

Habitat complexity facilitates coexistence in a tropical ant community

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Abstract The role of habitat complexity in the coexistence of ant species is poorly understood. Here, we examine the influence of habitat complexity on coexistence patterns in ant communities of the remote Pacific atoll of Tokelau. The invasive yellow crazy ant, *Anoplolepis gracilipes* (Smith), exists in high densities on Tokelau, but still coexists with up to seven other epigeic ant species. The size-grain hypothesis (SGH) proposes that as the size of terrestrial walking organisms decreases, the perceived complexity of the environment increases and predicts that: (1) leg length increases allometrically with body size in ants, and (2) coexistence between ant species is facilitated by differential habitat use according to body size. Analysis of morphological variables revealed variation inconsistent with the morphological prediction of the SGH, as leg length increased allometrically with head length only. We also experimentally tested the ability of epigeic ants in the field to discover and dominate food resources in treatments of differing rugosity. *A. gracilipes* was consistently

the first to discover food baits in low rugosity treatments, while smaller ant species were consistently the first to discover food baits in high rugosity treatments. In addition, *A. gracilipes* dominated food baits in planar treatments, while smaller ant species dominated baits in rugose treatments. We found that the normally predictable outcomes of exploitative competition between *A. gracilipes* and other ant species were reversed in the high rugosity treatments. Our results support the hypothesis that differential habitat use according to body size provides a mechanism for coexistence with the yellow crazy ant in Tokelau. The SGH may provide a mechanism for coexistence in other ant communities but also in communities of other terrestrial, walking insects that inhabit a complex landscape.

Keywords *Anoplolepis gracilipes* · Discovery-dominance trade-off · Invasive ants · Morphology · Size-grain hypothesis

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Introduction

Interspecific competition plays a key role in structuring ant communities (Blüthgen and Fiedler 2004; Blüthgen et al. 2004; Davidson 1998; Lach 2005; Savolainen and Vepsäläinen 1988). Coexistence in ant communities can be mediated by trade-offs in competitive abilities, for example the ability to discover versus the ability to dominate and consistently recruit to a food resource (the discovery–dominance trade-off; Fellers 1987). Most field studies of recruitment dynamics have been conducted in two dimensional environments, with food baits placed on the ground or on tree trunks, but at the scale of an individual ant landscapes are much more

complex. Moreover, ants vary substantially in size (Hölldobler and Wilson 1990), and this variation may affect the ways they interact with the landscape. Until recently the effects of body size and habitat complexity have been considered in isolation, but recent experimental evidence suggests that the interaction between these factors may have a strong influence on the composition of ant communities (Farji-Brener et al. 2004).

The size-grain hypothesis (SGH) proposes that as the size of a terrestrial, walking organism decreases, the landscape is perceived as more complex (rugose) (Kaspari and Weiser 1999). Larger organisms can decrease the rugosity of the environment and run over an otherwise complex landscape by having longer legs, effectively reducing the cost of locomotion. However, smaller organisms with shorter legs can benefit from enhanced penetration of environmental interstices where they may find food or refuge and avoid the cost associated with the construction of long legs. The SGH predicts that across species the benefits of increased penetration or enhanced running speed should result in leg lengths that increase disproportionately with body size (allometrically; Kaspari and Weiser 1999). To test this prediction, Kaspari and Weiser (1999) measured 135 ant species and compared this data to published measurements for mammals. They found that ants, but not mammals, displayed allometric scaling of leg length to body mass. This scaling might reflect a stronger change in landscape complexity at the scale of ants compared to mammals (Kaspari and Weiser 1999).

If leg lengths and body sizes of ant species are selected for their ability to maximise efficiency of locomotion in habitats of differing rugosity, then smaller species should not only have shorter legs, but should use interstitial habitats or demonstrate competitive advantages in these areas, and larger ants should demonstrate advantages in more planar environments (Farji-Brener et al. 2004; Kaspari and Weiser 1999). To the best of our knowledge, the ability of ants of different sizes to access food resources in environments of differing rugosity has only once been previously tested. Farji-Brener et al. (2004) found leaf litter ants that discovered food baits in rugose environments first were 42% smaller than the ants that first discovered food baits in planar environments. If assortative habitat use according to body size in ant communities is widespread it has important implications for understanding the role of interspecific competition in structuring these communities.

