

Research article

Community level impacts of an ant invader and food mediated coexistence

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Abstract. Ant invasions exert a range of effects on recipient communities, from displacement of particular species to more complex community disruption. While species loss has been recorded for a number of invasion events, a little examined aspect of these invasions is the mechanisms for coexistence with resident ant species. The yellow crazy ant, *Anoplolepis gracilipes* (Smith), is considered one of the world's worst ant invaders and has recently undergone rapid population growth in Tokelau. We surveyed the ground-dwelling ant fauna in two plots on each of five invaded and three uninvaded islands across two atolls in Tokelau to examine community characteristics of the ant fauna in areas with and without yellow crazy ants. We also used three types of food bait (tuna, jam and peanut butter) to experimentally test if species are able to coexist by consuming different food resources. *Anoplolepis gracilipes* was found to coexist with two to six other ant species at any one site, and coexisted with a total of 11 ant species. Four species never co-occurred with *A. gracilipes*. Non-metric multi-dimensional scaling showed significant differences in community composition and the relative abundance of species between areas that had, and had not, been invaded by *A. gracilipes*. The number of other ant species was significantly lower in communities invaded by the yellow crazy ant, but did not decline with increasing *A. gracilipes* abundance, indicating that impacts were independent of population density. The yellow crazy ant dominated all tuna and jam baits, but had a low attendance on peanut butter, allowing four other ant species to access this resource. Our results demonstrate community level impacts of an ant invader on a tropical oceanic atoll and suggest that differing use of food resources can facilitate coexistence in ant communities.

Keywords: *Anoplolepis gracilipes*, interspecific competition, food preference, invasive species, ant mosaic hypothesis.

Introduction

Ant invasions are known to adversely affect vertebrates and invertebrates (Haines et al., 1994; Feare, 1999; Hoffman et al., 1999), but the most commonly reported impact is a reduction in the abundance and diversity of native or resident ants (Erickson, 1972; Holway, 1999; Helms and Vinson, 2001; Wetterer et al., 2001; Holway et al., 2002; Lester and Tavite, 2004). The success of ant invaders has largely been attributed to superior competitive abilities (Holway, 1999; Holway et al., 2002), which is associated with high relative abundance (Palmer, 2004). Numerical dominance at food resources might allow invasive ants to break the trade-off between exploitative and interference competitive abilities (the discovery-dominance trade-off; Fellers, 1987) that appears to normally constrain ant populations (Davidson, 1998), and so dominate available food sources to the exclusion of other species. Although displacement of native ants is common, it is also typical for a number of ant species to coexist with the invader, even when the introduced species is in extremely high population densities (Helms and Vinson, 2001; Holway et al., 2002; Lester and Tavite, 2004; Abbott, 2006).

Tropical ant communities are thought to be structured by asymmetric competitive interactions, resulting in dominance hierarchies and strong distinctions between dominant and subordinate species (Majer, 1972; Morrison, 1996; Andersen 1997; Blüthgen and Fiedler, 2004; Blüthgen et al., 2004). Stronger competitors are able to monopolise stable and rewarding resources, such as

honeydew, and occupy mutually exclusive territories or partition food with other dominants. Subordinate species are able to access food resources that the dominant species have left unattended and thus can monopolise some foods while sharing others with dominants (Blüthgen et al., 2004). However, patterns of food resource use are also dependent upon a species' physiological capacity and nutritional requirements, seasonality, and recent dietary intake (Stein et al., 1990; Blüthgen and Fiedler, 2004; Lach, 2005). Ant species that coexist with an invader might exhibit complementary dietary preferences or undergo dietary shifts to avoid competitive interactions with the invader.

The yellow crazy ant, *Anoplolepis gracilipes* (Smith), is a tramp ant that has spread to tropical Asia, islands in the Pacific and Indian Oceans, and mainland Australia (Passera, 1994; Wetterer, 2005). It is considered one of the world's six worst ant invaders (Holway et al., 2002), and negative impacts of invasion have been reported from a number of areas including Christmas Island (O'Dowd et al., 2003; Abbott, 2004, 2005), Seychelles Islands (Haines et al., 1994; Feare, 1999), India (Rao and Veeresh, 1991), and Tokelau (Lester and Tavite, 2004).

