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The ants of Tokelau

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Abstract This paper combines published and new collection records to provide a comprehensive list of ant species collected on Tokelau, a Pacific island nation with the world's smallest land area. Twenty-eight ant species have been recorded since the late 1950s, 10 in recent surveys, and the majority of which are tramp species. Known invasive species such as *Anoplolepis gracilipes*, *Monomorium pharaonis*, *Pheidole megacephala*, and *Tapinoma melanocephalum* are present but currently appear to have a limited distribution on two of the three atolls. There are no ant species endemic to Tokelau, but two Pacific endemics, and 11 Pacific natives; 26 listed ant species are present in Samoa, which is the likely point of origin for most of Tokelau's ant fauna. Pitfall trap collections from three visits between 2002 and 2005 highlight how different sampling intensities and locations alter the species accumulation rate and species richness and diversity estimates. The relationship between total ant species and land area of Pacific islands is linear, but combined with earlier records, this study reports more ant species from Tokelau than the analysis predicts. This study indicates the remote and small nation of Tokelau is as susceptible to invasive species as other larger, more populated, land masses in the Pacific.

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INTRODUCTION

Ants are a ubiquitous component of terrestrial invertebrate faunas on islands and mainlands (Hölldobler & Wilson 1990). However, current information on the ant fauna of Pacific islands is focused on the main island groups including Hawaii, Samoa, Tonga, Fiji, Marquesas, and the Society Islands (Wilson & Taylor 1967; Morrison 1997; Wetterer 2002; Wetterer & Vargo 2003; Ward & Wetterer 2006). Because most colonists have arrived from the west on prevailing ocean currents, islands in the western Pacific have rich native ant faunas. In contrast, those islands east of New Zealand, Rotuma, Samoa, and Tonga are thought to have few if any native ant species (Wilson & Taylor 1967). But the dramatic increase in movement of people and cargo throughout the Pacific has been coupled with an increase in the abundance of tramp ant species on frequently-visited islands (Wilson & Taylor 1967; Wetterer 1997; Wetterer 2002).

Tokelau lies directly north of Samoa, located at the hypothesised limit of native ants in the Pacific. It consists of three isolated low-lying oceanic atolls; Atafu, Nukunonu, and Fakaofo. Each atoll is home to around 500 people, who inhabit only one or two islets out of many in the group. Until recently, the ant fauna of Tokelau has been sparsely documented, but a recent population explosion of the invasive yellow crazy ant, *Anoplolepis gracilipes* (Smith), on two atolls led Lester & Tavite (2004) to suggest that their increase in abundance has changed the composition and dynamics of the ant fauna there. Similar to Hawaii, Tokelau's recorded ant fauna is comprised primarily of non-native species (Wilson & Taylor 1967; Dale 1959; Hinckley 1969; Lester & Tavite 2004). Ants have arrived on Tokelau via several pathways over the past decade, so it is not surprising Tokelau shares common ant species with

