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ANTS OF THE NATIONAL PARK OF AMERICAN SAMOA

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ABSTRACT

American Samoa makes up the eastern end of the Samoan Archipelago. On the islands of Tutuila, Ta'ū and Ofu, the National Park of American Samoa (NPSA) protects about 4,000 ha of coastal, mid-slope and ridge-top forest. While the ant fauna of the Samoan Archipelago is considered relatively well documented, much of NPSA has never been surveyed for ants, leaving the fauna and its distribution poorly known. To address this shortfall, we systematically surveyed ants within the Tutuila and Ta'ū units of NPSA using standard methods (hand collecting, litter sifting, and baits) at 39 sites within six vegetation types ranging from 8 to 945 m elevation. Forty-four ant species were identified, 19 of which are exotic to the Samoan Archipelago. Two notoriously aggressive species, *Anoplolepis gracilipes* and *Pheidole megacephala* were detected at two and seven sites, respectively. Both of these species largely excluded all other ants from bait, although their impact on ant community composition is unclear. A suite of habitat variables measured at each site was assessed to explain park-wide ant distributions. Of eight variables evaluated, only elevation was associated with ant community structure, as the ratio of native to exotic ant species increased significantly with elevation on Tutuila. Our survey documented two species not previously reported from American Samoa. *Strumigenys eggersi*, detected at 12 sites, appears to be a new immigrant to the Pacific Basin. A species of *Pheidole* was collected that likely represents an undescribed species. *Solenopsis geminata*, an aggressive species first reported on Tutuila in 2002, was not detected during our survey.

INTRODUCTION

Ants are important elements of nearly all terrestrial faunas and occupy habitats ranging from wet tropical forest to arctic tundra. In the tropical forest of Amazonia, ant abundance can reach 8 million individuals per hectare and their biomass can comprise as much as one-third of the total animal biomass (Hölldobler and Wilson 1990). Worldwide, ants are represented by nearly 15,000 species and subspecies (Bolten *et al.* 2007). Ant communities on oceanic islands are generally less diverse than they are in similar habitats on continents, and island assemblages are often dominated by exotic species (Wilson and Taylor 1967). In the western Pacific Ocean, ant species richness is largely proportional to island size (Ward and Wetterer 2006) although field studies are continuing to identify new species (Sarnat and Moreau 2011, Lucky and Sarnat 2010). Ants of the Samoan Archipelago are considered well known compared to other Pacific island groups (Wilson and Taylor 1967, Kami and Miller 1998, Wetterer and Vargo 2003). Overall, more than 40 species are considered native to the archipelago, with 12 species thought to be endemic. Unfortunately, an additional 26 exotic species have been recorded, several of which are considered invasive and potentially damaging to the native environment.

Invasive ants are among the greatest threats to ecosystem integrity in much of the Pacific Basin, including the Samoan Archipelago (Holway *et al.* 2002, Wetterer and Vargo 2003, Wetterer 2007). The aggressive nature of many of these species, combined with their ability to live in high densities over extensive areas, often results in large-scale reductions in biodiversity and disruption of ecosystem processes (e.g., Porter and Savignano 1990, O'Dowd *et al.* 2003). The relatively small size and fragile nature of many island ecosystems makes them particularly vulnerable to the effects of invasive ants. The ecological impact of many invasive ants found in the Samoan Archipelago is poorly understood, but several species are known to have profound

negative impacts in other habitats where they have invaded. The most damaging species are the big-headed ant (*Pheidole megacephala*) and yellow crazy ant (*Anoplolepis gracilipes*). Each of these species has been documented to reduce abundances and diversity of native arthropods, including other ants (big-headed ant: Haskins and Haskins 1965, Heterick 1997, Gillespie and Reimer 1993, Hoffman *et al.* 1999, LaPolla *et al.* 2000; yellow crazy ant: Haines *et al.* 1994, Green *et al.* 1999). Less studied, the tropical fire ant (*Solenopsis geminata*) also appears to be a threat to native arthropod communities as well as ground-nesting seabirds and turtles (Wetterer and O'Hara 2002, Plentovich *et al.* 2009). Identifying the extent to which these species have penetrated native habitat is an important first step toward understanding the threat they pose to forest ecosystems in the Samoan Archipelago.

The most ecologically intact and important habitat in American Samoa is protected by the National Park of American Samoa (NPSA). The park encompasses numerous offshore islets and over 40 km² of habitat on the islands of Tutuila, Ta'ū and Ofu, which preserves significant stands of mixed-species, paleotropical rainforest. Compared to many other lowland forests in the Pacific Basin, habitats in NPSA are relatively healthy and support 36 resident species of land and seabirds, 3 native bats and 12 native reptiles (Craig 2009). However, alien species are still a common feature of forest communities and are considered the primary threat to the park. Therefore, management priorities include preventing establishment of additional species and controlling or eradicating those that are already present. While most of the emphasis has been on identifying invasive plants, invasive ants are recognized as a threat of high priority (Peter Craig, NPSA, personal communication).

The primary objective of this study was to provide, for the first time, an extensive survey of the ant fauna found in NPSA. Our strategy was to sample across all habitats within the park to identify distributions of native and exotic species and to observe potential interactions among species. We also aimed to determine whether key characteristics of park habitats could be used to explain ant distributions and faunal assemblages. Finally, we focused on identifying how the most aggressive exotic species interacted with native and other exotic species to better enable NPSA managers to understand the threat these species pose to park resources.

METHODS

Study Area

The U.S. Territory of American Samoa is located approximately 3,700 km southwest of Hawai'i, and along with the independent nation of Samoa, comprises the Samoan Archipelago (Figure 1). Overall, American Samoa occupies about 200 km² of land, with the island of Tutuila comprising 53% of the total, Ta'ū 18%, and the adjacent islands of Ofu and Olosega together comprising 13%. Collectively, the islands of Ta'ū, Ofu and Olosega make up the Manu'a group and are located about 95 km east of Tutuila. The climate of American Samoa is hot, humid and rainy year-round, with daily temperatures averaging about 21 °C and annual rainfall totaling > 300 cm (Craig 2009). The topography is generally steep with the few existing foot trails largely limited to ridge tops and valleys. The highest point in the territory is the summit of Mt. Lata on Ta'ū (966 m) and the highest point on Tutuila is Mt. Matafao (653 m).

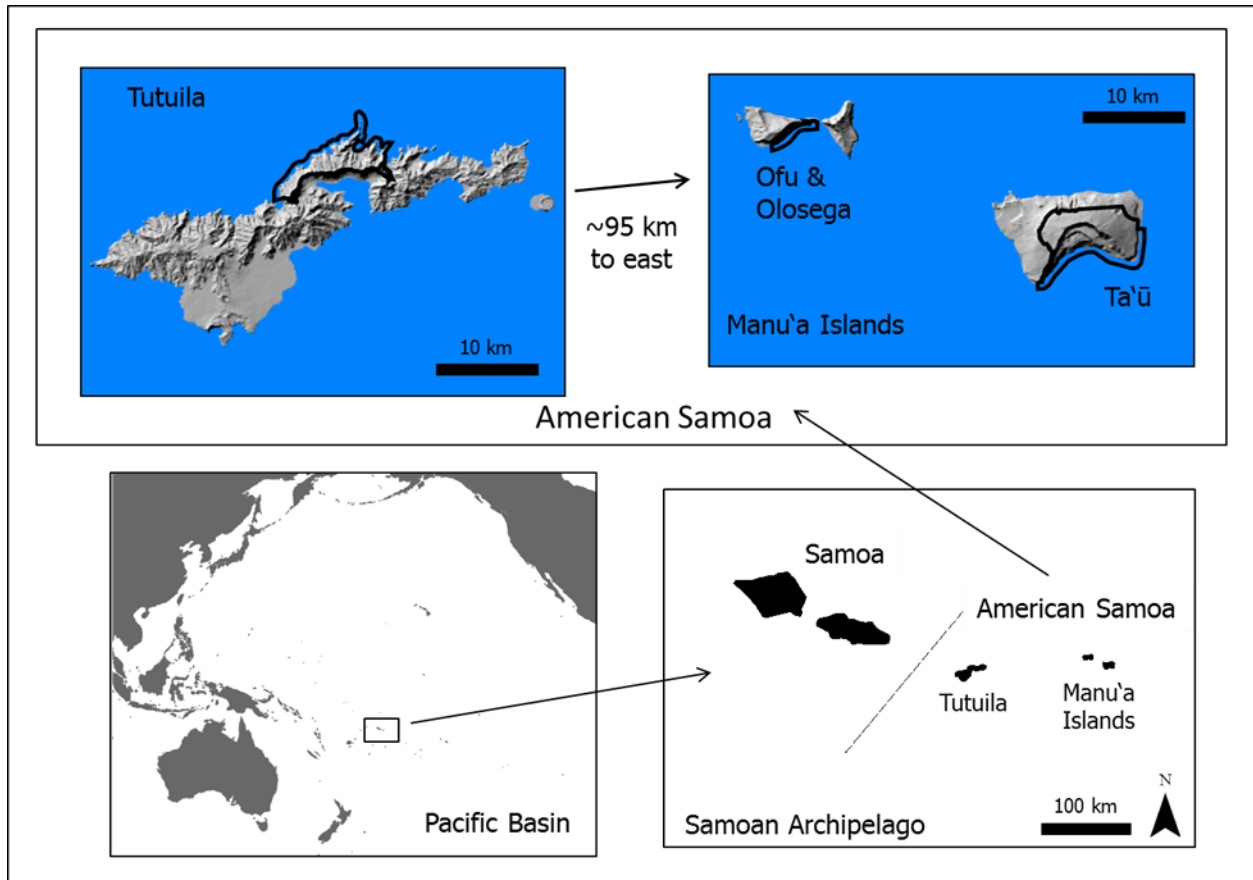


Figure 1. American Samoa comprises the easternmost islands of the Samoan Archipelago and consists of Tutuila, Ofu, Olosega and Ta'u. The National Park of American Samoa is outlined in black in the top two images.

Surveys for ants were conducted at a subset of sites established by the National Park Service Vegetation and Mapping Program (Green et al. 2014) and were chosen to represent a variety of habitats and elevations. During 14–27 July and 4–12 December 2010, and 20–31 July 2011, we surveyed ants at 22 of these sites on Tutuila and 17 sites on Ta'u. Due to the difficulty accessing Ofu, we did not include that section of the park during our systematic survey, although we did conduct a brief general survey of the small, coastal section of the park. Each study site occupied an area approximately 1,256 m² (20-m radius) around the gps point identifying the site.

A geographic information system vegetation base layer was used to categorize each of the 39 survey sites into discrete habitat types (U.S. Forest Service 2014). The classification scheme was based on Whistler (2002) and summarized in Liu *et al.* (2011). Using this system, vegetation types that we surveyed for ants included littoral strand (9 sites), Rhus secondary forest (15 sites), montane scrub (1 site), rainforest (8 sites), secondary scrub (2 sites) and summit scrub (4 sites; Figure 2). Sites ranged from 8 to 945 m elevation.