Yellow crazy ant invasions can result in dramatic ecological shifts in the surrounding communities. On Christmas Island, *A. gracilipes* has killed millions of native red land crabs, subsequently modifying the dynamics of rainforest regeneration in invaded areas and facilitating secondary invasions by the giant African land snail (O'Dowd et al., 2003). Yellow crazy ants can also change local invertebrate communities and kill young birds and reptiles (Haines et al., 1994; Feare, 1999; Hill et al., 2003; Lester and Tavite, 2004). The yellow crazy ant has been in Tokelau since at least the 1930's (Wilson and Taylor, 1967), but has recently undergone rapid population growth and become an agricultural and household pest (Lester and Tavite, 2004) since the apparent introduction of a new haplotype (Abbott et al., in press). A recent survey showed that despite attaining high densities, particularly on village islands, *A. gracilipes* was coexisting with several other ant species (Lester and Tavite, 2004). *Anoplolepis gracilipes* was observed to dominate plant exudates and homopteran aggregations, and was also seen feeding on lizard and insect carcasses, indicating that both sugar and protein food sources are an important part of the diet.

Although the impacts of invasive ants and mechanisms of invasion have received considerable attention, the mechanisms for coexistence between invaders and resident ants have not. In addition, while impacts of ant invaders are well documented for some species, such as *Linepithema humile* (Mayr) and *Solenopsis invicta* Buren, (Holway et al., 2002), records of the impacts of yellow crazy ant invasions on resident ant communities are not. In the present study we aimed to examine ant community characteristics in areas with and without the yellow crazy ant and determine patterns of coexistence with *A. gracilipes* in Tokelau, testing the following hypotheses: 1) that areas where *A. gracilipes* is present

have fewer other ant species than areas where *A. gracilipes* is absent; 2) that the composition of ant communities where *A. gracilipes* is present differs to communities in which *A. gracilipes* is absent; and 3) that species coexisting with *A. gracilipes* do so by consuming different food resources.

Materials and methods

Study site

Tokelau is located 483 kms north of Samoa (approximately 9°45'S, 171°35'W) and is comprised of three low-lying coral atolls: Atafu, Nukunonu and Fakaofu. The atolls are 50–100 kms apart and each is made up of 38–51 islands surrounding a shallow lagoon, with one or two islands on each atoll being permanently inhabited. Tokelau lies in the southeast trade wind belt and has a moist tropical climate year round (mean annual temperature 28°C; mean annual rainfall >3000 mm; Mueller-Dombois and Fosberg, 1998). The vegetation of the islands, dominated by the coconut palm, *Cocos nucifera*, is low in diversity and typical of small Pacific atolls.

The yellow crazy ant was first recorded on Tokelau in the 1930's but only became problematic for villagers in the past five years (Wilson and Taylor, 1967; Lester and Tavite, 2004). The ants have 'farmed' scale insects on crop plants to the extent that crops have collapsed, and high ant abundance means that any food left out, for example drying fish, is almost immediately covered in ants. In addition the ants cause direct nuisance to humans by crawling over people, particularly young children. Of the three atolls, only the southernmost two (Nukunonu and Fakaofu) have been invaded by *A. gracilipes* (Abbott et al., 2006).

Community composition of the ground-dwelling ant fauna

To assess the composition of the ground-dwelling ant fauna, two 15 m x 15 m plots were established on each of eight islands (four invaded and two uninvaded on Nukunonu Atoll, one invaded and one uninvaded on Fakaofu Atoll). The plots were haphazardly located at least 40 m apart in the inner forest area. Within each plot all trees above 5 cm diameter-at-breast-height were identified. Five pitfall traps were placed haphazardly throughout the plot and one-third filled with Gault's solution, an insect killing agent and preservative (Walker and Crosby, 1988). Pitfall traps are commonly used to sample ant communities and haphazard or random placement is essential to ensure that the results are not biased by being located near to nest entrances (Bestelmeyer et al., 2000). The pitfall traps were plastic cups 9 cm tall, 7.5 cm diameter at the top, tapered to 5 cm diameter at the bottom and placed flush with the ground surface. The pitfalls were only left out for 24 hrs due to the speed at which they can fill up with *A. gracilipes* (Lester and Tavite, 2004). Data were collected between 27th November and 13th December, 2004. Samples were identified using the keys of Wilson and Taylor (1967) and Bolton (1977), and representative specimens deposited at Te Papa, the Museum of New Zealand, Wellington.