The yellow crazy ant, *Anoplolepis gracilipes* (Smith), has been considered one of the world's six worst ant invaders (Holway et al. 2002) and is now widespread throughout islands of the Pacific and Indian Oceans (Wetterer 2005). It was first recorded in Tokelau, a

series of three low-lying atolls in the Pacific Ocean, in the 1930s (Wilson and Taylor 1967), but has recently undergone rapid population growth and has become an agricultural and household pest (Lester and Tavite 2004). Recent surveys showed that *A. gracilipes* was coexisting in some areas with up to seven other ant species (Lester and Tavite 2004; Sarty 2005).

The forest floor environment in Tokelau is a spatially complex array of coral rubble of different sizes and organic debris including leaf litter, coconut husks, logs and twigs. Fallen logs, twigs and leaf litter provide both planar and highly rugose environments for the foragers of different sized ant species. If smaller ants are able to coexist with *A. gracilipes* by accessing food sources in rugose environments, where *A. gracilipes* either cannot or does not forage or recruit, they should be faster at discovering these resources. Conversely, the SGH predicts that the yellow crazy ant should be faster at discovering food resources in low rugosity environments, such as in large environmental interstices or on top of leaf litter or coral rubble.

In this study we tested two predictions of the SGH in epigeic ant communities invaded by the yellow crazy ant in Tokelau and hypothesised that: (1) the ant species of Tokelau, display an allometric relationship between body mass and leg length as predicted by the SGH; (2) smaller ant species discover food baits in rugose environments faster than *A. gracilipes*, and conversely, *A. gracilipes* discovers food baits in planar environments faster than smaller ants; and (3) smaller ant species dominate food resources in rugose environments without being displaced by *A. gracilipes*.

Materials and methods

Tokelau lies 483 km north of Samoa in the Pacific Ocean (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 km apart and each is made up of 38–51 islands surrounding a shallow lagoon, one or two of which are permanently inhabited on each atoll. The islands are generally small in size and Tokelau's total land area is approximately 12 km². Tokelau lies in the southeast trade wind belt and has a humid tropical climate that displays little seasonal variation (mean annual temperature 28°C, mean annual rainfall 3,000 mm; Mueller-Dombois and Fosberg 1998). Of the three atolls, only the southernmost two (Nukunonu and Fakaofu) have been invaded by *A. gracilipes* (K.L. Abbott et al., unpublished data).

The islands of Tokelau are comprised of coral rubble of varying size with poorly developed soil overlying

beach rock (Parham 1971). The islands are low-lying (≤ 5 m above sea level) and narrow. The vegetation is low in diversity and typical of small Pacific atolls (Mueller-Dombois and Fosberg 1998; Parham 1971).

Allometric scaling of morphology

Morphological measurements of ants were made on head length, head width, pronotum width and total hind leg length (femur + tibia + tarsus), following methods used by previous authors to investigate allometries predicted by the SGH (Espadaler and Gómez 2001; Farji-Brener et al. 2004; Kaspari and Weiser 1999; Parr et al. 2003). Specimens were sourced from pitfall trap surveys on Nukunonu and Fakaofu atolls in June and July 2004. Between 14 and 30 ants were selected per species to allow testing of differences between islands prior to testing allometric relationships at the species level. We measured 3–20 specimens from each island where they were found. Only those species of which at least three complete specimens were available were measured, so 4 out of 16 species were not measured [*Tetramorium simillimum* (Smith), *Ponera swezeyi* (Wheeler), *Rogeria stigmatica* Emery, and *Strumigenys godeffroyi* Mayr]. We made linear measurements on ants suspended in 70% ethanol using a dissecting microscope fitted with a graticule division scale at between 10 and 50 \times magnification, depending upon ant size.

After testing within species for differences in linear measurements between islands using one-way ANOVA, two species were split into separate morphological groups as linear measures were significantly different between island populations [*Pheidole umbonata* Mayr, and *Paratrechina vaga* (Forel)]; thus, 14 species groups were used in this analysis. There were no other differences between island populations ($P > 0.05$). Three to six ant specimens (depending on availability of complete specimens) were randomly selected from each species or morphological group for weighing. The ants were desiccated in a drying oven at 60°C for approximately 44 h, cooled to room temperature and individually weighed using a Sartorius microbalance sensitive to 0.1 μg .