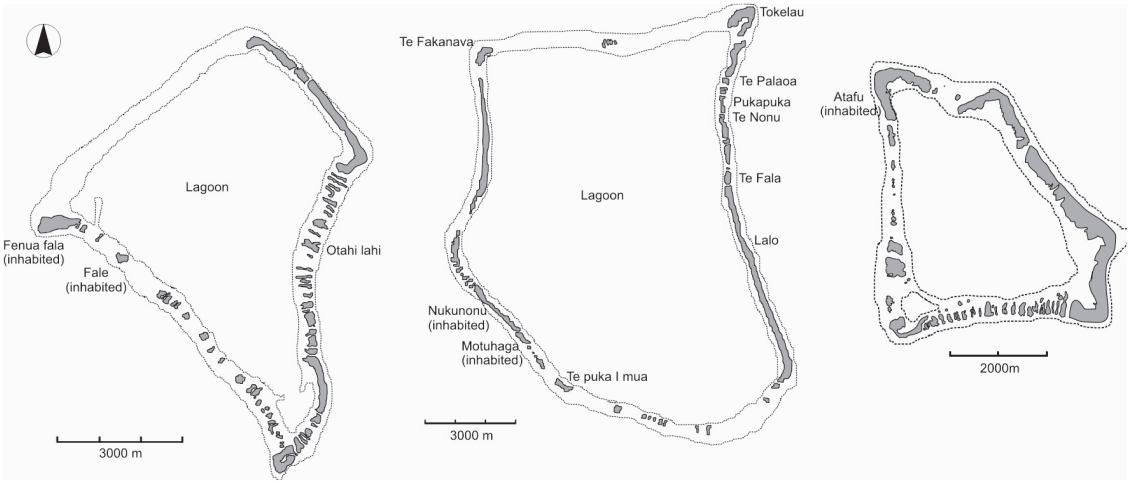

Fig. 1 Map of Fakaofo (southernmost), Nukunonu (middle), and Atafu (northernmost) Atolls, which comprise the three-atoll system of Tokelau. Each atoll is separated from the next by c. 60–90 km. Fakaofo lies 493 km north of Samoa in the Pacific Ocean. Different scales required by space constraints.

these countries. However, the major pathway of biological introduction in recent years has been Samoa, whose ant fauna has been relatively well studied (Wetterer & Vargo 2003).

This paper examines the ant fauna of Tokelau. We augment published records with records of ant species collected in pitfall traps, at food baits and during hand collections on Nukunonu Atoll, and limited sampling on Fakaofo and Atafu Atolls during visits to Tokelau in November 2002 (Atafu Atoll only), November–December 2004 (both Nukunonu and Fakaofo Atolls) and June–July 2005 (Nukunonu Atoll only). First, we aim to provide a comprehensive list of all ant species recorded to date. Second, we examine how three pitfall trap collections (2002–05) differ in their rate of species accumulation and subsequent overall species richness and diversity estimates, and how using only one set of results would have changed the outcome of a faunal list. Finally, we include Tokelau in an analysis of the ant species-area relationship for Pacific islands.

METHODS AND MATERIALS

Tokelau is located 483 km north of Samoa (c. 9°45′S, 171°35′W), where each of the three low-lying coral atolls are composed of between 31 and 58 islets, which combined make up 12 km^2 of terrestrial habitat (Fig. 1). The atolls lie in the south-east trade wind belt and enjoy a moist tropical climate year round (mean annual temperature 28°C; mean annual rainfall >3000 mm; Mueller-Dombois & Fosberg 1998), therefore, collections were considered not to be season-sensitive. The islets of each atoll are comprised of coral rubble of varying size with poorly developed soil overlying coral reef rock. They are low-lying (≤5 m a.s.l.) and narrow, thus are exposed to salt-laden south-easterly winds. The vegetation is low in diversity and typical of small Pacific atolls (Mueller-Dombois & Fosberg 1998). The forest of the inner island is dominated by the coconut palm (*Cocos nucifera*) with other common tropical trees reaching the canopy (*Cordia subcordata*, *Pisonia grandis*, *Guettarda speciosa*, *Pandanus* spp.). The bird's nest fern (*Asplenium nidus*) constitutes the majority of the groundcover layer. The vegetation closer to the beach tends to be denser and more diverse (e.g., *Scaevola taccada*, *Morinda citrifolia*) with little or no soil (Parham 1971). Some plants (e.g., *C. nucifera*, *M. citrifolia*, and *A. nidus*) produce floral/extra floral nectar and support small populations of honeydew-producing hemipteran insects (Homoptera).

Data compilation

No previous surveys of Tokelau have looked specifically at the ant fauna. Here we supplement historic records (Dale 1959; Hinckley 1969; Wilson & Taylor 1967) with current collections to provide an up to date list of the ant species collected on Tokelau. The data used in this study consists of records from both

published (Lester & Tavite 2004) and unpublished collections between 2002 and 2005 by three different authors using a variety of collection techniques. Previous authors (Dale 1959; Hinckley 1969) surveyed a variety of arthropods using opportunistic hand collection techniques, thus records of ant species present by these authors are not comprehensive, but are nonetheless presented in Table 1.