To test the hypothesis that *A. gracilipes* reduced ant species richness in invaded areas, we compared the number of other ant species present in invaded and uninvaded plots using a nested one-way ANOVA (island nested within presence/absence of yellow crazy ants) (R Development Core Team, 2005). We then used a nested generalised linear model (plot nested within island) to test the hypothesis that the total number of other ant species in invaded plots declined with increasing mean abundance of *A. gracilipes* in each plot. Differences in ant community composition and species abundance between invaded and uninvaded plots, and between atolls, were tested on untransformed data using non-metric multidimensional scaling (nmMDS), and analysis of similarity (ANOSIM). The sample units used for these analyses were the abundance of ant species in each separate pitfall trap. We excluded the abundance of *A. gracilipes* from this analysis, and instead

used its presence/absence as a factor, because the variable of interest is the community of other ant species, and the presence/absence of *A. gracilipes* would skew the results. In these analyses, a Global R value above 0 indicates that the groups are different, and the stress value indicates the degree to which the model provides a good fit to the data (stress values < 0.2 are considered acceptable). The contribution of each species to differences between plots was determined using SIMPER analysis (Primer 5 for Windows v 5.2). We also tested for differences in species abundance and composition in vegetation communities between invaded and uninvaded plots using ANOSIM to see if differences between ant communities might be explained by differences in vegetation.

Food resource use

In each of the 16 plots (two on each of eight islands) four bait stations were observed for 60 minutes at which time all ants at each bait type were counted and samples collected for identification. Each bait station consisted of three bait cards with one of tuna (tinned in oil), apricot jam, or peanut butter as an attractant. These bait types are commonly used to attract ants in ecological studies, contain differing amounts of protein, fat and carbohydrates and are assumed to approximate different food sources in the environment (Fellers, 1987; Farji-Brener et al., 2004; Thomas and Holway, 2005). The baits were placed on 10 cm x 10 cm laminated white paper bait cards laid in a triangle, each card was approximately 15 cm from each of the others; each bait station was haphazardly placed at least 2.5 m from the other bait stations.

To test the hypothesis that coexisting ants in invaded communities use different food resources to *A. gracilipes*, we performed a log-linear regression on the total number of bait cards of each type occupied by *A. gracilipes* versus all other ant species. Whenever a species was present on the bait card, it was considered occupied by that species. On the occasions where both yellow crazy ants and another ant species occurred simultaneously on the bait card (12 times), both were considered to be occupying that card. We also applied log-linear regression to the total number of individuals of *A. gracilipes* versus

individuals of all other ant species present at each bait type, pooled across all replicates (R Development Core Team, 2005).

To test the hypothesis that the presence of *A. gracilipes* affected the types of baits attended by other ant species and their abundance at those baits, we compared the effects of food type and the presence of *A. gracilipes* on the total number of individual ants (excluding *A. gracilipes*) present at each bait type in invaded versus uninvaded plots using log-linear regression. For this analysis, we pooled the number of individuals of all other ant species together at each food type in invaded versus uninvaded plots; therefore, this analysis did not distinguish different species or islands. Similarly, we used log-linear regression to test the effects of food type and presence of *A. gracilipes* on the number of baits occupied by other ant species. Because more invaded plots were sampled than uninvaded plots, and five tuna baits in invaded plots were disturbed by rats or lizards, counts in all four analyses were weighted by the total number of baits of each type sampled.

Results

Community composition of the ground-dwelling ant fauna

A total of 16 ant species were recorded, none of which are unique to Tokelau (Table 1). Two species are Pacific endemics [*Tetramorium tonganum* Mayr, and *Ponera swezeyi* (Wheeler)], the remainder are either exotic or native to the Pacific and are now widespread in the region and other tropical areas (Wetterer and Vargo, 2003; Abbott et al., 2006).