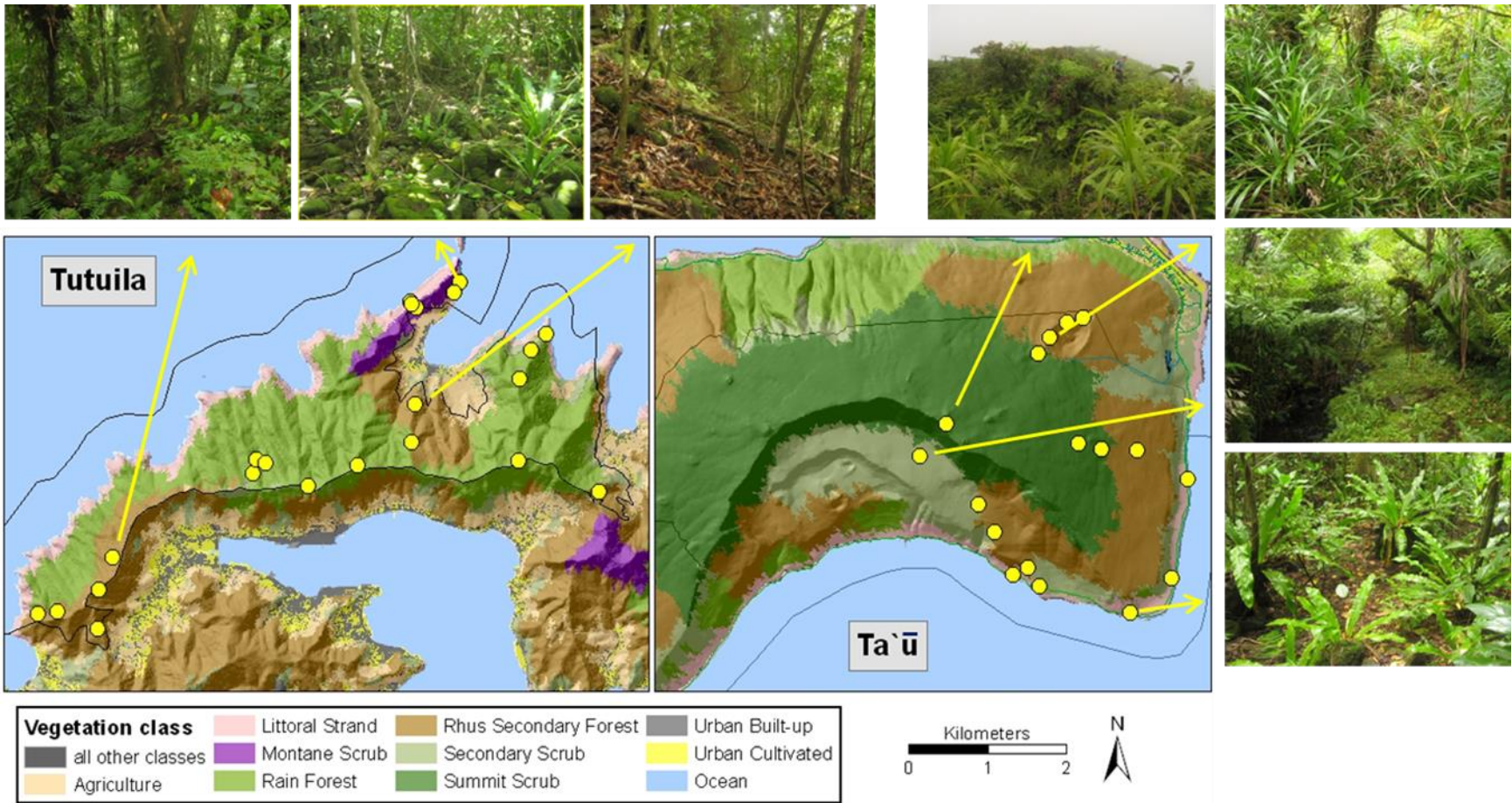


Figure 2. Location of 39 sites surveyed for ants in several vegetation types on the Tutuila and Ta'u units of National Park of American Samoa. The photographs show typical habitat structure in several vegetation types and were taken at site centers. The black polygon on each map represents the park boundary.

Collection Methods

Ants were systematically surveyed on each site using three standard methods: baiting, hand searching, and litter sifting (Figure 3). Baiting is effective at collecting species that recruit most aggressively to ephemeral food resources and is commonly used to compare competitive dominance among ant species (Lester *et al.* 2009, Cerdá *et al.* 2012). Hand searching is an efficient method of detecting a wide range of species that are either active on foliage and ground surfaces or that live primarily in wood or under rocks. Litter sifting primarily targets small, cryptic species that live on the forest floor and are often undetected by other methods. Pitfall traps also are frequently used to survey ant communities, but they were not used in this study due to the steep terrain and regular heavy rain that would have flooded the traps and rendered them ineffective.

Bait. Each bait consisted of approximately 5 g of canned tuna (mixed in its oil) placed on a 5 x 7 cm paper card in an open plastic petri dish nestled within the leaf litter on the ground. Baits were placed in all four quadrants of the site, each 20 m distant from the site center. After 60 minutes, the petri dishes containing ants and remaining bait were capped with their lids and sealed with rubber bands. The petri dishes were then frozen, and ants were subsequently identified and counted in the lab.

Hand searching. At each site, ants were located by searching over the foliage of plants, on bark surfaces, within decomposing branches and logs, and under rocks for one person-hour (generally 2 people for 0.5 hour each). Ants were collected using an aspirator.

Litter sifting. The collection of ants within leaf litter was guided using a 0.25 m² pvc sampling frame that we haphazardly tossed onto eight sample points within each site. At each sample point, all leaf litter and small twigs within the frame were collected and placed into a sifting bag that was used to separate ants from the coarse debris, thereby reducing the volume of the sample (Bestelmeyer *et al.* 2000). The top portion of the sifting bag contained a barrier of 1.3 x 1.3 cm hardware mesh onto which the litter was placed; when the bag was vigorously shaken, ants and small fragments of litter passed through the mesh and into a 3.8-l zip lock bag secured to the bottom of the sifting bag. In the lab, this residue was placed into Winkler sacks, or in a few instances when Winkler sacks were unavailable, Berlese funnels (Figure 3; Bestelmeyer *et al.* 2000). Ants exiting the litter residue were collected into vials containing a mixture of propylene glycol and water (30:70) for 24–48 hours or until the litter became dry to the touch. Ants species were identified using keys in Wilson and Taylor (1967) and the Pacific Invasive Ant key (Sarnat 2008) and by comparison to voucher material held within the collection at the USDA Entomology Lab at American Samoa Community College (ASCC). The provenance (native or non-native status) of each species was based on Wetterer and Vargo (2003) and Wilson and Taylor (1967). *Nylanderia bourbonica* and *N. vaga* were difficult to differentiate; our determinations all resulted in *N. vaga*, but *N. bourbonica* also may have existed in the samples.

Data Analysis

We did not compare overall abundances of ants among species or sites because the effectiveness of the methods used to collect ants varied among species to unknown degrees. Therefore, we limited our community-wide analysis to species richness and the presence or absence of ants at each site. However, we did measure ant abundance at bait cards to



Figure 3. Techniques used to survey ants included tuna bait (4 baits/site; A), hand searching (one person-hour; B) and litter sifting (eight 0.25 m² samples; C). Ants were extracted from litter in the lab using Winkler sacks and Berlese funnels (D; right and left, respectively).

determine relative levels of aggression among species and their ability to dominate food resources. Values of means (\pm SEM) are provided where appropriate.

Habitat analysis

Several environmental variables were used to evaluate whether location and habitat structure could explain ant distributions. Broad-scale variables included island and habitat type, while site-specific variables included elevation, plant species richness, and percent cover of the forest canopy, rocks, litter, coarse woody debris, and vegetation measured at ground level. Response variables were total ant species richness and the ratio of native ant species to exotic ant species. The ratio of native to exotic ants provided an index of exotic ant invasion.

The habitat type for each site was determined using Liu *et al.* (2011) while habitat variables were obtained from the National Park Service Vegetation and Mapping Program (Green *et al.* 2014). Site-specific data were unavailable for two sites on Ta'ū and one site on Tutuila; therefore, those sites were not included in some of the analyses.

Effect of habitat

Principle components analysis (PCA) was used to evaluate relationships among the study sites and the six site-specific variables measured at each site. A product of this analysis, a two-

dimensional biplot, was used to visualize the relationships among the sites and the habitat variables. The biplot axes represent the two principal components that explained the greatest proportion of the variability found in the dataset. Distinct patterns among sites relative to the habitat variables (e.g., some sites closely clustered near variables) suggest the existence of a significant relationship between sites and habitat variables and warrant subsequent post-hoc analyses of how the ant assemblages were influenced by the habitat variables. In contrast, dispersed or random patterns among sites suggest that the habitat variables have insufficient power to explain ant distributions. PCA was performed using the statistical program R version 3.1.0 (R Core Team 2014) using the ADE4 library (Dray and Dufour 2007).

Effect of elevation

Analysis of covariance was used to determine whether a relationship existed between elevation and ant species richness and elevation and the ratio of native to exotic ant species. Island (Tutuila and Ta'ū) was considered a factor variable (a type of categorical variable) that could potentially interact with elevation to identify island-specific differences. The ratio of native to exotic species was modeled as having normal, random error, and our interpretation of diagnostic plots indicated little departure from that assumption. The total number of ant species was modeled as a Poisson process using a logarithmic link function. The pure Poisson model was overdispersed, so the final model was fit as a quasi-Poisson family with a dispersion parameter of 0.58. The models were fit in the R statistical environment version 3.1.0 (R Core Team 2014).

Species co-occurrence patterns

Patterns of co-occurrence among ant species were interpreted to infer antagonistic interactions and possible exclusion of ant species from sites. For example, widespread species would be expected to co-occur with a large number of other species because they occupy a wide range of habitats that likely support locally-distributed ants. However, aggressive ant species may exclude other ant species from sites, thereby reducing the number of co-occurrences. To search for such patterns, a co-occurrence matrix was constructed in which 1 (co-occurrence) and 0 (not found together) represented all possible pairwise combinations of ant species. The matrix was sorted by the number of 1's in a species' column to reveal patterns of co-occurrence and exclusion.

Dominance at baits

The number and composition of ants detected at bait cards containing tuna indicated the relative ability of ant species to monopolize an ephemeral food resource. One measure of dominance was the proportion of each ant species on a bait card. We limited this to those ant species that were detected on at least eight bait cards.

We also utilized binary logistic regression to assess dominance between ant species. Based on interactions between pairs of species, we estimated the probability that one species (A) was numerically dominant over another species (B) by calculating the likelihood that an individual ant (belonging to species A or B) detected at a bait card belonged to species A. The prevalence of each species was modeled as a series of binomial trials, with each bait station representing an individual trial. As an example, consider two stations: the first has 60 individuals of species A and 40 of species B, the second station has four and six of A and B, respectively. A naïve approach would calculate the two stations as 60% to 40% (A to B) at station 1 and 40% to 60% at station 2 with no evidence that either species was dominant over the other. Binomial regression allows the differing sample sizes to be taken into account while calculating the

probability that one species prevails over the other. Because 11 different binomial regressions were run, the threshold of significance was adjusted with a Bonferroni correction to $P = 0.004$ to produce an experiment-wise significance threshold of $P = 0.05$. Analyses were run using the R statistical environment (R Core Team 2014). Analyses were limited to the six species that comprised $> 1\%$ of all ants at bait cards, were found on at least two plots, and for which eight or more pairwise interactions occurred. Pairwise comparisons among *Nylanderia vaga*, *Pheidole oceanica*, *Pheidole sexspinosa* and *Pheidole umbonata* were only made for sites at which *Anoplolepis gracilipes* and *Pheidole megacephala* were absent since the latter two species largely excluded all other ants from bait.

RESULTS

Over the study, 19,761 ants representing 44 species were collected using the three standard sampling methods. Of the 44 species, 22 are considered native to American Samoa, 20 exotic, and two of unknown origin (Table 1). The Tutuila unit supported 40 species while 32 species were found on the Ta'ū unit. Both native and exotic species were widespread in the park (Figures 4–16). The most frequently collected species was the exotic *Nylanderia vaga* (found at 39 sites; Figure 6), followed by the native *Nylanderia minutula* (36 sites; Figure 6) and *Pheidole umbonata* (34 sites; Figure 9), non-native *Strumigenys rogeri* (29 sites; Figure 10), native *Pheidole oceanica* (28 sites; Figure 9) and non-native *Technomyrmex vitiensis* (26 sites; Figure 4). In contrast, 20 species were uncommon, found at five or fewer sites (9 native, 11 exotic). The highly aggressive, exotic *Anoplolepis gracilipes* (Figure 5) and *Pheidole megacephala* (Figure 9) were found at two and seven sites, respectively.

