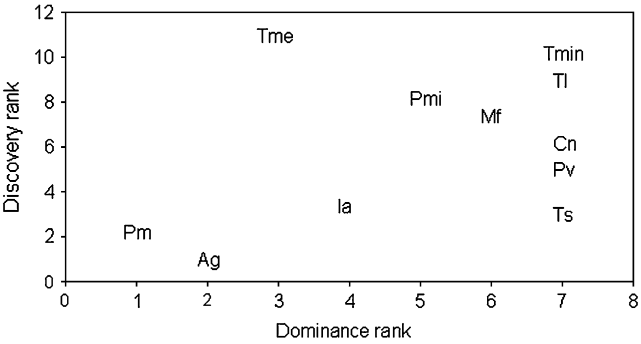

Fig. 2 – The relationship between exploitative and interference competition. Species are ranked by dominance – the ability to exclude species from resources (proportion of baits monopolised after 60 min) and discovery – a measure of the ability to find and exploit resources quickly (proportion of occurrence at baits at 12 min). Spearman rank correlation = 0.165. Species codes are given in Table 6.

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