Anoplolepis gracilipes varied in relative abundance between islands, but where it occurred it was always the most abundant species in the pitfall traps (Table 1). The mean abundance of *A. gracilipes* in the pitfall traps ranged from 3.6 ± 1.2 to 2108.2 ± 529.8 per plot (mean of five pitfall traps \pm SE). Densities in plots within islands were usually comparable, with the exception of the island of Nukunonu where the plots differed in mean *A. gracilipes* abundance by two orders of magnitude (mean 38 ± 19.2 SE to 1049.4 ± 614.9). The islands of Nukunonu and Fenua Fala had the highest abundances of *A. gracilipes*; one and both plots on each island respectively had a mean *A. gracilipes* abundance >1000 individuals.

Species richness (excluding *A. gracilipes*) was significantly lower in plots invaded by *A. gracilipes* (mean species richness in invaded and uninvaded plots was 3.5 and 4.5 respectively, one-way nested ANOVA, $F_{1,8} = 7.5$, $p = 0.025$). However, the effect of yellow crazy ants on the number of other ant species differed between islands ($F_{6,8} = 6.67$, $p = 0.009$). The number of other ant species present in invaded plots did not decline with increasing *A. gracilipes* abundance in pitfall traps ($Z_{4,9} = -0.04$, $p = 0.97$, Fig. 1), indicating another factor is driving differences in the effect of *A. gracilipes* between islands.

Anoplolepis gracilipes was found to co-occur with between two and six other ant species in each plot, with a total of 11 ant species persisting in the presence of the invader (Table 1, Fig. 1). Six ant species were found only in invaded plots, compared with four species that were found only in uninvaded plots. Five

Table 1. Mean abundance of ant species on islands of Tokelau that have been invaded by *Anoplolepis gracilipes*, or remain uninvaded. Five and three islands were sampled respectively. Data are mean (\pm SE) from 10 pitfall trap collections on each island, which were then averaged across islands with and without *A. gracilipes*. *Tapinoma melanocephalum* was collected from bait cards only, so is not included in this table. NP = Not Present

Species	Invaded		Uninvaded	
<i>Anoplolepis gracilipes</i>	463.54	(137.71)	NP	
<i>Tetramorium lanuginosum</i>	16.90	(4.21)	NP	
<i>Pheidole oceanica</i>	0.80	(0.23)	2.57	(0.55)
<i>Tetramorium bicarinatum</i>	NP		2.15	(1.00)
<i>Pheidole umbonata</i>	1.35	(0.80)	0.67	(0.37)
<i>Tetramorium tonganum</i>	1.27	(0.43)	NP	
<i>Paratrechina vaga</i>	0.60	(0.20)	1.05	(0.66)
<i>Pheidole sexspinos</i>	0.60	(0.23)	1.00	(0.33)
<i>Tetramorium simillimum</i>	0.60	(0.40)	NP	
<i>Paratrechina longicornis</i>	NP		0.50	(0.17)
<i>Anochetus graeffei</i>	0.47	(0.19)	NP	
<i>Monomorium floricola</i>	0.36	(0.11)	0.40	(0.16)
<i>Strumigenys godeffroyi</i>	NP		0.20	(0.20)
<i>Rogeria stigmatica</i>	0.20	(0.20)	NP	
<i>Ponera swezeyi</i>	0.20	(0.20)	NP	