The total number of species found at each site varied considerably, ranging from 18 near the southwestern boundary of the park on Tutuila to five on the summit of Mt. Lata on Ta'ū (Figure 16). Overall, the mean number of species on Tutuila (12.8 ± 0.6) was indistinguishable from that on Ta'ū (13.0 ± 0.7 ; t-test, $t = -0.61$, $P = 0.54$). In contrast, the mean percentage of native ant species differed between islands, with significantly more native species found on Ta'ū than on Tutuila (69.7 ± 1.8 and 57.4 ± 3.5 , respectively; t-test, $t = -3.13$, $P = 0.004$). The mean number of ant species collected within each vegetation type was generally similar, ranging from $13.7 (\pm 0.6)$ in *Rhus* secondary forest to $11.0 (\pm 2.0)$ in secondary scrub (Figure 17). Native species were dominant in each vegetation type (range 54.4–69.6%) except in montane scrub, where exotic species comprised 66.7% of the fauna.

Table 1. Native and exotic ant species collected in the National Park of American Samoa and the number of sites where species were detected on the Tutuila and Ta'ū units. Twenty-two sites were surveyed on Tutuila and 17 sites were surveyed on Ta'ū.

Species	Code ⁴	Tutuila	Ta'ū	Species	Code ⁴	Tutuila	Ta'ū
Native species				Non-native species			
<i>Anochetus graeffei</i> Mayer	ANOC	1	2	<i>Anoplolepis gracilipes</i> (F. Smith)	ANGR	1	1
<i>Camponotus chloroticus</i> Emery	CACH	10	11	<i>Cardiocondyla emeryi</i> Forel	CAEM	1	0
<i>Camponotus flavolimbatus</i> Viehmeyer ¹	CAFL	5	0	<i>Cardiocondyla obscurior</i> Wheeler	CAOB	1	0
<i>Carebara atoma</i> (Emery)	CAAT	7	1	<i>Cardiocondyla</i> sp.	CARD	4	2
<i>Nylanderia minutula</i> (Dlussky)	NYMI	20	16	<i>Cerapachys biroi</i> Forel	CEBI	1	0
<i>Odontomachus simillimus</i> F. Smith	ODSI	11	12	<i>Hypoponera punctatissima</i> (Roger)	HYPU	2	0
<i>Ectomomyrmex insulanus</i> (Mayr)	ECIN	0	1	<i>Monomorium floricola</i> (Jerdon)	MOFL	8	4
<i>Pheidole</i> Mt. Lata	PHML	0	1	<i>Nylanderia vaga</i> (Forel)	NYVA	22	17
<i>Pheidole oceanica</i> Mayr	PHOC	13	15	<i>Paratrechina longicornis</i> (Latreille)	PALO	3	0
<i>Pheidole sexspinosa</i> Mayr	PHSE	13	9	<i>Pheidole megacephala</i> (Fabricius)	PHME	7	0
<i>Pheidole umbonata</i> Mayr	PHUM	17	17	<i>Pseudoponera stigma</i> (Fabricius)	PSST	0	2
<i>Ponera incerta</i> (Wheeler)	POIN	6	3	<i>Solenopsis papuana</i> Emery	SOPA	2	2
<i>Rogeria stigmatica</i> Emery	ROST	9	7	<i>Strumigenys eggersi</i> (Emery)	STEG	10	2
<i>Strumigenys godeffroyi</i> Mayr	STGO	5	10	<i>Strumigenys membranifera</i> (Emery)	STME	0	2
<i>Sylophopsis australica</i> (Forel)	SYAU	7	6	<i>Strumigenys rogeri</i> Emery	STRO	19	10
<i>Tetramorium insolens</i> (F. Smith)	TEIN	2	0	<i>Tapinoma melanocephalum</i> (Fabricius)	TAME	8	10
<i>Tetramorium pacificum</i> Mayr	TEPA	10	9	<i>Technomyrmex vitiensis</i> Mann	TEVI	14	12
<i>Tetramorium tonganum</i> Mayr	TETO	8	12	<i>Tetramorium bicarinatum</i> (Nylander)	TEBI	2	6
<i>Vollenhovia</i> nr. <i>denticulata</i> Emery	VODE	1	4	<i>Tetramorium lanuginosum</i> Mayr	TELA	4	0
<i>Vollenhovia</i> nr. FJ05 from Fiji ²	VOLL	1	0	<i>Tetramorium simillimum</i> (F. Smith)	TESI	4	0
<i>Vollenhovia pacifica</i> Wilson & Taylor ¹	VOPA	1	2				
<i>Vollenhovia samoensis</i> Mayr ³	VOSA	4	0	Species of uncertain status			
				<i>Hypoponera</i> sp.	HYP0	4	5
				<i>Ponera</i> sp.	PONE	6	10

¹Endemic to the Samoan Archipelago

²Described in Sarnat and Economo (2012)

³Endemic to the Samoan Archipelago and Tonga

⁴Species code used in Table 3

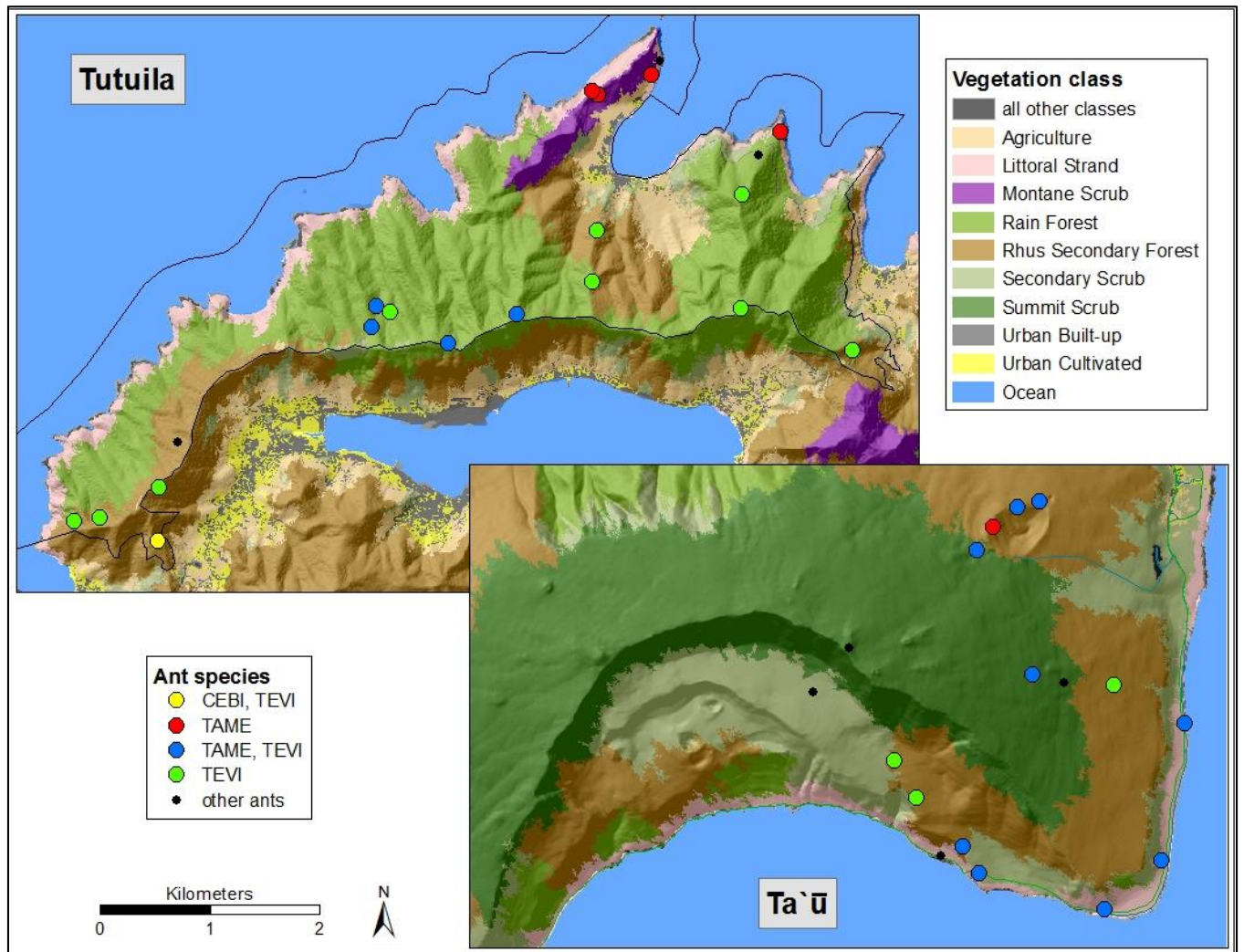


Figure 4. Sites where *Cerapachys biroi* (CEBI), *Tapinoma melanocephalum* (TAME) and *Technomyrmex vitiensis* (TEVI) were collected within the Tutuila and Ta'u units of National Park American Samoa.

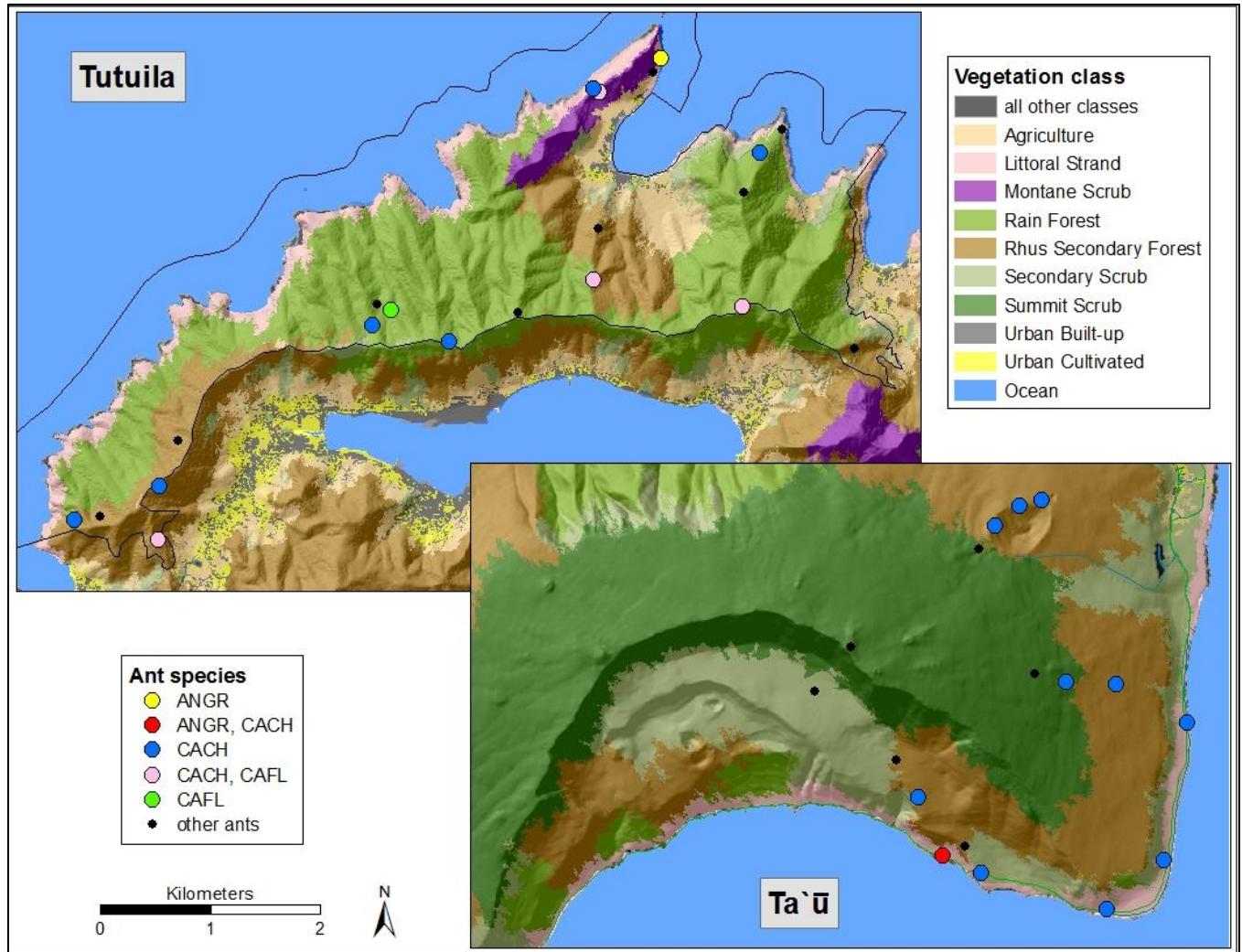


Figure 5. Sites where *Anoplolepis gracilipes* (ANGR), *Camponotus chloroticus* (CACH), and *Camponotus flavolimbatus* (CAFL) were collected within the Tutuila and Ta'u units of National Park of American Samoa.