The mean for each species group was determined for each of five measures: head length, head width, pronotum width, leg length, and mass. Previous studies have found positive correlations between dry body mass and each of head width, pronotum width and head length (Espadaler and Gómez 2001; Kaspari and Weiser 1999), thus all these four body measurements were used as indicators of body size. These values were used to investigate allometric relationships between leg

length and body size, and also between the different indicators of body size. Pairwise simple linear regressions were performed on \log_{10} -transformed data. Following a graphical analysis, those slopes that appeared allometric were tested for allometry with one-sided t tests, with a null hypothesis of isometry ($\beta = 0.333$ vs $\beta > 0.333$ for mass vs leg length; $\beta = 1$ vs $\beta > 1$ for linear measures; Kaspari and Weiser 1999).

Discovery of food baits

The SGH predicts that ants of different sizes use the same landscape differently, with smaller ants using interstices and larger ants using planar environments. To test the ability of ants of varying sizes to discover food resources in environments of differing rugosity, an experiment composed of five treatments was set up in a randomised block design. The treatments were designed to represent a gradient of environmental rugosity: highly rugose (small coral rubble matrix), medium rugosity (medium size rubble matrix), low rugosity (large rubble matrix), control (container with no coral rubble), and a planar environment (bait cards).

The experimental treatments consisted of baits placed in plastic containers filled with different sized coral rubble, which is typical of the substrate of Tokelau. Each plastic container was round, approximately 18 cm diameter, with ten 1-cm-diameter holes drilled around the bottom edge, approximately 4 cm apart. A separate chamber, 6 cm diameter with six 1-cm-diameter holes drilled around the bottom, was placed in the centre and contained food bait. The lid of the container was open above the central chamber to allow visual monitoring of the chamber and access to collect ants. Other ants were deterred from entering from above with Tanglefoot[®]. The top and bottom of each container was packed with cotton wool to ensure that ants were forced to travel through the rubble. The bait cards used to represent the planar environment were 10 \times 10 cm laminated white paper squares.

To standardise the gap sizes in each treatment, the coral rubble was progressively sifted through smaller wire mesh sieves. Standard gap sizes were verified by measuring 20 randomly selected gaps between adjacent rubble pieces from the outside of each treatment container. The mean gap size increased with the size of the rubble (small, 0.66 ± 0.05 cm; medium, 0.95 ± 0.05 cm; large, 1.23 ± 0.04 cm; values are mean ± 1 SE). The gap sizes were significantly different (one-way ANOVA on \log_{10} -transformed data, $F_{2,59} = 33$; $P < 0.001$).

The food baits placed in the central chamber or bait card were tuna (tinned in oil), peanut butter and aricot jam. These baits were chosen as they are

commonly used to attract ants (Farji-Brener et al. 2004; Fellers 1987; Thomas and Holway 2005) and attract a variety of different ant species on Tokelau (Sarty 2005). The baits were placed in small drops (approximately 2 ml each) adjacent to each other. The five treatments were laid out in random blocks (each 1 m²) on each of five invaded islands ($n=23$, 3–5 replicates per island). The blocks were haphazardly located at least 10 m apart and monitored until baits in all five treatments were discovered, up to a maximum of 5 h. The first ant to enter the central chamber (in containers) or touch the bait on the bait card was collected for identification and measurement. Specimens were identified using the keys of Wilson and Taylor (1967), and Bolton (1977).

A new body size index (BSI) was developed which better reflects the ability of ants to penetrate gaps in the environment. Measures used by previous authors, such as body mass (Kaspari and Weiser 1999) and body length (Farji-Brener et al. 2004), do not adequately represent body size as it relates to the ability to penetrate environmental interstices. Body mass indicates not only body size, but also degree of sclerotisation and ants of differing sizes and thickness of cuticle can be similar in weight. Moreover, intraspecific variation in body mass can be considerable (Zollikofer 1994). Body length by itself may affect the ability of an ant to move through environmental gaps once in them, but the ability of the ant to get into gaps is mostly controlled by its width. Therefore, an index comprised of head width and leg length, measures of minimum and maximum width, respectively, was used to represent the size of the ant as it relates to their ability to enter environmental gaps. Hind femur length was used as a proxy for total leg length as the two measures are strongly correlated (simple linear regression, untransformed data, $R^2=0.99$; $P<0.0001$). The final index was: $BSI = \text{head width} \times \text{hind femur length}$.