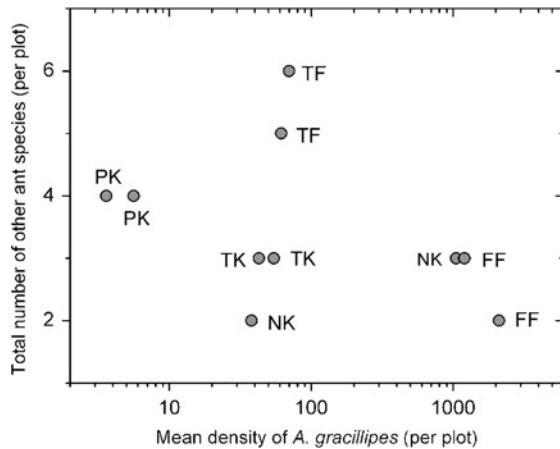


Figure 1. The total number of other ant species (excluding *A. gracilipes*) plotted against the mean abundance of *A. gracilipes* found in each of 10 invaded plots on two atolls in Tokelau. Each plot was 15 m x 15 m and contained five haphazardly placed pitfall traps. Two plots were placed on each of five islands invaded by *A. gracilipes*. Log-linear regression showed that the number of other ant species found did not decline significantly with increasing abundance of *A. gracilipes* ($p=0.97$). A log scale was used to differentiate points of similar value along the x axis. Nukunonu Atoll: PK = Pukapuka Island; TK = Tokelau Island; NK = Nukunonu Island; TF = Te Fala Island. Fakaofu Atoll: FF = Fenua Fala Island

species occurred in both invaded and uninvaded plots, four of which were more abundant in uninvaded plots (Table 1).

Ant community composition and abundance significantly differed between invaded and uninvaded plots and between atolls (Fig. 2; ANOSIM for atoll and presence of *A. gracilipes*, $p=0.001$, Global R 0.281 and 0.219 respectively). Uninvaded plots form distinct communities that are further differentiated between atolls, though there is some degree of overlap of invaded plots from both atolls (Fig. 2). Nukunonu uninvaded plots, and both invaded and uninvaded plots from Fakaofu, form a distinct cluster within the wider scatter of Nukunonu invaded plots. SIMPER analysis indicated that invaded and uninvaded plots were 89% dissimilar; over 40% of this was explained by just two species, *Pheidole oceanica* Mayr and *Tetramorium lanuginosum* Mayr. The former species being more than three times as abundant on uninvaded islands, and the latter not present on uninvaded islands at all. SIMPER analysis also revealed that ant communities on the two atolls were 86% dissimilar; over 60% of the difference was explained by four species (*Ph. oceanica*, *Pheidole sexspinosa* Mayr, *Pheidole umbonata* Mayr and *Te. lanuginosum*). Differences in ant communities between atolls were driven largely by differing relative abundances, as only *Te. lanuginosum* was not present on both atolls. Vegetation did not differ significantly between invaded and uninvaded plots or between atolls (ANOSIM for atoll $p=0.545$, and presence of *A. gracilipes*, $p=0.861$), so is unlikely to account for differences between ant communities, though we can not exclude the possibility that other factors may have been

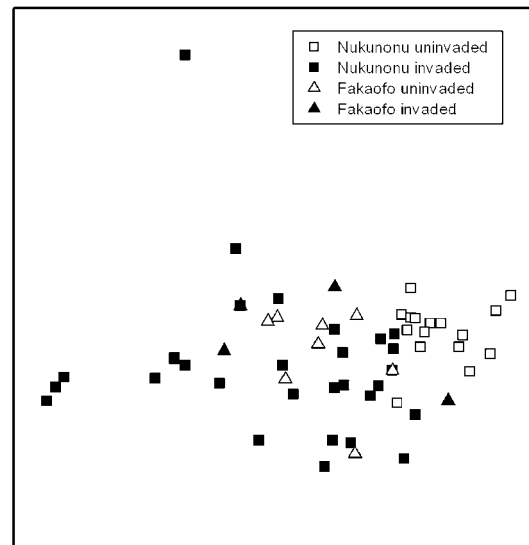


Figure 2. Non-metric multidimensional scaling (nmMDS) of ant community composition and abundance across two atolls in Tokelau (Nukunonu and Fakaofu). Solid symbols indicate presence of *Anoplolepis gracilipes*. Differences between atolls and between invaded and uninvaded plots were significant ($p=0.001$, stress=0.09; *A. gracilipes* abundance data were not included in the analysis, see Methods)

responsible for differences in coexistence between islands.