Data on the origin and status (extent of spread throughout Pacific region) of each species follow Wetterer & Vargo (2003). Species considered widespread are present in both eastern and western Polynesia and in a total of at least eight countries.

Ant collection methods

We used three different methods to collect ant specimens on Tokelau; pitfall trapping, attraction to food baits and hand collecting. Pitfall traps were placed haphazardly in groups of three to five in both urban and forested areas across both Fakaofo and Nukunonu Atolls. Two islands on Fakaofo Atoll and nine islands on Nukunonu were surveyed over the two visits. The pitfall traps were plastic cups 9 cm tall, 7.5 cm diameter at the top and tapered to 5 cm diameter at the bottom. The cups were placed flush with the ground surface, one-third filled with Gault's solution, an insect killing agent and preservative (Walker & Crosby 1988), and left out for 24 h due to the speed at which they can fill up with *A. gracilipes* (Lester & Tavite 2004).

Food baits were used in two ways; first, single baits of tinned tuna in oil on 10 × 10 cm white laminated cards (bait cards hereafter) were haphazardly placed and left out for at least 2 h on the inhabited islands of all atolls. Second, bait stations combining three types of food bait (tinned tuna in oil, apricot jam, and peanut butter on one bait card each) were haphazardly placed in two 15 × 15 m plots on eight islands across both Nukunonu and Fakaofo atolls. Within each plot, we placed the three bait cards in groups of four (bait stations hereafter); each bait type was c. 15 cm apart, while each set of three baits was at least 2.5 m apart within the plot. The bait stations were laid out for 1 h and individuals of each different ant species to visit each bait type were collected for identification.

Hand collections were a mix of extensive searches and opportunistic collections on the ground and vegetation. Our hand collections spanned nine islands on Nukunonu Atoll, three islands on Fakaofo Atoll and one on Atafu Atoll. Five different people performed the collections over the visits. All ant specimens were preserved in ethanol (c. 70%) and identified to species under a binocular microscope by the authors. Ants were identified using the keys of Wilson & Taylor (1967) and Bolton (1977). Nomenclature, where modified since Wilson & Taylor (1967), follows Agosti & Johnson (2005), except for *Monomorium liliuokalanii*, which is used under suggestion by Bolton (1987), that all *M. monomorium* specimens he examined from Oceania were actually *M. liliuokalanii*. This is likely true for Tokelau.

Species richness, diversity and accumulation on Nukunonu Atoll

Sampling effort and method can influence outcomes of species lists such as these (Agosti et al. 2000). We estimated total species richness on three separate sampling occasions (2002–05) for Nukunonu Atoll using the Michaelis-Menten species richness estimators in *EstimateS* (Colwell 2005) to compare how using different datasets could influence our resultant list. In addition, alpha species diversity (that of the entire atoll), using the same data combined, was calculated using the Shannon index by *EstimateS*. Species accumulation curves are presented as sampled-based rarefaction curves, where the curves were computed by repeated re-sampling of all pooled samples (individual pitfall traps) on Nukunonu Atoll only on the three sampling occasions. The collection conducted in 2002 was conducted on one island only (Lester & Tavite 2004), while pitfall trapping in 2004 and 2005 were across six and nine islands respectively. All species richness, diversity, and accumulation analysis was carried out using *EstimateS* (Colwell 2005). The patchiness parameter in *EstimateS* was set to 0.8 to highlight the influence of nests in the spatial aggregation of samples (Chazdon et al. 1998).

We analysed the relationship between the area of an island and (a) the number of Pacific native + endemic species it supports, and (b) the total number of species recorded on that island. Data for nine Pacific islands were taken from Ward & Wetterer (2006). A log-linear regression was performed on the number of taxonomic divisions (ant species or subspecies) versus the terrestrial area of the island.