Due to non-normality of the size data, the size of the first ant to enter each treatment was analysed using Friedman's test (S-PLUS 2003), a non-parametric alternative to a blocked ANOVA design, with replicate as the blocking variable and treatment (small, medium, large, control and bait card) as factor.

Dominance of food baits

We used the rubble filled containers that represented a high rugosity (small coral rubble matrix), a low rugosity (large rubble matrix) and a planar environment (bait card) to test if small ants can not only discover but also dominate food resources in highly rugose environments. Each treatment was laid out in a randomised

block design and observed for 5 h, after which the abundance of each ant species at the baits in each treatment was counted and specimens collected for identification. The baits used were the same and were applied in the same way as for the discovery experiment. This experiment was replicated 20 times across two islands on Nukunonu Atoll, Nukunonu and Motuhaga.

The number of times each treatment was dominated by *A. gracilipes* versus other ant species after 5 h was analysed using a chi-squared test. Dominance, for the purpose of this analysis, was defined numerically; the species present in the highest abundance was considered dominant. One replicate (small grain size) was excluded from this analysis because, after 5 h, *A. gracilipes* and *Te. simillimum* were both present at the bait (each on a separate food type) in equal numbers.

Results

Allometric scaling of morphology

All morphological variables were positively correlated with leg length (Table 1). Head length displayed the strongest relationship to leg length ($R^2=0.736$; $\beta=1.47\pm 0.25$; $P<0.0001$) and was the only variable that displayed a statistically significant allometric relationship. The slopes for leg length against mass, head width and pronotum width all indicated allometric relationships (as $\beta>0.33$ for mass, and $\beta>1$ for both linear measures) but were not significantly different from the null hypothesis of isometry (Fig. 1). All four body size measures were positively and strongly correlated with each other and all were isometric.

A. gracilipes had the largest BSI of any ant species to be measured in this analysis (1.22), almost twice that of the next largest species, *Anochetus graeffei* Mayr (0.69). Although it was not the largest species in mass, head width, head length or pronotum width, its mean leg length was 2.2 mm longer than that of any other species measured in this study.

Morphological differences between *Ph. umbonata* populations between two invaded islands on Nukunonu atoll and the uninvaded island on Fakaofu atoll were significant for all variables. These differences were consistent with differences in worker size and colour noted by Wilson and Taylor (1967) between *Ph. umbonata* populations in central and eastern Polynesia. This suggests that *Ph. umbonata* invaded Tokelau at least twice, from different source populations. Intraspecific differences in *Pa. vaga* are more likely to represent unresolved taxonomy of this species group (Lester