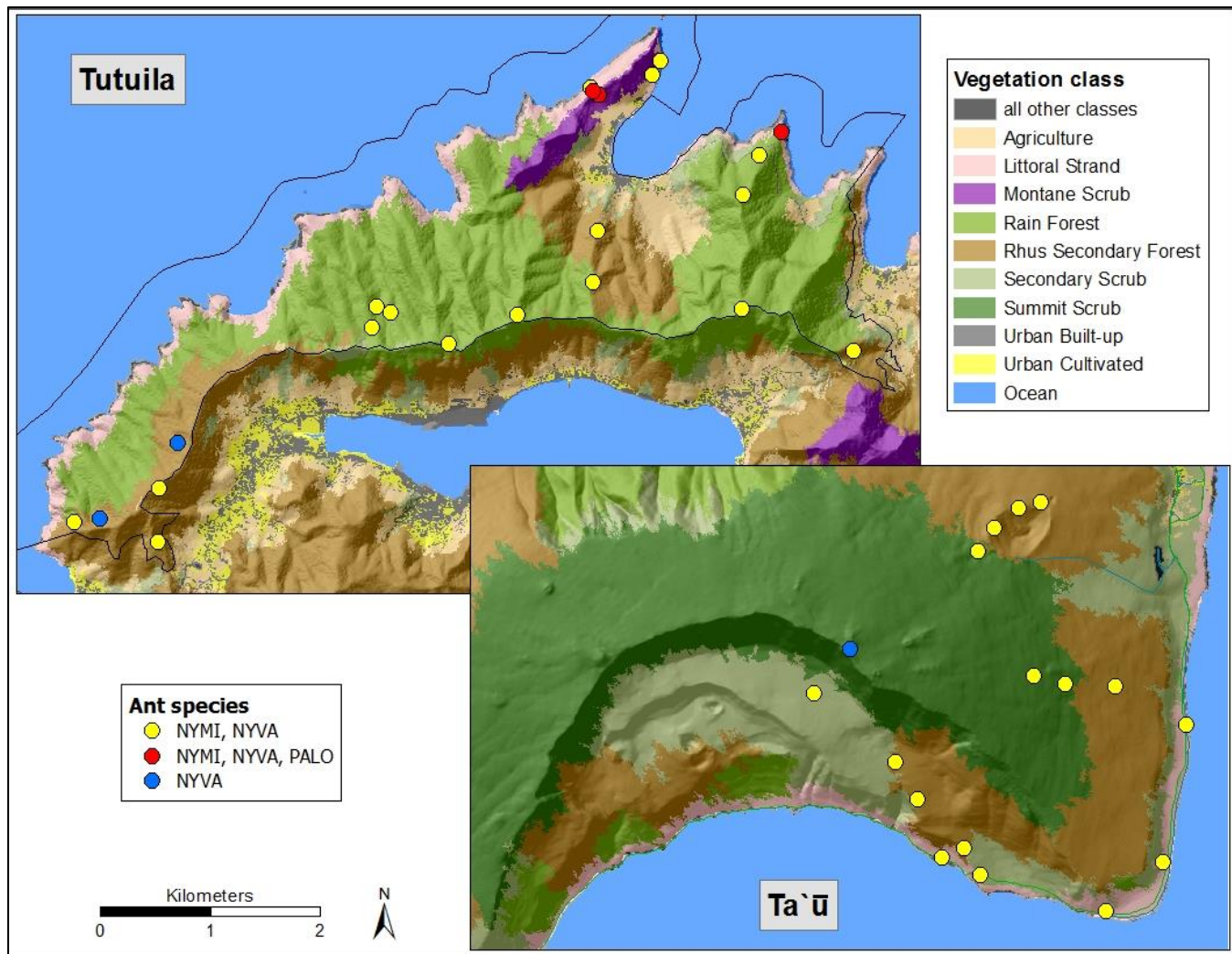


Figure 6. Sites where *Nylanderia minutula* (NYMI), *Nylanderia vaga* (NYVA), and *Paratrechina longicornis* (PALO) were collected within the Tutuila and Ta'u units of National Park of American Samoa.

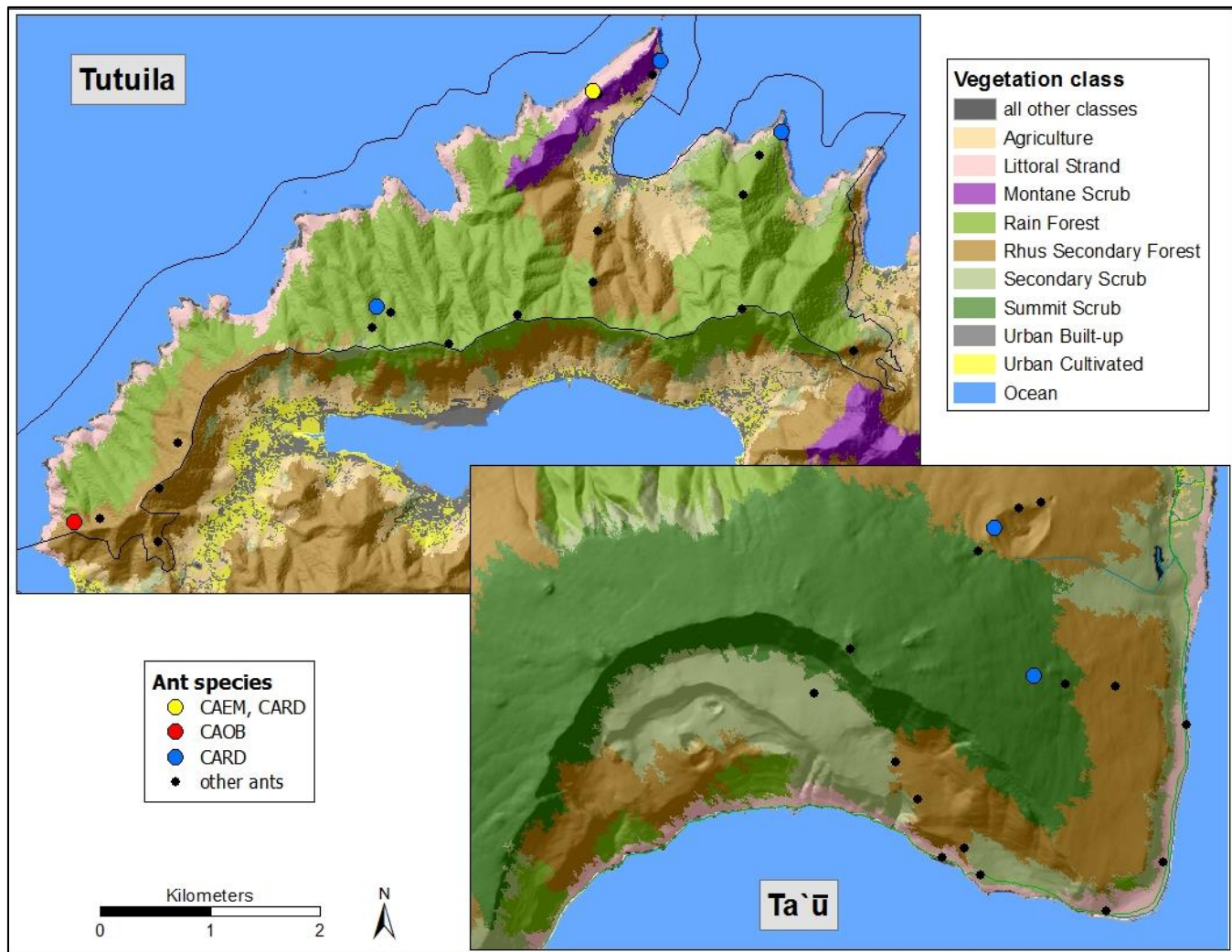


Figure 7. Sites where *Cardiocondyla emeryi* (CAEM), *Cardiocondyla obscurior* (CAOB), and *Cardiocondyla* sp. (CARD) were collected within the Tutuila and Ta'u units of National Park of American Samoa.