RESULTS

Recent collections (2002–05) sampled 10 species not previously recorded on Tokelau, bringing the total number of ant species collected to 28 for the three atolls combined (Table 1). Thirteen species are considered exotic to the Pacific, while 11 are native to

the region. Where the origin of the species is known (23/28), 15 species are thought to have originated in Asia, while only two species, *Tetramorium tonganum* and *Ponera swezyi*, are regional endemics. Of the 13 confirmed exotic species, three have been introduced from Africa. Twenty-six of the 28 species are widespread throughout the Pacific region.

During collections for this study, 12 ant species were collected using three methods: pitfall trapping, food baits, and hand collections. Six species were collected during hand collections only, and three species were collected only in pitfall traps, however, no ant species was collected exclusively from food baits. Hand collecting yielded a total of 25 species;

Table 1 Compiled data on the presence and distribution of ant species on Tokelau showing species origin, present status in the Pacific, method of specimen collection, presence on each atoll and the reference from which the record is derived. Nomenclature follows Agosti & Johnson (2005). –, data unknown.

		Status[b]				Collection method[c]			Atolls[d]			
Species	Origin[a]	W	N	E	X	P	B	H	A	F	N	References[e]
Subfamily Dolichoderinae												
Iridomyrmex anceps (Roger)	–	W				P		H			N	5, 7
Tapinoma melanocephalum (Fab.)	Asia	W			X	P	B	H	A	F	N	3, 4, 5, 6, 7
Tapinoma minutum Mayr*	Asia	W	N			P		H	A		N	4, 7
Technomyrmex albipes (Smith)	Asia	W	N					H		F		1
Subfamily Formicinae												
Anoplolepis gracilipes (Smith)	Asia/Africa	W			X	P	B	H		F	N	3, 5, 6, 7
Camponotus chloroticus Emery	Asia	W	N					H			N	3, 7
Paratrechina bourbonica (Forel)	Asia	W			X	P	B	H			N	3, 5, 7
Paratrechina longicornis (Latr.)	Asia	W			X	P	B	H	A	F	N	1, 4, 5, 6, 7
Paratrechina vaga (Forel)	Asia	W			X	P	B	H	A	F	N	1, 4, 5, 6, 7
Subfamily Myrmicinae												
Cardiocondyla nuda (Mayr)*	Africa	W			X	P		H			N	7
Monomorium floricola (Jerdon)	Asia	W			X	P	B	H		F	N	1, 5, 6, 7
Monomorium liliuokalanii Forel*	–	W	N					H			N	7
Monomorium pharaonis (Linn.)*	Asia	W			X			H	A		N	4, 7
Pheidole fervens Smith	Asia	W			X	P		H		F	N	1, 7
Pheidole megacephala (Fab.)	Africa	W			X			H	A		N	2, 3, 4
Pheidole oceanica Mayr	PNG	W	N			P	B	H		F	N	1, 5, 6, 7
Pheidole sexspinosa Mayr*	PNG	W	N			P	B	H		F	N	6, 7
Pheidole umbonata Mayr	PNG	W	N			P	B	H		F	N	5, 6, 7
Rogeria stigmatica Emery	–	W	N			P					N	5, 6, 7
Strumigenys godeffroyi Mayr*	Asia	W	N			P		H			N	6, 7
Strumigenys sp. 1*				–		P					N	7
Tetramorium bicarinatum (Nyl.)	–	W			X	P	B	H	A	F	N	1, 4, 5, 6, 7
Tetramorium lanuginosum Mayr	Asia	W			X	P	B	H			N	5, 6, 7
Tetramorium simillimum (Smith)	Africa	W			X	P		H	A	F	N	1, 4, 5, 6, 7
Tetramorium tonganum Mayr*	Pacific	W		E		P	B	H			N	6, 7
Subfamily Ponerinae												
Anochetus graeffei Mayr*	Asia	W	N			P		H			N	6, 7
Odontomachus simillimus Smith	Asia	W	N					H		F	N	3
Ponera swezeyi (Wheeler)*	Pacific			E		P				F		6

*Denotes collections from 2002 to 2005.

[a]Africa, Pacific, Papua New Guinea (PNG)—after Wetterer & Vargo (2003).