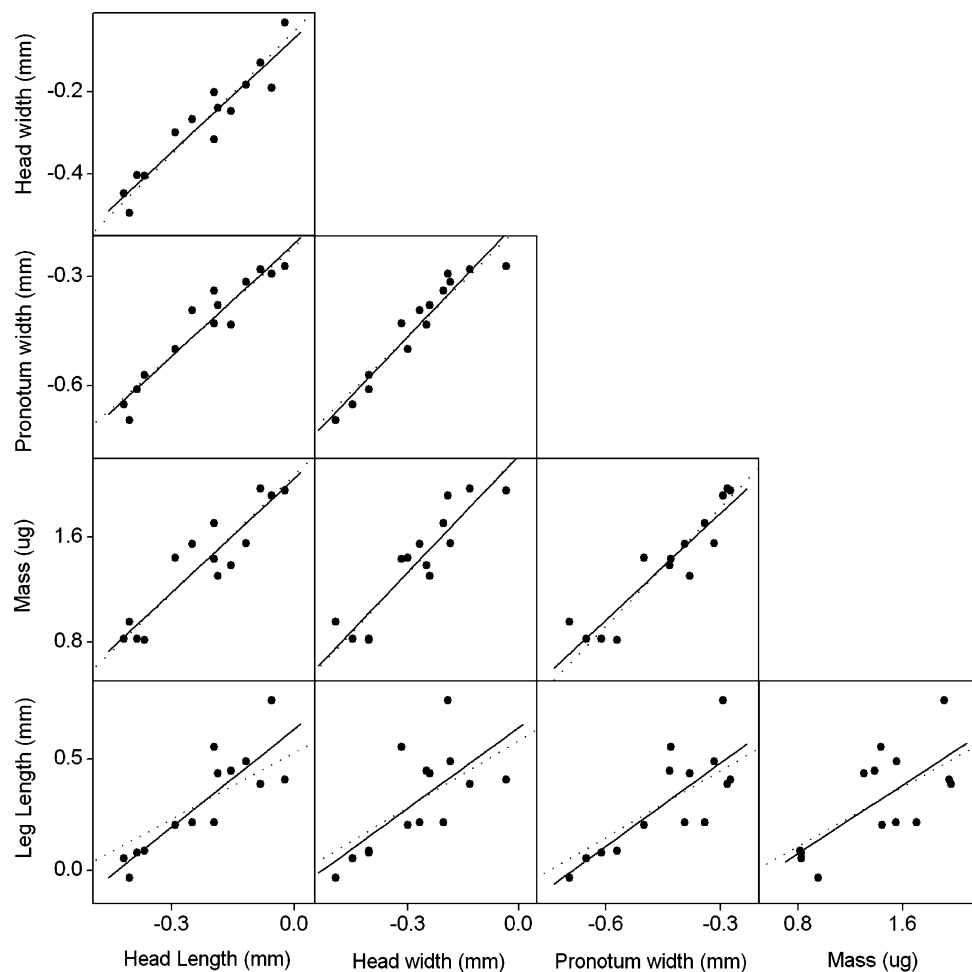


Fig. 1 Pairwise scatterplots of the five morphological measures made on 14 ant species or morphological groups from Tokelau. Simple linear regressions were performed on each pair of variables using \log_{10} -transformed data. The *solid line* represents a linear regression on the data; the *dotted line* is the expected

(isometric) relationship in the absence of allometric scaling. All regressions were statistically significant (all $P < 0.01$). Only head length versus leg length was significantly allometric. Regression results are presented in Table 1

2005), and our specimens might include two or more as yet undescribed species.

Discovery of food baits

The BSI size class distribution of the first ants to discover all treatments was bimodal, with *A. gracilipes* forming a separate and larger size group (Fig. 2). Each mode (all other ant species and *A. gracilipes*) formed its own normal distribution (one-sample Kolmogorov–Smirnov test $P > 0.1$).

The mean BSIs of the first ants to discover each treatment were significantly different ($\chi^2_4 = 41.6$, $P < 0.0001$; Fig. 3), with mean BSI increasing with decreasing rugosity. *A. gracilipes* was the first species to discover food in the planar treatments (bait cards), and other, smaller ant species were the first to discover food in the most rugose environments 22 and 21 times,

respectively (Table 2). Smaller ants first discovered the medium rugosity treatment 16 times, but the large size grain treatment was most often discovered by *A. gracilipes* (17 vs 6). Of the other ant species to discover the baits, *Tetramorium lanuginosum* Mayr, was the most common, discovering 12 small, 9 medium, 4 large, and 1 control treatment. *Monomorium floricola* (Jerdon), was the first ant to discover a bait only once (small rugosity treatment). *A. gracilipes* was the first ant to discover both the bait cards and control treatments (empty container) 22 times each, indicating that the experimental chamber itself had little or no effect on the discovery of food by ants of different sizes.

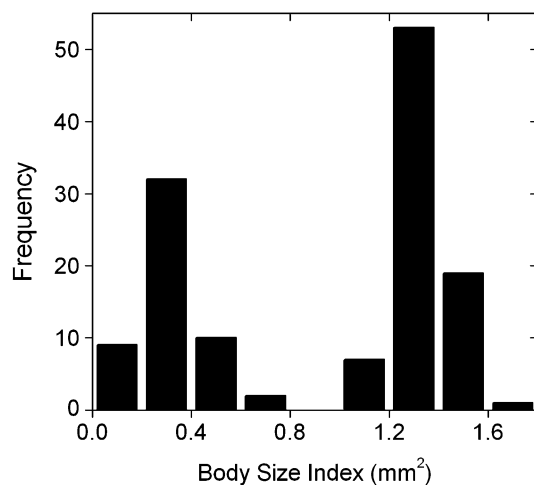
Dominance of food baits

Small ant species dominated baits in rugose treatments significantly more often than did *A. gracilipes*,