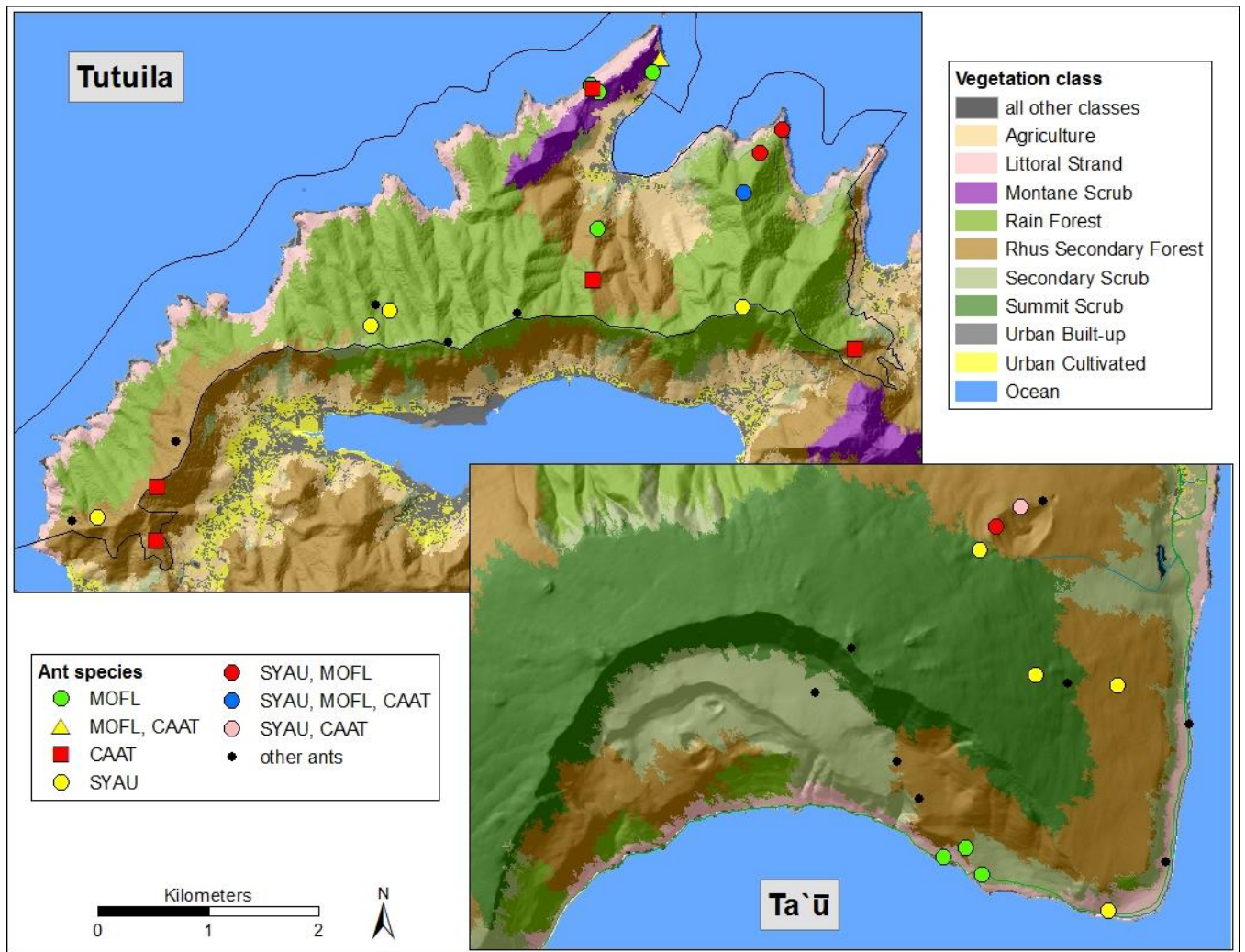


Figure 8. Sites where *Carebara atoma* (CAAT), *Monomorium floricola* (MOFL), and *Sylophopsis australica* (SYAU) were collected within the Tutuila and Ta'u units of National Park of American Samoa.

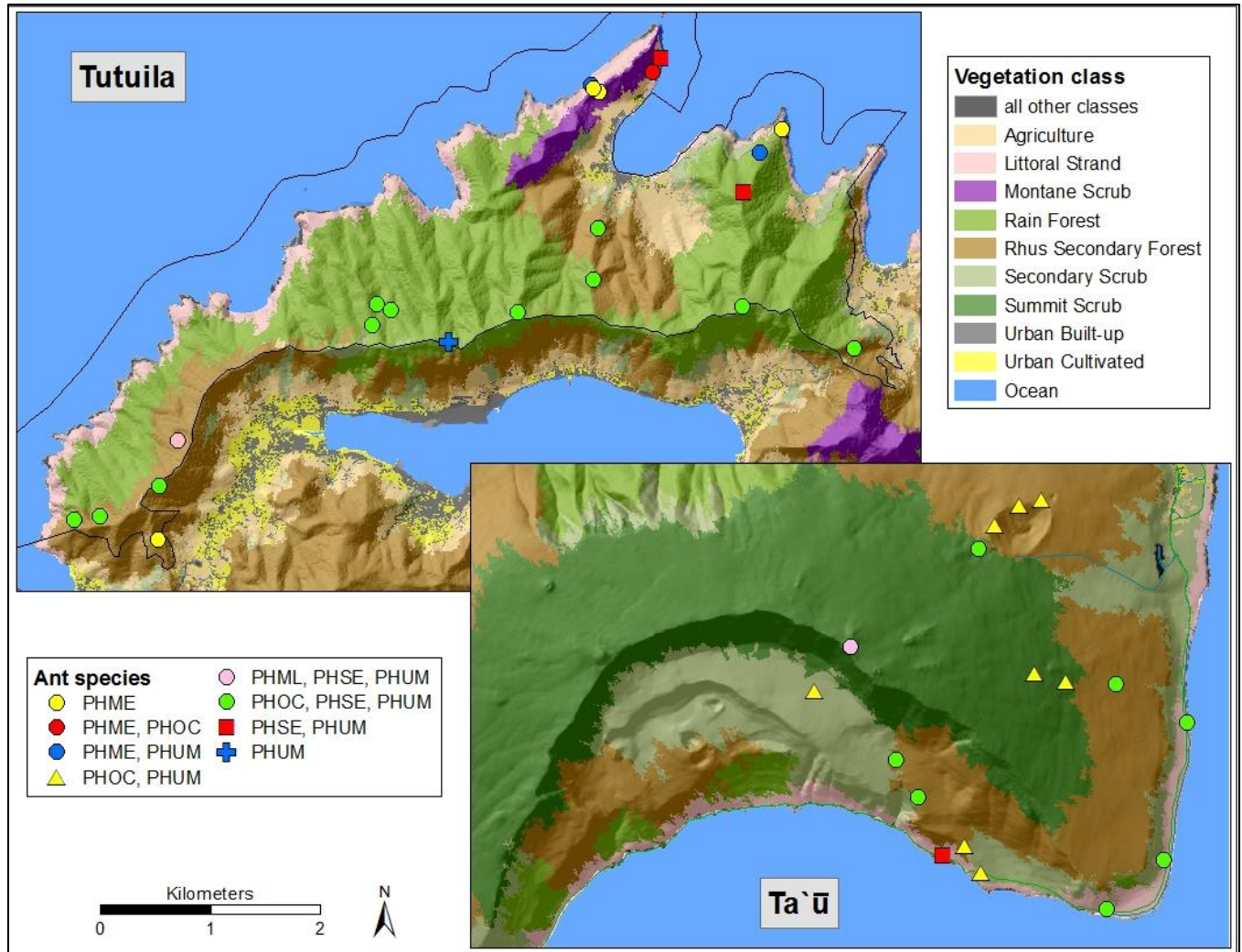


Figure 9. Sites where *Pheidole megacephala* (PHME), *Pheidole* Mt. Lata (PHML), *Pheidole oceanica* (PHOC), *Pheidole sexspinosa* (PHSE), and *Pheidole umbonata* (PHUM) were collected within the Tutuila and Ta'u units of National Park of American Samoa.

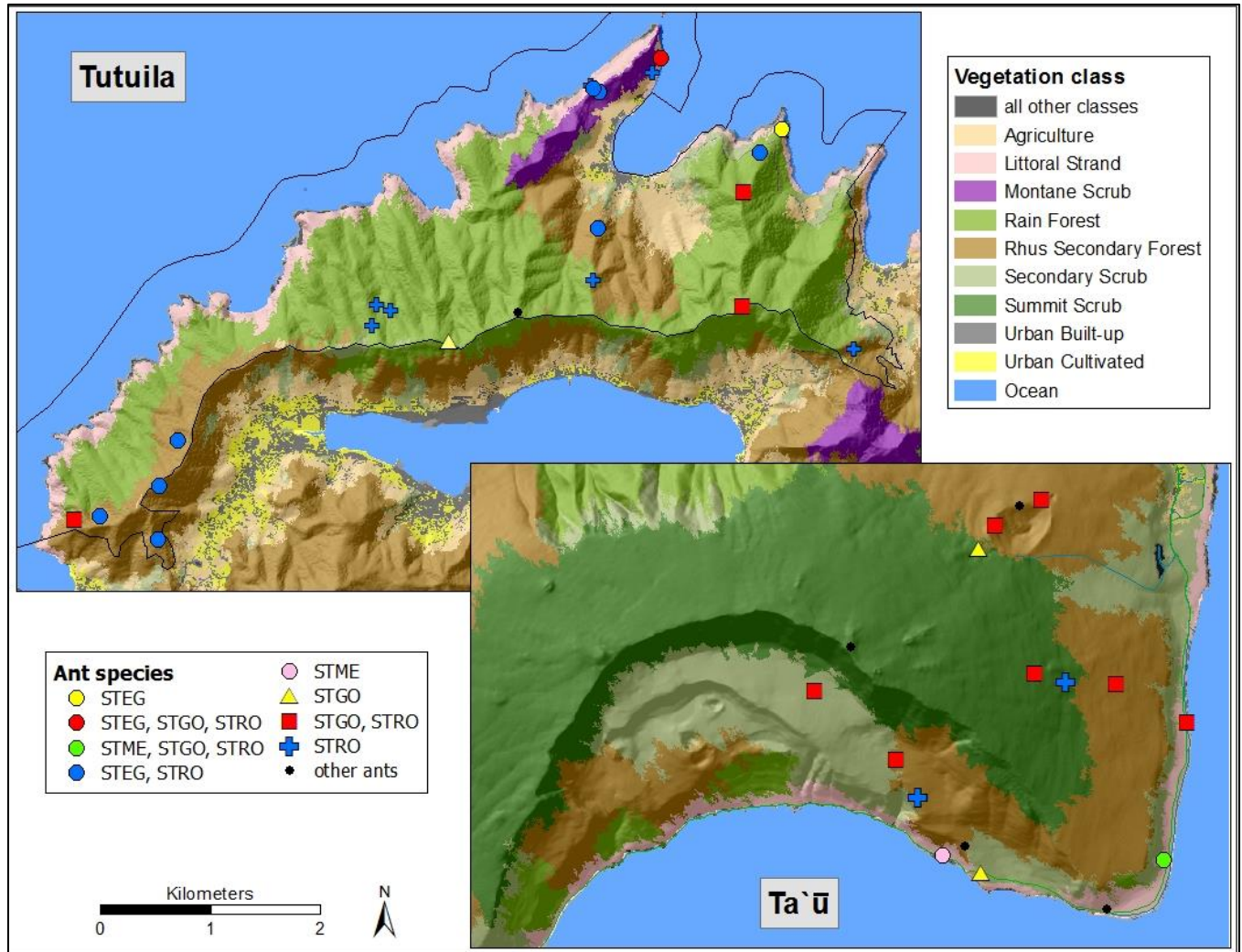


Figure 10. Sites where *Strumigenys eggersi* (STEG), *Strumigenys godeffroyi* (STGO), *Strumigenys membranifera* (STME), and *Strumigenys rogeri* (STRO) were collected within the Tutuila and Ta'u units of National Park of American Samoa.