[b]W, widespread in Pacific region; N, native to Pacific; E, endemic to Pacific; X, exotic to Pacific—after Wetterer & Vargo (2003).

[c]P, pitfall traps; B, bait; H, hand collected. See Methods for further details.

[d]Presence of species on the three atolls of Tokelau: A, Atafu Atoll; F, Fakaofo Atoll; N, Nukunonu Atoll.

[e]References from which records came: 1, Wilson & Taylor (1967); 2, Dale (1959); 3, Hinckley (1969); 4, Lester (unpubl. data); 5. Lester & Tavite (2004); 6, Sarty (2005); 7, this study.

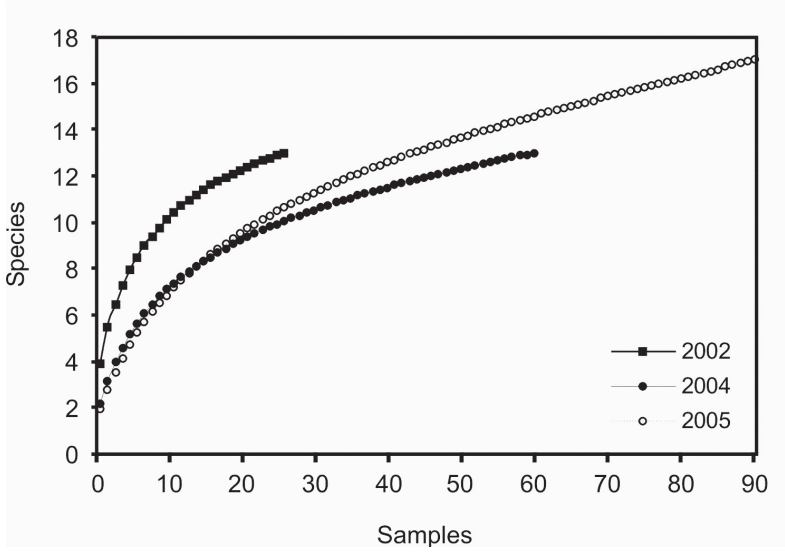

Fig. 2 Sample-based rarefaction curves for pitfall trap collections over three visits to Nukunonu Atoll. In 2002 Nukunonu Island and Motuhaga were sampled with 26 pitfall traps placed randomly without examination for nests (Lester & Tavite 2004). In 2004, six islands were sampled with 10 pitfall traps placed in two plots in the interior of each island. Sampling in 2005 followed the same protocol as in 2004, but across nine islands on Nukunonu Atoll.

pitfall trapping detected 22 species, while food baits resulted in only 12 records.

Three earlier records are unverified by recent collections. Wilson & Taylor (1967) documented *Technomyrmex albipes* on Fakaofo Atoll, a species that was not detected in any collections between 2002–05. Fakaofo was not widely surveyed, however, and this species may have avoided detection or been locally absent where collections were made. *Odontomachus simillimus* was recorded by Hinckley (1969) but not recorded in the recent surveys. Because *O. simillimus* is a conspicuous species, it is unlikely that it avoided detection, and it may now be absent from Tokelau. *Pheidole megacephala* was found on Nukunonu Atoll by both Dale (1959) and Hinckley (1969), but was only found on Atafu in recent collections. As Nukunonu is the most intensively surveyed atoll from the recent collections, it is likely that this species is now rare or absent on Nukunonu Atoll.

The species accumulation curves for three separate pitfall trap collections on Nukunonu Atoll only show how the rate of species accumulation and total species richness estimation changes with time and sampling intensity (Fig. 2), and how using one sampling event might have changed the results of this list. Sampling in 2002 was concentrated on two inhabited islands (Nukunonu Island and Motuhaga). The estimated total species richness from this sampling period was 12.3, compared to 13.3 in 2004 from sampling less intensively across six islands, and 17.2 sampling at the same intensity as in 2004 but across nine islands. However, species diversity was approximately equal in all sampling years (Shannon index 0.28, 0.31, and 0.29 in 2002–05, respectively).