Food resource use

In invaded plots, *A. gracilipes* occupied more bait cards than any other ant species ($p < 0.0001$) and significantly affected the bait type occupied by other ant species ($p=0.001$; Tables 2 and 3). Across all species, there was no difference in the overall number of each bait type occupied ($p=0.85$), indicating that all bait types were recruited to by at least one of the species groups (*A. gracilipes* or other ant species). Yellow crazy ants were significantly more abundant at the baits ($p < 0.0001$) and also significantly affected the abundance of other species at the baits ($p < 0.0001$; Table 3). *Anoplolepis gracilipes* dominated tuna and jam baits in all invaded plots, being most abundant on tuna baits, though usually had few or no recruits to peanut butter (Table 2). The presence and abundance of other ant species at the baits displayed the inverse pattern to the preferences of *A. gracilipes*, with other ant species being most abundant on peanut butter, then jam, and least common on tuna baits.

Baits in uninvaded plots were dominated by two of the species that never co-occurred with yellow crazy ants (Table 2). *Tetramorium bicarinatum* dominated all but four bait cards of all 16 bait stations in uninvaded plots on Nukunonu. Other species to access baits in uninvaded plots on Nukunonu included *Ph. oceanica* (peanut butter twice, jam once) and *Paratrechina vaga* (Forel) (jam five times). On Fakaofu atoll, *Pa. longicornis* dominated five

Table 2. Mean abundance of each ant species present at each bait type in plots invaded and uninvaded by *A. gracilipes*. Values in parentheses are the number of each bait type occupied by that species. Results of the log-linear analyses are presented in Table 3. An asterisk indicates the species was found in both invaded and uninvaded plots

Species	Invaded			Uninvaded		
	Tuna	Jam	Peanut butter	Tuna	Jam	Peanut butter
<i>Anoplolepis gracilipes</i>	58.9 (35)	40.6 (40)	9.4 (26)			
<i>Pheidole sexspinosa</i> *			11.3 (3)			27.0 (4)
<i>Pheidole umbonata</i> *		4.0 (1)	22.5 (2)			8.0 (2)
<i>Monomorium floricola</i> *	3.0 (1)	5.0 (2)	12.3 (6)			
<i>Tetramorium tonganum</i>			3.0 (1)			
<i>Tetramorium bicarinatum</i>				82.0 (16)	40.0 (14)	123.9 (15)
<i>Pheidole oceanica</i> *				15.5 (2)	11.0 (2)	25.5 (2)
<i>Paratrechina longicornis</i>				122.0 (6)	40.0 (3)	
<i>Tapinoma melanocaphalum</i>				3.0 (1)	103.0 (2)	
<i>Paratrechina vaga</i> *					12.4 (5)	
Number of baits samples	35	40	40	24	23	23

Table 3. Results of log-linear regressions on bait experiment: the upper panel shows the effects of species group (*Anoplolepis gracilipes* and other ant species) and bait type on the number of baits occupied and the abundance of ants at the baits in invaded plots. The lower panel shows the effects of the presence of *A. gracilipes* and bait type on the number of baits occupied by other ant species (all ant species other than *A. gracilipes*), and the total number of individuals of other ant species at the baits. Values shown are χ_{df} , p

Plots invaded by <i>A. gracilipes</i>	Species group		Bait type		Interaction	
Number of baits occupied	68.8 ₁	< 0.01	0.3 ₂	0.85	15.1 ₂	< 0.01
Ant abundance at the baits	4821.4 ₁	< 0.01	1797.7 ₂	< 0.01	234.1 ₂	< 0.01
Invaded vs. uninvaded plots	<i>A. gracilipes</i>		Bait type		Interaction	
Number of baits occupied by other ant species	65.6 ₁	< 0.01	1.9 ₂	0.38	9.7 ₂	< 0.01
Abundance of other ant species at the baits	8508 ₁	< 0.01	545.5 ₂	< 0.01	182.2 ₂	< 0.01

tuna and five jam baits (out of eight bait stations) in uninvaded plots but never recruited to peanut butter. Peanut butter baits on Fakafo were occupied by *Ph. sexspinosa* (five times) and *Ph. umbonata* (twice). A total of seven species were found on baits in uninvaded plots, almost twice that found in *A. gracilipes* invaded plots.

Other ant species occupied fewer bait stations in invaded, compared to uninvaded, plots ($p < 0.0001$) and were generally restricted to peanut butter baits in invaded plots ($p = 0.008$). There was no difference in the number of each bait type occupied in invaded compared to uninvaded plots, indicating that no bait type was unacceptable in either community ($p = 0.381$; Table 3). The abundance of other ant species at bait cards was significantly reduced in the presence of *A. gracilipes*, higher on peanut butter baits in invaded plots, and highest on tuna and peanut butter baits in uninvaded plots ($p < 0.0001$).