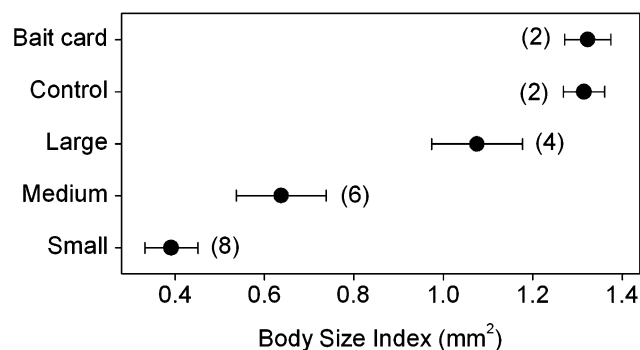
Table 1 Results of pairwise simple linear regressions of five morphological measures made on 14 ant species or morphological groups from Tokelau

Morphological variable	β	1SE	R^2
Head length			
Head width	0.926	0.091	0.896
Pronotum width	1.035	0.093	0.911
Mass	2.915	0.359	0.846
Leg length	1.470	0.254*	0.736
Head width			
Pronotum width	1.062	0.092	0.918
Mass	2.963	0.379	0.836
Leg length	1.206	0.367	0.474
Pronotum width			
Mass	2.710	0.317	0.859
Leg length	1.247	0.280	0.623
Mass			
Leg length	0.384	0.110	0.505

All slopes were significantly different from 0 ($P < 0.01$). Data used were the mean of each measure for each species or morphological group, and were \log_{10} -transformed. An allometric relationship occurs where slopes significantly differ from $\beta=1$ for linear measures, and $\beta=0.33$ or 3.03 if mass is on the x or y axis, respectively, and is indicated by an asterisk

**Fig. 2** The bimodal size class distribution of body size index (head width \times hind femur length) of all first ants to discover treatments. Each mode forms its own normal distribution (one-sample K-S test $P > 0.1$). *Anoplolepis gracilipes* makes up the largest group (>0.88 mm²); the eight other ant species are grouped in the smaller size classes (<0.88 mm²)

and *A. gracilipes* dominated food in the planar treatments significantly more often than other ant species ($\chi^2_2=28.2$, $P < 0.0001$; Table 3). *Monomorium floricola* and *Te. lanuginosum* were the most commonly found species in the small and large treatments, achieving numerical dominance on 12 and 11 treatments respectively, out of a total of 60 trials (3 treatments \times 20 replicates).

**Fig. 3** Body size index (BSI) of the first ants to discover food baits in each treatment (BSI = head width \times hind femur length). Treatments consisted of coral rubble filled containers and decreased in rugosity from small to bait card (no container). The BSI was calculated for each individual ant, values shown are mean \pm 1 SE. BSI's were significantly different across all treatments (χ^2 test $P < 0.0001$). The number of species that first discovered each treatment is shown in brackets. $n=23$

After 5 h, 19 out of 60 trials (31.6%) were dominated by a different species to the species that discovered it. This changeover occurred nine times in the small treatment, eight times in the large treatment, and least often on the bait card (twice). *Monomorium floricola* extirpated *A. gracilipes* from the bait card on both occasions. These replicates were close to each other in an area of high *M. floricola* abundance. *M. floricola* extirpated other ant species from small and large treatments five times each, and was extirpated by other species only once (small treatment). *A. gracilipes* replaced

Table 2 The number of times each ant species discovered the food baits in the central arena of each treatment

Species	Small	Medium	Large	Control	Bait card
<i>Anoplolepis gracilipes</i>	2	7	17	22	22
<i>Tetramorium lanuginosum</i>	12	9	4	1	0
<i>Tetramorium simillimum</i>	2	2	1	0	0
<i>Pheidole umbonata</i>	2	2	1	0	0
<i>Pheidole oceanica</i>	2	2	0	0	0
<i>Cardiocondyla nuda</i>	1	1	0	0	0
<i>Monomorium floricola</i>	1	0	0	0	0
<i>Paratrechina vaga</i>	1	0	0	0	0
<i>Pheidole sexspinosa</i>	0	0	0	0	1