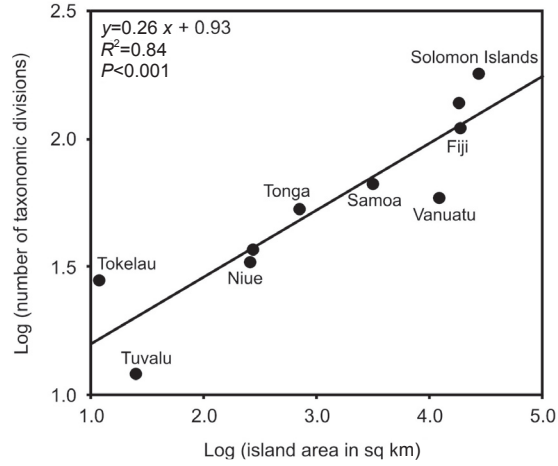

Fig. 3 Log-linear regression analysis of total ant taxonomic divisions versus area relationship on Pacific islands. Data taken from Ward & Wetterer (2006).

With the inclusion of Tokelau in the analysis, there was a positive log-linear relationship between the number of native and endemic ant species (taxonomic divisions native and endemic to the Pacific) on an island and its land area ($y = 0.36x + 0.41$, $R^2 = 0.84$, $P < 0.001$). Similarly, there was a good correlation between the total number of ant taxonomic divisions supported by an island and its area ($y = 0.26x + 0.93$, $R^2 = 0.83$, $P < 0.001$; Fig. 3).

DISCUSSION

Twenty-eight ant species have been recorded from Tokelau as a result of our work and that of previous studies, 13 of them considered either endemic (*Tetramorium tonganum* and *Ponera swezyi*) or native to the Pacific region (Wilson & Taylor 1967; Dale 1959; Hinckley 1969; Lester & Tavite 2004). Twenty-six species are widespread throughout the Pacific and most are considered "tramp" species, closely associated with human movement (Passera 1994). Twenty-six species recorded on Tokelau are also present in Samoa (Wetterer & Vargo 2003), which is the nearest and most frequently used port used for transportation of cargo and people to the Tokelau atolls. That these boats are likely to be the primary method for ant introductions was evidenced by the observation of individuals of *Camponotus* spp. on the deck of one of the boats by Hinckley (1969), and more recently, nests of three species found on fresh produce in 2002 (Lester & Tavite 2004). Considering the logistical difficulties of fumigation or other treatment at Tokelau ports, quarantine officials have become particularly scrupulous when checking cargo from vessels from Samoa. Of concern is the potential for invasion of the little red fire ant *Wasmannia auropunctata* (Roger), established in several Pacific island groups including New Caledonia (Jourdan 1997; Le Breton et al. 2005) and Tahiti (Le Breton 2005).

Within Tokelau, despite the unequal sampling intensities, differences in the ant distribution between the three atolls are apparent. Common, and widely distributed tramp species such as *Paratrechina longicornis* and *Tapinoma melanocephalum* are present on all three atolls. However, only two of the three atolls currently have the yellow crazy ant, *Anoplolepis gracilipes*, which is considered one of the six most widespread, abundant, and damaging invasive ant species worldwide (Holway et al. 2002), and included in the list of 100 of the world's worst invasive alien species (Lowe et al. 2000). Its presence on Tokelau was recorded in 1934 (Wilson & Taylor 1967), and it appears to be the only ant species that has increased in abundance and become an environmental and social pest on Tokelau (Lester & Tavite 2004). Where it is abundant, it forms associations with honeydew-producing scale insects that can destroy fruit crops, irritates chickens and pigs, and even drives them away from their dwellings; it runs over food and people, and threatens the outdoor Polynesian lifestyle. Another of the six most invasive species is the big headed ant *Pheidole megacephala*, though our records indicate that this also has a limited distribution to two of the three atolls. Why the ant faunas have not homogenised between atolls within Tokelau remains unclear. These three atolls are spatially close, with similar climate, soil and vegetation characteristics (Parham 1971). However, propagule pressure is known to influence the outcome of introductions of plants and animals (Lonsdale et al. 1999; Hee et al. 2000; Leung et al. 2004; Lester 2005; Memmott et al. 2005), and differences in introduction rates of ants to the different atolls are likely to influence establishment success there. It is also likely that existing ant communities on each island will influence the ant faunal composition and may even restrict the establishment of new species. For example, a significant negative relationship was found between increasing *A. gracilipes* densities and species diversity on Nukunonu Atoll (Lester & Tavite 2004).