Only *Ph. sexspinosa* and *Ph. umbonata* were able to access baits in both invaded and uninvaded plots. *Pheidole sexspinosa* was in higher abundance at baits in uninvaded plots but was only ever found on peanut butter (Table 2). *Pheidole umbonata* was in higher abundance at baits in the presence of *A. gracilipes* and was most

commonly found on peanut butter baits, appearing on only one jam bait and no tuna baits (Table 2). Both species occupied the same food types in both invaded and uninvaded plots, indicating no shift in diet to allow coexistence with *A. gracilipes*.

Discussion

The most widely documented effect of ant invasions is the reduction in species richness of the resident ant community (Erickson, 1972; Holway, 1999; Helms and Vinson, 2001; Wetterer et al., 2001; Holway et al., 2002; Lester and Tavite, 2004), a finding that is supported by our results. In addition, our results show that while the yellow crazy ant is exerting community level impacts on resident ant communities, these effects are not attributable to exclusion of a particular species at any site. Conversely, a total of 11 species coexisted with the yellow crazy ant and six of these were only found in yellow crazy ant-invaded sites. Studies on *S. invicta* invaded ant communities report up to 37 coexisting ant species (Helms and Vinson, 2001; Morrison and Porter, 2003), and positive associations between species richness of ants and other arthropods,

and the density of *S. invicta* (Morrison and Porter, 2003). Coexistence with invasive ants may be more prevalent than currently understood, and will most likely vary as a function of time (Helms and Vinson, 2001; Morrison and Porter, 2003). Other studies on coexistence between invasive and native ants have implicated non-overlapping habitats, strong competitive abilities (Wetterer et al., 2001) and temperature dependent surface activity (Helms and Vinson, 2005) to enable coexistence. However, these mechanisms are unable to explain the observed coexistence in Tokelau as coexisting ants are active in the same places and at the same times as *A. gracilipes*, and are also inferior interference competitors, as observed by consistent dominance of the baits by *A. gracilipes*.

Research focussed on mechanisms for displacement of native species by invasive species has highlighted the importance of numerical abundance in allowing the invader to make up for competitive deficiencies (Holway et al., 1998, 2002). However, our results suggest that a factor other than abundance is altering the impact of the yellow crazy ant between islands. A recent study highlighted associations between different genetic haplotypes in the Nukunonu yellow crazy ant population, differing densities of yellow crazy ants, and differing impacts on the ant community (Abbott et al., in press). While the mechanism for haplotypes giving rise to differing population densities and the associated community impacts has not been demonstrated, this provides a potential explanation for the lack of correlation between yellow crazy ant abundance and impact on the local ant communities. In contrast to the results of this study, Lester and Tavite (2004) found a negative relationship between *A. gracilipes* abundance and the number of co-occurring ant species on Tokelau. However, samples for that study were collected from the range of only one of the haplotypes reported in the Abbott et al. (in press) study, indicating that the effect of *A. gracilipes* haplotype on community impact may be greater than the effect of *A. gracilipes* abundance at a broader spatial scale.

Differential food resource use has been documented in a range of ant communities, including granivorous, nectarivorous (Blüthgen et al., 2004) and omnivorous ant guilds (Savolainen and Vepsäläinen, 1988). An emerging theme from these studies is that patterns in the use of food resources depend on the competitive outcomes between dominant and coexisting subordinate species, such that subordinate species show a high degree of overlap in resource use amongst themselves, and are largely excluded from stable carbohydrate resources. We identified three dominant species (*A. gracilipes*, *Te. bicarinatum*, and *Pa. longicornis*), which showed complementary patterns of food resource use with subordinate species. In invaded plots, subordinate species showed high overlap in attendance at peanut butter, with tuna and jam monopolised by *A. gracilipes*, while in uninvaded plots overlap was higher between species, indicating that *Pa. longicornis* and *Te. bicarinatum* do not exert the same

degree of influence over the respective communities. A previous survey in Tokelau showed *Te. bicarinatum*, but not *P. longicornis*, coexisted with *A. gracilipes* (Lester and Tavite, 2004), supporting the suggestion from our results that the latter is excluded from invaded areas.