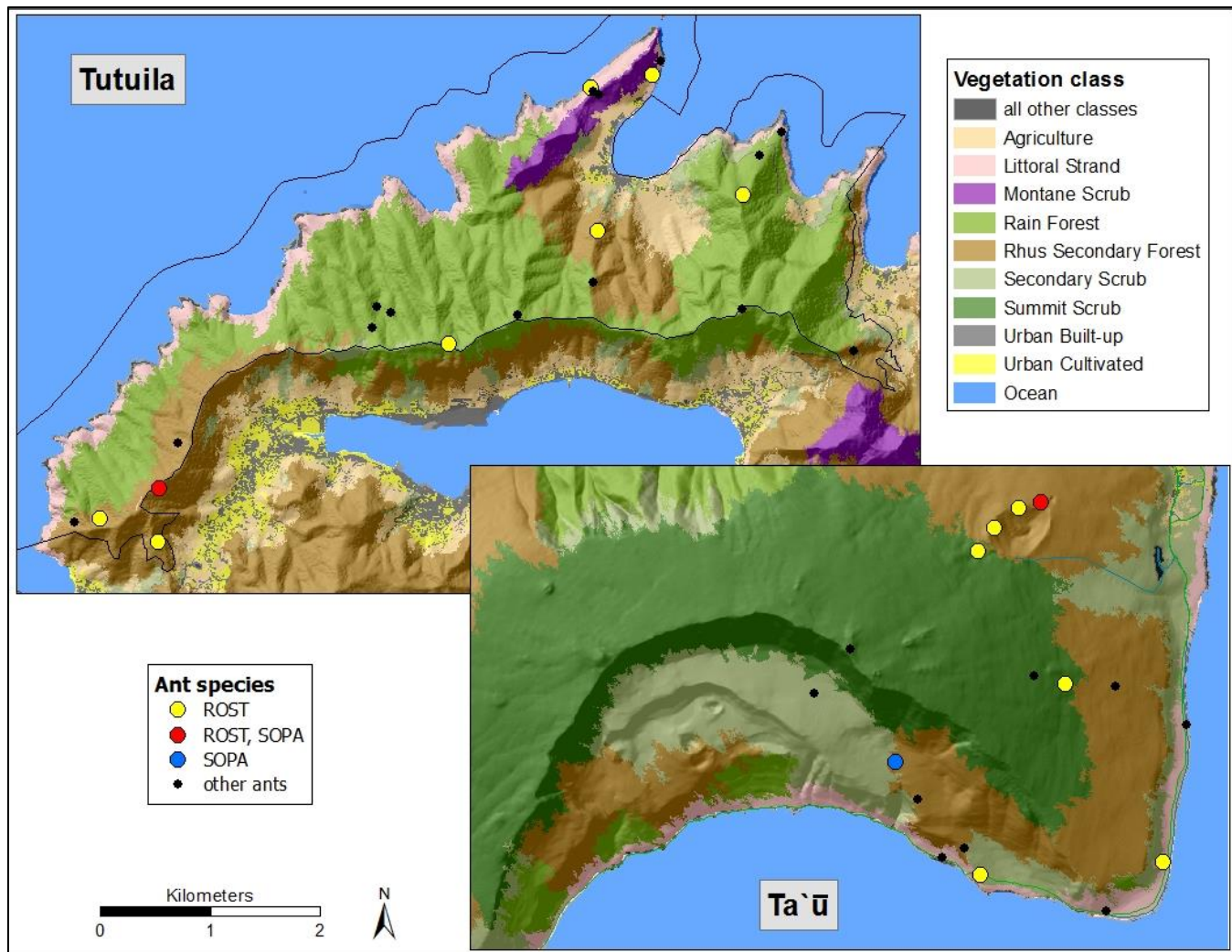


Figure 11. Sites where *Rogeria stigmatica* (ROST) and *Solenopsis papuana* (SOPA) were collected within the Tutuila and Ta'u units of National Park of American Samoa.

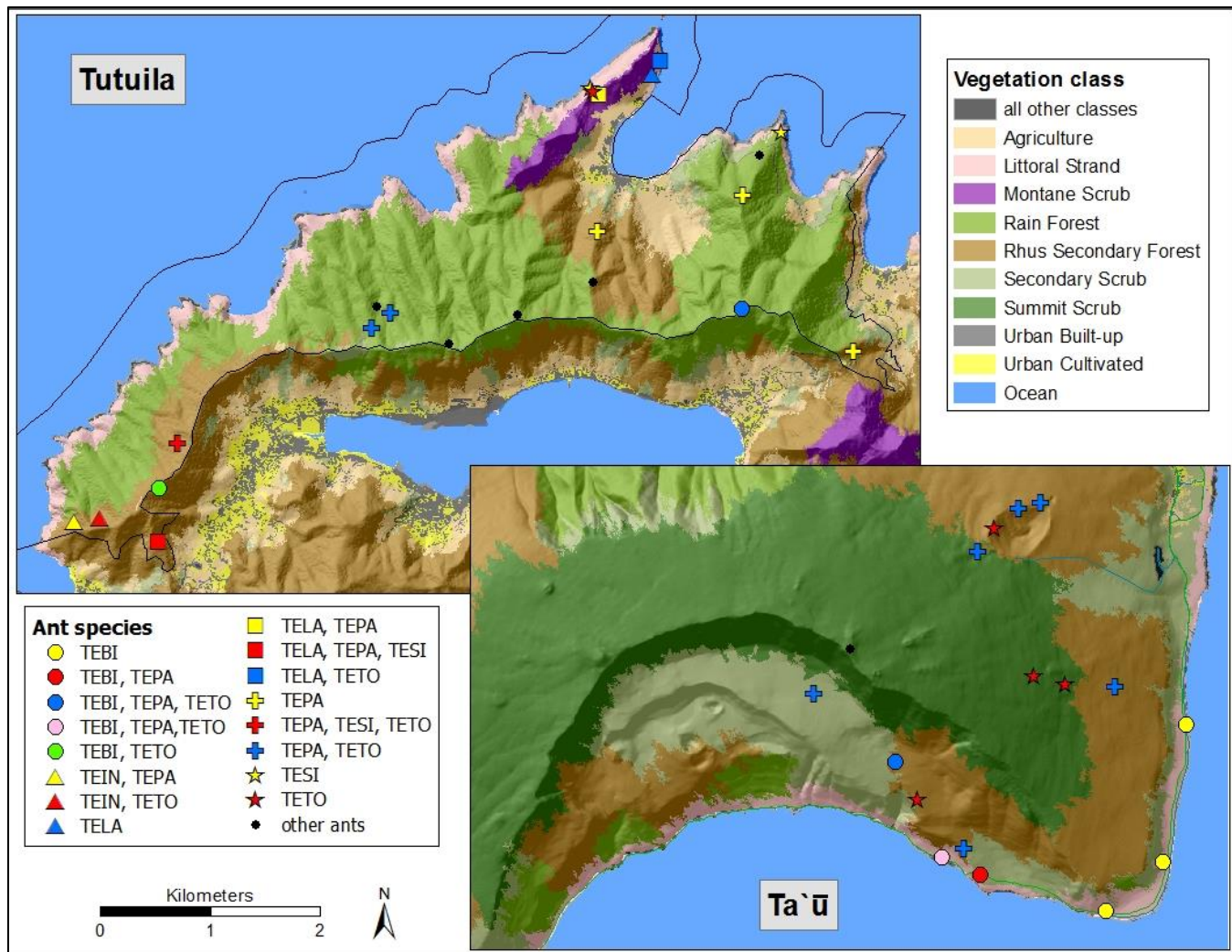


Figure 12. Sites where *Tetramorium bicarinatum* (TEBI), *Tetramorium insolens* (TEIN), *Tetramorium lanuginosum* (TELA), *Tetramorium pacificum* (TEPA), *Tetramorium simillimum* (TESI), and *Tetramorium tonganum* (TETO) were collected within the Tutuila and Ta'u units of National Park of American Samoa.

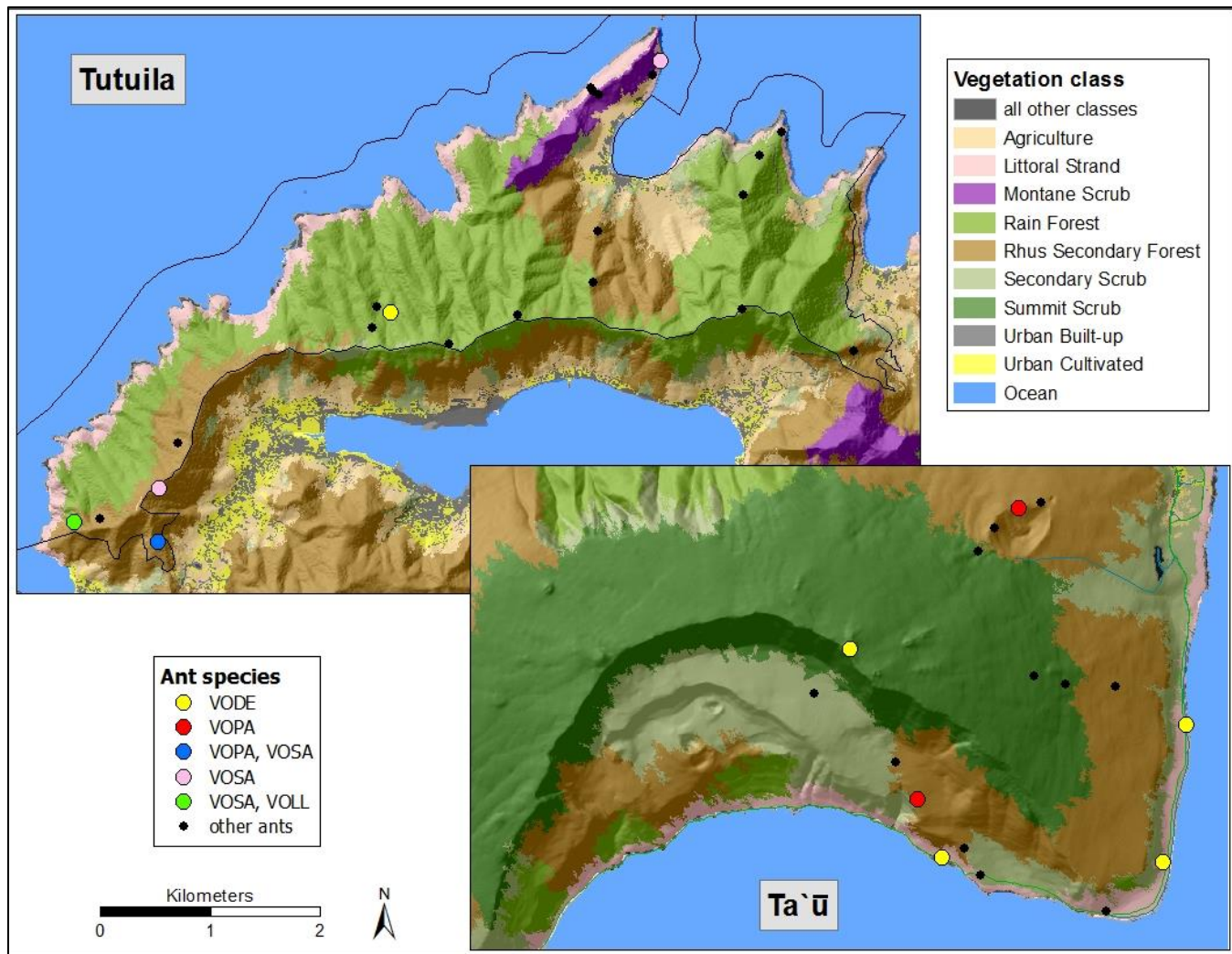


Figure 13. Sites where *Vollenhovia* nr. *denticulata* (VODE), *Vollenhovia pacifica* (VOPA), *Vollenhovia samoensis* (VOSA), and *Vollenhovia* nr. FJO5 from Fiji (VOLL) were collected within the Tutuila and Ta'u units of National Park of American Samoa.