The observed differences in ant fauna between atolls may also be attributed to sampling effects in this study, as indeed we have shown how sampling effects on Nukunonu would have changed results should only one sampling event have been used. The most intensive sampling in our work has been on Nukunonu Atoll. Similarly, Hinckley (1969) spent 3–4 days on Atafu and Fakaofo, but 36 days on Nukunonu. As a result 26 of the 28 species recorded on Tokelau have been at one time on Nukunonu Atoll. Our estimates put the current species richness of Nukunonu at a total of c. 17 species. Some species, such as *P. megacephala*, that were previously recorded on Nukunonu are now likely absent. On other less intensively sampled atolls, species in addition to those listed here are likely to be discovered with more thorough searching. We are, however, confident of results such as *A. gracilipes* being absent from Atafu. *Anoplolepis gracilipes* is a large, abundant and readily observable species likely to have been noted by residents or by collectors.

Should further sampling be conducted on Tokelau, results from Table 1 indicate that a combination of sampling methods will most likely yield the highest species richness, although no species was caught exclusively at food baits. Species such as *Technomyrmex albipes* are primarily arboreal and are not often observed in pitfall traps (Lester & Keall 2005). Similarly, *Camponotus chloroticus* was only ever observed in Tokelau foraging aboreally. Sampling techniques such as Winkler extraction are suggested to be more effective than pitfall traps for

ant sampling (Delabie et al. 2000), and it is possible that this method would result in higher richness and diversity on Tokelau. However, the combination of hand collecting, pitfall trapping and food baits used in this study is likely to be effective in ant faunal assessments.

Both the number of Pacific native and endemic ant species, and the total number of ant species on Tokelau reported here are higher than expected, based on Ward & Wetterer's (2006) native and endemic species-area regression equation (four species). This is most likely due to the intensive sampling effort that occurred over the 3-year period, but also due to regular human trafficking of goods to and from Tokelau during the last decade. Considering its isolation, small size and location at the hypothesised limit of native ants in the Pacific, human-mediated transport of tramp ants to Tokelau constitutes the most likely explanation for the high number of ant species recorded. The inclusion of this additional point in the analysis allows predictions to be made for islands with small land areas, but also reflects the intensive searching that can be carried out on a small land area with limited habitat diversity on the Tokelau atolls, and indeed low-lying oceanic atolls elsewhere (Simberloff 1974). The islets on each atoll are no greater than 5 m in elevation and are all less than 200 m wide. While there are some changes in vegetation across the width of the islands, associated with the lagoon or ocean side of the islet, it is our experience that no individual ant species is restricted to any particular vegetation type.

Studies documenting faunal compositions are useful for several purposes. These lists provide biodiversity managers with information regarding the conservation status of different areas. No endemic or endangered ant species have been observed on Tokelau, but our data are indirectly useful for other taxa. For example, the Tokelau atolls are used by a range of migratory birds (Wodzicki & Laird 1970). *Anoplolepis gracilipes* is known to negatively influence bird populations (Feare 1999) and hence vigilance on Atafu in searching for this species may be of international importance. Such faunal lists as ours will also aid in "before and after" comparison studies, as a result of invasion or habitat change such as by global warming. The invasion of *A. gracilipes* on Nukunonu and Fakaofo Atolls is currently considered Tokelau's primary environmental problem. In spite of its small size and remote nature, Tokelau is as susceptible to invasion by ants as other larger nations in the Pacific.

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