Invasive ants are commonly omnivorous, consuming insect and animal prey and feeding on plant and homopteran exudates (Holway et al., 2002; Helms and Vinson, 2003; Kaplan and Eubanks, 2005). Previous studies have shown that sugary liquids and animal proteins, as opposed to lipids, form the bulk of food brought back to *A. gracilipes* nests (Haines and Haines, 1978; Rao and Veeresh, 1991) and in previous food choice experiments, *A. gracilipes* recruited strongly to sugary and proteinaceous baits (Rao and Veeresh, 1991; Abbott, 2004). It appears that the patterns of food resource use observed in this study are driven by the preferences of the yellow crazy ant, not by any trade-off in competitive ability between *A. gracilipes* and any other species, a pattern consistent with other studies of food resource use amongst coexisting ant species (Blüthgen et al., 2004).

Species coexistence can also be mediated by differential responses to environmental heterogeneity. For example, variation in moisture and temperature can limit the distribution of Argentine ants and facilitate coexistence with native ants that are better adapted to hot, dry conditions (Holway et al., 2002). In addition, patchiness in habitat disturbance apparently mediates the relative distributions of two fire ant species in woodland and wetland areas (Tschinkel, 1987). However, environmental heterogeneity at smaller spatial scales is also likely to play a role in the coexistence of ants with *A. gracilipes*.

The size-grain hypothesis (SGH; Kaspari and Weiser, 1999) proposes that species can coexist in the same landscape by using different sized spaces in the substrate according to body size. In a recent test of the SGH in the same ant communities of Tokelau, Sarty et al. (2006) demonstrated that smaller ant species are able to access food resources in interstitial environments where *A. gracilipes* is at a competitive disadvantage. In addition, several species that accessed tuna, jam and peanut butter food baits in the most rugose treatments of the SGH experiment are recorded in the present study only on peanut butter. Sarty et al.'s (2006) SGH experiment effectively acts as an exclusion filter for the yellow crazy ant, allowing coexisting species to express food preferences in the absence of the dominant competitor (Sarty, 2005). Comparing the results of these two studies suggests not only that *M. floricola*, *Ph. umbonata* and *Ph. sexspinosa* were restricted to peanut butter by asymmetric competition rather than inherent food requirements, but also that at least two mechanisms of coexistence are acting simultaneously in these communities: exploitation of underutilised food resources and differential use of the forest floor landscape according to body size.

Coexistence between *A. gracilipes* and other ant species has been documented in other studies (Greenslade,

1971; Morrison, 1996; Lester and Tavite, 2004; Abbott, 2006), but the mechanisms for coexistence between *A. gracilipes* and other ant species have not been investigated. In a focus on patterns of coexistence, rather than displacement, our study highlights the potential for numerous species to coexist with high-density invaders and provides a mechanism both for the exclusion and coexistence of species dependent on food preferences and/or needs.

The yellow crazy ant poses a significant risk to many areas including Pacific islands where it is still in low densities, islands where it has not yet established, and other climatically suitable areas such as moist tropical regions of Mexico and Africa (Wetterer, 2005). The interactions between invasive ants and resident ant communities, particularly on oceanic islands, need to be better understood if we are to manage the risk of further invasions and protect natural ecosystems, human well being and global biodiversity. While the wider application of these findings to other invaded ant communities deserves further testing, this study, in conjunction with previous work, allows us to predict the potential effects of an *A. gracilipes* invasion on recipient ant communities. It appears that larger, competitively dominant ant species that display preferences for sugary and proteinaceous foods are more likely to be displaced by *A. gracilipes*. Conversely, those species that exploit interstitial habitats and alternative food sources may coexist with *A. gracilipes*. The ability to predict the effects of invasive species can potentially play an important role in conservation and biosecurity management by enabling identification of species that are at risk of competitive displacement. This could be used to prioritise conservation efforts in the face of an invasion and aid in the protection of global biodiversity.

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