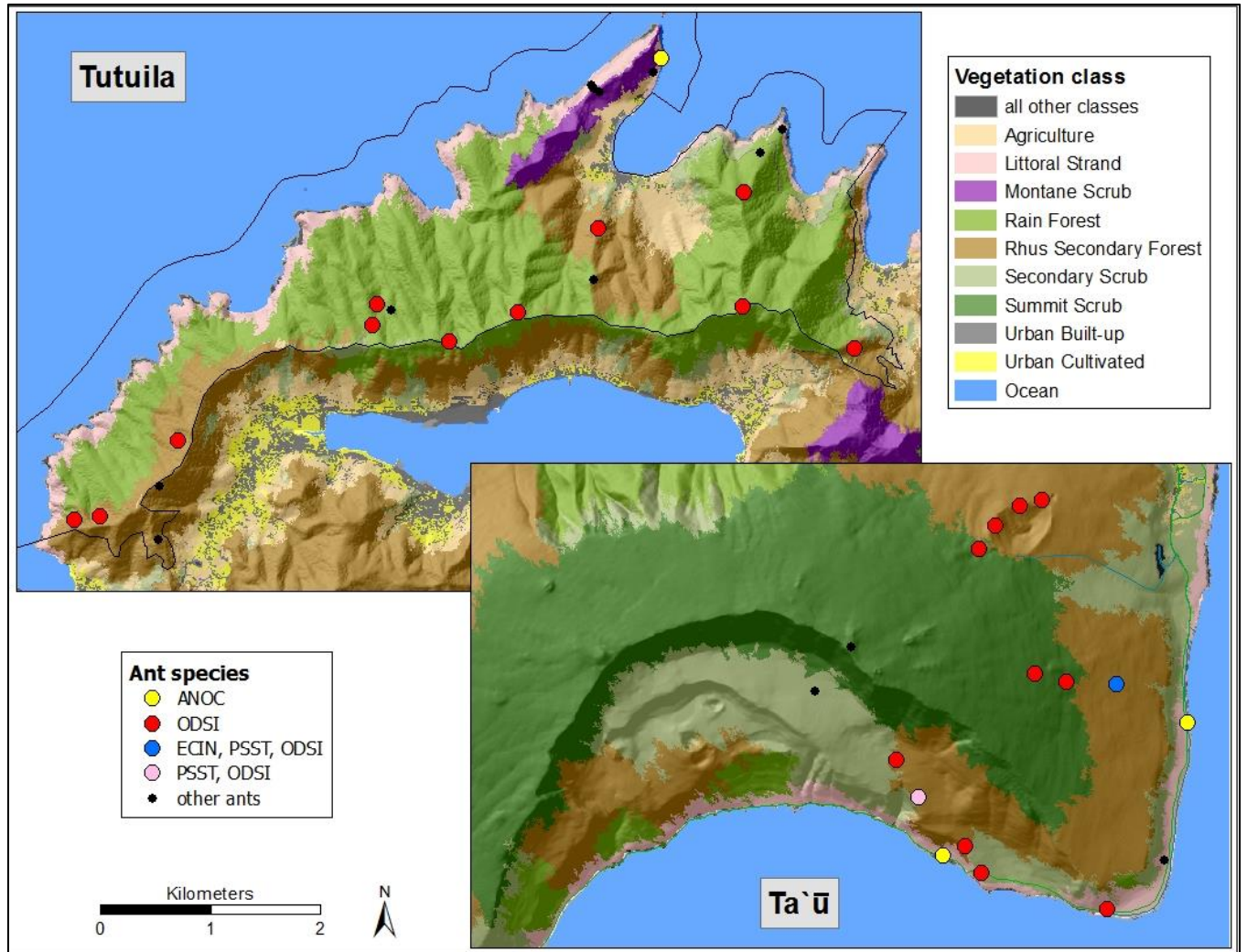


Figure 14. Sites where *Anochetus graeffei* (ANOC), *Ectomomyrmex insulanus* (ECIN), *Odontomachus simillimus* (ODSI), and *Pseudoponera stigma* (PSST) were collected within the Tutuila and Ta'u units of National Park of American Samoa.

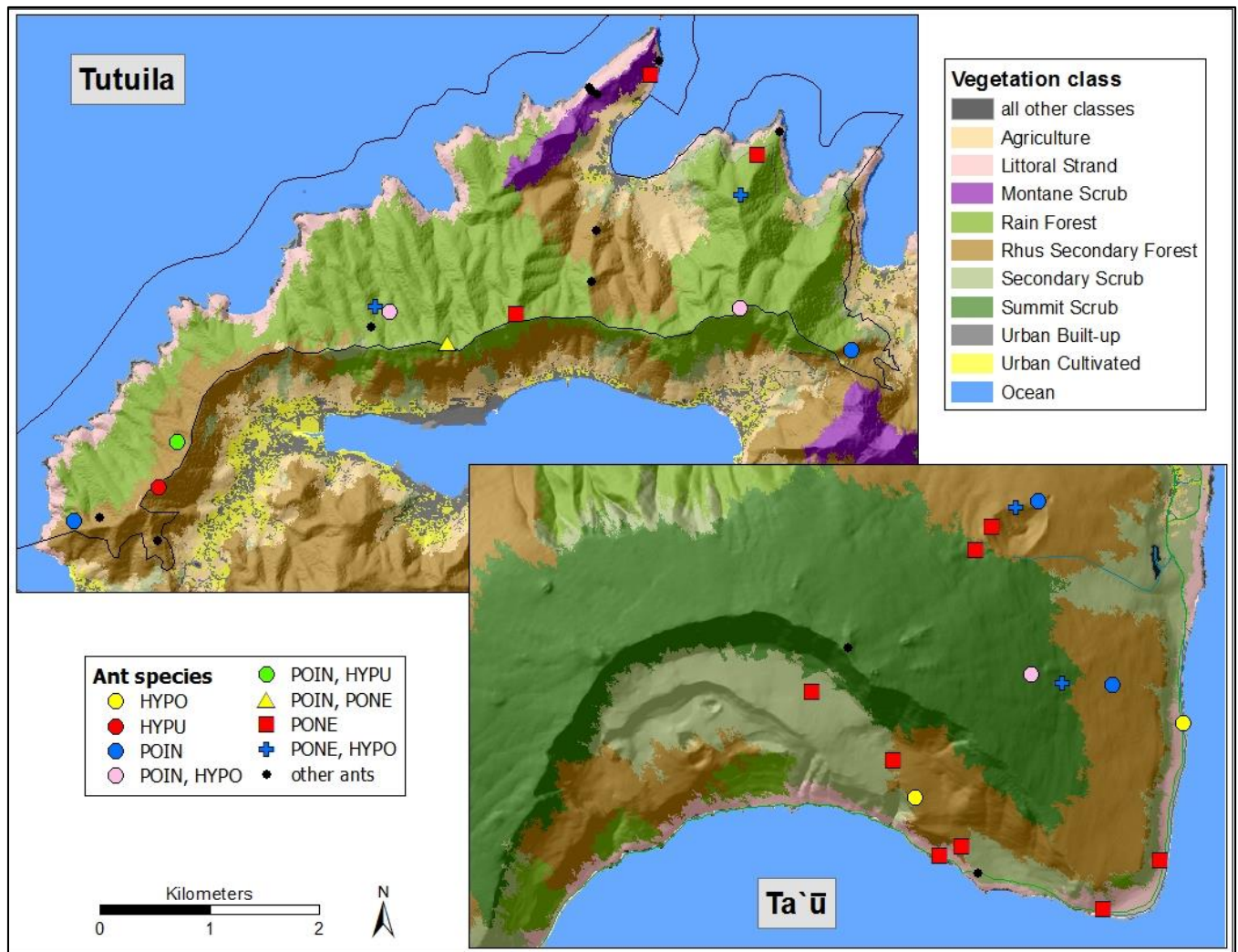


Figure 15. Sites where *Hypoponera* sp. (HYPO), *Hypoponera punctatissima* (HYPV), *Ponera incerta* (POIN), and *Ponera* sp. (PONE) were collected within the Tutuila and Ta'u units of National Park of American Samoa.

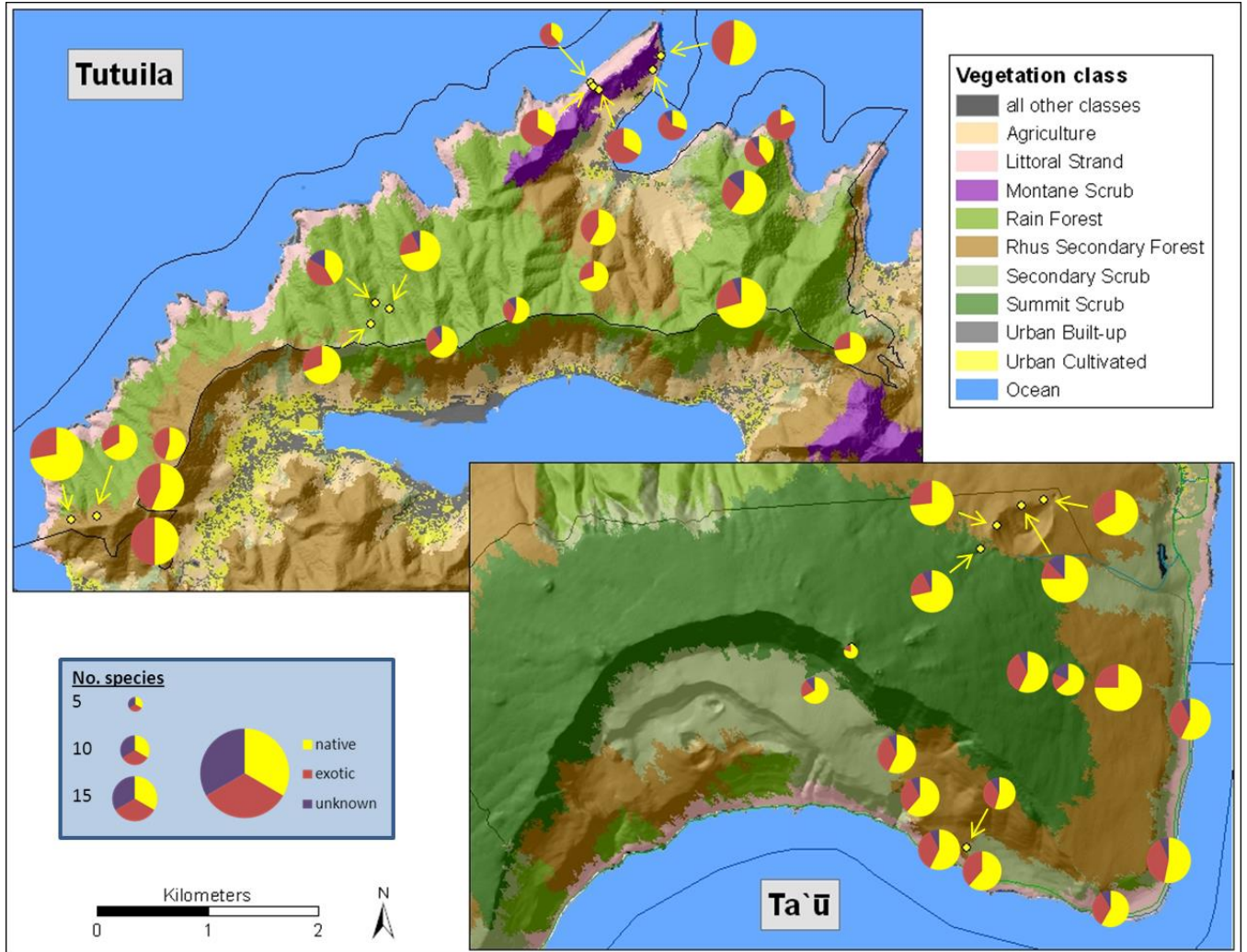


Figure 16. Total number of ant species (size of circle) and relative abundances (proportion of colored circle sections) of species considered to be native (yellow), exotic (red) or of unknown origin (purple) detected at survey sites on Tutuila and Ta'u units of National Park of American Samoa.

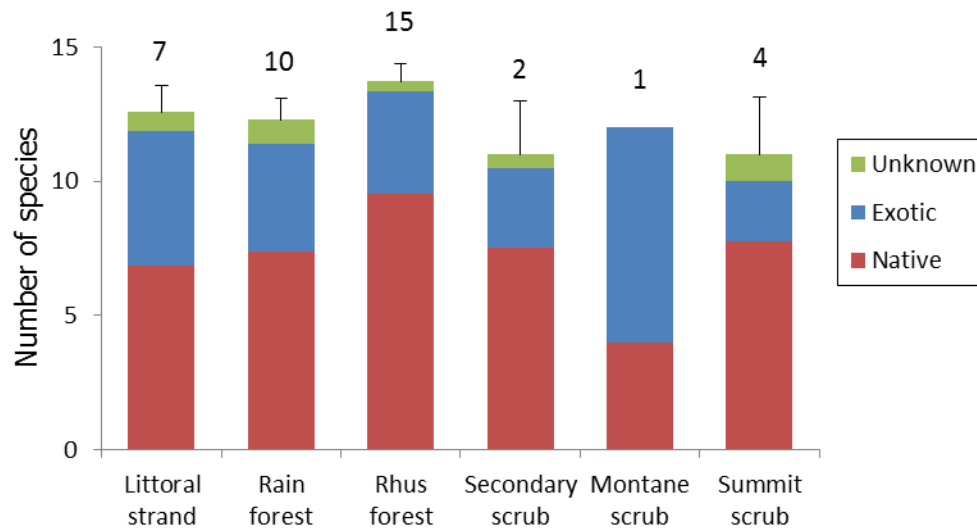


Figure 17. Mean (\pm SEM) number of ant species found in the six vegetation types sampled in the National Park of American Samoa. The mean proportion of species considered native, exotic and of unknown origin at each site is also presented. The number above each bar indicates the number of plots sampled in that vegetation type.