Small, medium and large treatments consisted of coral rubble filled containers. The treatments decreased in rugosity from small to control (empty container) and bait card (no container). $n=23$

Table 3 The number of times each ant species numerically dominated food baits in each treatment after 5 h

Species	Small	Large	Bait card
<i>Anoplolepis gracilipes</i>	2	11	18
<i>Monomorium floricola</i>	5	5	2
<i>Tetramorium lanuginosum</i>	7	4	0
<i>Tetramorium simillimum</i>	3	0	0
<i>Pheidole umbonata</i>	3	0	0
<i>Pheidole sexspinosa</i>	1	0	0

The small and large treatments consisted of coral rubble filled containers; all treatments had centrally placed food baits. Treatments decreased in rugosity from small to bait card. Differences in species dominating each treatment were significant (*A. gracilipes* vs all other species pooled, $P < 0.0001$). At one small treatment both *Te. simillimum* and *A. gracilipes* were co-dominant (small $n=21$, large $n=20$).

other ant species in both the small and large treatments twice each.

Discussion

Perhaps the major challenge in community ecology is to understand factors that confer persistence and stability (May 1973; McCann et al. 1998). Our results highlight how habitat complexity facilitates resource use by a variety of species, and inhibits domination by one or two abundant species. Numerically dominant species are unable to access all habitats thereby providing other species with a refuge and an arena for resource acquisition. Habitat heterogeneity is likely to be a major factor facilitating coexistence in ant communities on Tokelau and elsewhere.

Allometric scaling of morphology

The SGH makes two broad predictions: (1) that across ant species leg length increases allometrically with body size (evolutionary); and (2) that ant species use the same landscape differently according to body size (ecological). However, these two components are distinct and it is possible to find support for the ecological component, even if the evolutionary prediction is unsupported by the data. This is the first study of the SGH that has not found a significant allometric relationship between leg length and body mass (Kaspari 1999; Parr 2003; Espadaler 2001). There are three possible and not mutually exclusive explanations for this

result: (1) the sample size was too small ($n=14$) and so weakened the statistical tests, (2) our sample set was biased towards small ants and so the relationship was not as apparent, and (3) body mass is a poor indicator of body size. However, if the primary selection pressure determining relative leg length and body size is the ability to walk over, compared to the ability to walk through, a rugose environment then the allometric relationship should hold regardless of sample size or size range of the samples used. The reason why only head length displayed an allometric relationship with leg length in this study is unclear, particularly given the strong correlations between all four indicators of body size in this analysis.

The ant species in this study showed considerable variation in leg length and body mass that cannot be explained by the SGH. For example, *An. graeffei* weighed more than three times as much as *Paratrechina longicornis* (Latreille), but its legs were shorter by 1 mm. The former species is a cryptic ambush predator, whereas *Pa. longicornis* is a competitively dominant, fast moving, omnivorous species (Lester and Tavite 2004). Other factors important to the success of ants, such as foraging strategy and behaviour are also likely to be influencing the evolution of leg length and body size. For example, both body size and leg morphology affect running speed (Zollikofer 1994), and body size is also related to colony size, tolerance to desiccation, and one-on-one fighting ability (McGlynn 1999), all of which are important in foraging and aggressive interactions. Our results highlight the amount of deviation from the SGH's prediction of allometry that must be considered in future tests.

The discovery–dominance trade-off

The ability to break the trade-off between exploitation and interference competitive abilities has been demonstrated for the Argentine ant, *Linepithema humile*, (Holway 1999; Human and Gordon 1996) and is thought to be driven by numerical dominance (Brightwell 2002; Holway 1999). Previous studies have documented the strong exploitative abilities of *A. gracilipes*, in terms of the ability to quickly discover and recruit to food baits (Lester and Tavite 2004), and the ability to quickly consume food resources (Lach 2005; Lester and Tavite 2004). The yellow crazy ant may be superior at exploitation competition in particular due to three main factors: (1) its long legs allow it to run quickly over a complex environment, (2) the consumption of plant and homopteran exudates allows heightened levels of foraging and recruitment activity (Davidson 1998), and (3) its distensible gaster enables it to hold

higher quantities of liquid foods than some other invasive ant species (Lach 2005). However, our results show that these potential advantages in planar environments are effectively disadvantages in rugose environments, allowing other ant species to access food resources in environmental interstices that would otherwise be dominated by the yellow crazy ant.

The interspecific fighting abilities of *A. gracilipes* have not, to the best of our knowledge, been empirically examined. The yellow crazy ant sprays formic acid when fighting and, although it engages in contact combat in intraspecific aggression assays, it does not appear to use these tactics during interspecific fights. Observations of interspecific fighting in the field, however, such as the displacement of *A. gracilipes* by *M. floricola* on several occasions in areas of high *M. floricola* density, suggest that, like the Argentine ant, numerical dominance is necessary for the yellow crazy ant to win battles with other abundant species. In addition, Morrison (1996) found that *A. gracilipes* on Moorea was superior at exploitation but not interference competition, suggesting that a superior fighting ability is not ubiquitous for the species.

Patterns of ant recruitment consistent with the trade-off between the abilities to discover or dominate food resources were strongest in the most rugose environment. Species turnover was highest in the small size-grain treatment; thus coexistence by the discovery-dominance trade-off might be a dominant force in the community of smaller, litter foraging ant species. The two most common species to discover and dominate the rugose treatments, *Te. lanuginosum* and *M. floricola*, displayed different foraging and recruitment strategies. *Te. lanuginosum* was often the first ant to discover baits in small treatments in both the 'discovery of food baits' and the 'recruitment to food baits' experiments, demonstrating strong exploitative competition abilities. Foragers were abundant on the ground and on trees, but recruitment was weak (maximum 35 at once). *M. floricola* was rarely the first ant to discover food baits, but displaced other ant species, particularly *Te. lanuginosum*, often enough to end up dominating 12 baits. *M. floricola* was usually in higher abundance at baits (maximum 105), tended to recruit quickly, and appeared to be a strong interference competitor. Therefore at least two mechanisms for coexistence appear to be operating simultaneously in these ant communities: (1) differential access to food resources based on habitat rugosity, between the yellow crazy ant and coexisting epigeic ant species, and (2) temporal turnover of species coexisting with the yellow crazy ant at food resources in rugose environments. In addition, different food preferences may also be promoting coex-

istence with *A. gracilipes* in these communities (Sarty 2005).

The results presented here support the findings of previous field studies on the SGH. Farji-Brener et al. (2004) found a clear size difference between those species that discovered food baits in rugose, compared to planar treatments. In addition, Yanoviak and Kaspari (2000) found leaf litter ants displayed a bimodal body size distribution while arboreal ants formed a unimodal distribution. This was attributed to there being two habitats in the leaf litter; one within and one on top of the leaf litter (rugose and planar respectively), while the surfaces of tree stems and leaves constitute a predominantly planar environment. The bimodal distribution of BSI's found in this study (*A. gracilipes* vs all other ant species) corresponds to that found by Yanoviak and Kaspari (2000) and is directly related to landscape use. Yellow crazy ants used the planar and low rugosity treatments, while virtually all the other ants represented in the graph used the higher rugosity treatments. Taken together, the results of these three studies provide strong support for the hypothesis that two distinct habitats exist within the forest floor landscape and that ant species segregate into these habitats based on body size.

The differential effects of habitat complexity on interspecific competition in ants have been largely ignored from experimental tests but are likely to have an important effect on the outcomes of such interactions (Lach 2005). We have shown that the normally predictable outcomes of interspecific competition are reversed in a more complex habitat. In addition, the SGH provides a mechanism for coexistence between a large and highly abundant invasive ant species and the smaller and less abundant species of the ant community, while the discovery-dominance trade-off may facilitate coexistence amongst the latter. The ant communities of Tokelau are recently assembled but are typical of ant communities throughout the Pacific. These results allow us to make more accurate predictions of the effects of *A. gracilipes*, and other similar invasive ant species, on recipient ant communities elsewhere in the world. Moreover, these results provide encouragement for the investigation of the SGH as a mechanism for coexistence in communities of other terrestrial, walking insects that inhabit a complex landscape, particularly in more diverse communities where a larger and more continuous body size range is represented.

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