Habitat Analysis

Effect of habitat

Principle component analysis of the six habitat variables measured at the study sites found 62% of the total variation within the dataset to be accounted for by the first two axes (39% and 23%, respectively; Table 2). The percent cover of rock and vegetation contributed most strongly to Axis 1 while the percent cover of rock, and to a lesser extent, the percent cover of the canopy and coarse wood debris, contributed to Axis 2. In general, no clear patterns emerged among survey sites relative to the habitat variables (Figure 18).

Table 2. Principal component loadings for the six habitat variables measured along each axis and the amount of the total variation in the dataset explained by each axis.

Habitat variable	Axis 1	Axis 2	Axis 3	Axis 4	Axis 5	Axis 6
Canopy cover (%)	-0.42	0.28	0.29	-0.75	0.33	-0.04
Number of plant species	-0.43	-0.40	0.05	-0.22	-0.77	0.06
Rock cover (%)	0.34	0.63	0.23	-0.09	-0.44	0.48
Litter (%)	-0.59	0.05	0.06	0.44	0.23	0.63
CWD (%)	-0.05	0.13	-0.91	-0.29	0.00	0.24
Vegetation (%)	0.41	-0.59	0.15	-0.32	0.22	0.56
Variation explained	39%	23%	18%	10%	8%	1%

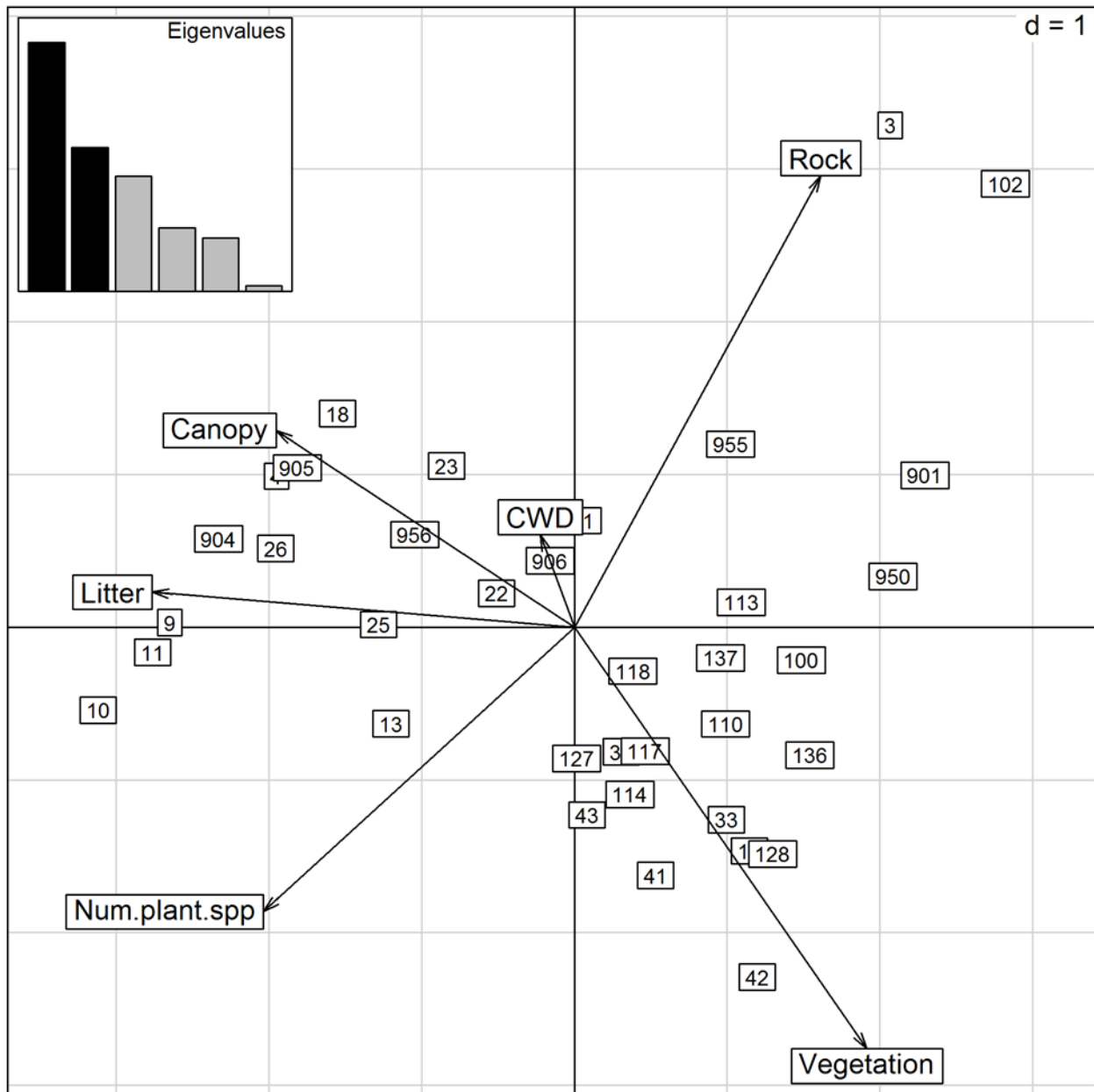


Figure 18. Biplot of the six habitat variables measured at each site. The axes shown are the first (horizontal) and second (vertical) principal components. The 36 sites where habitat measurements were recorded are shown as numbered boxes. Arrows indicate the relative contribution of each habitat variable to the principal component axes. The inset histogram shows the relative proportion of the total variation accounted for by each principal component. Black bars indicate the axes displayed in the biplot.

Effect of elevation

Analysis of covariance revealed no effect of elevation on the total number of ant species ($P = 0.3046$), although elevation did have a significant influence on the ratio of native to exotic ants ($P < 0.001$). The interaction between island and the ratio of native to exotic ants was not significant indicating a similar pattern for Tutuila and Ta'ū. The linear relationship between elevation and number of ant species was slightly positive on Tutuila and slightly negative on Ta'ū (Figure 19). The linear relationship between elevation and the ratio of native to exotic species was positive on the Tutuila and Ta'ū units (Figure 19).

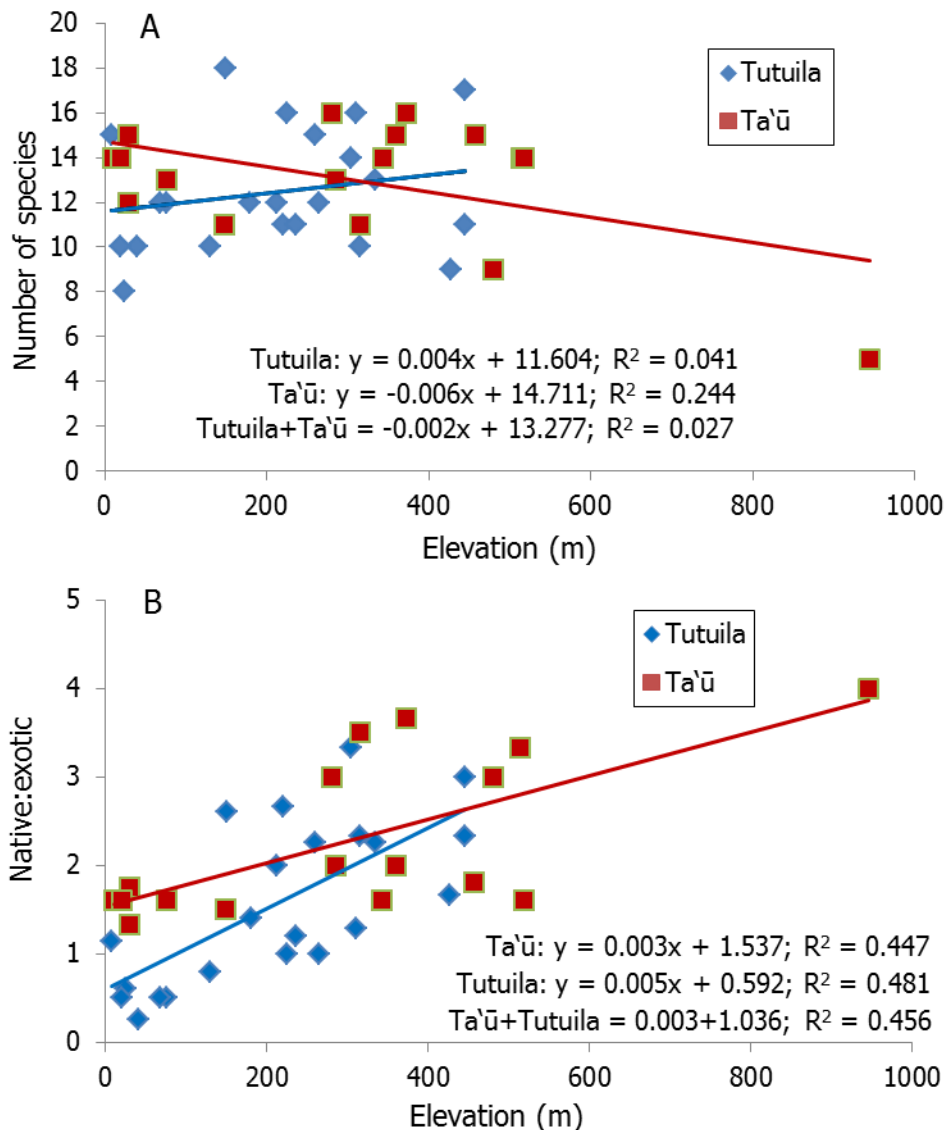


Figure 19. Relationships between elevation and ant species richness (A) and the ratio of native to exotic ant species (B) for sites in the Tutuila and Ta'ū units of the National Park of American Samoa. Best-fit linear regression lines are shown for each island.

Species co-occurrence patterns

Overall, 8 of 11 frequently co-occurring species were native; only *Nylanderia vaga* (NYVA), *Strumigenys rogeri* (STRO), and *Technomyrmex vitiensis* were exotic (Table 3). The widespread *Odontomachus simillimus* (ODSI; found on 23 sites) shared sites with 33 other ant species, but it was not found in the presence of *Pheidole megacephala* (PHME) or *Anoplolepis gracilipes* (ANGR). *Tetramorium tonganum* (TETO; found on 20 sites) co-occurred with all ant species except four uncommon species while *Pheidole sexspinosa* (PHSE; found on 22 sites) co-occurred with all ant species except five uncommon species, including *P. megacephala*. Rare species, such as *Pheidole* Mt. Lata, *Cardiocondyla emeryi* and *Cerapachys biroj*, co-occurred with few other species (4, 11 and 15, respectively). *Pheidole megacephala* was found at seven sites but co-occurred with 25 other species.

Dominance at bait cards

Fourteen ant species were collected at bait cards, but six species, comprising 91.2% of the total number of individuals found, were found on at least eight bait cards (Figure 20). Of these six, *Pheidole megacephala* and *Anoplolepis gracilipes* were most dominant, comprising $93.9 \pm 4.2\%$ and $93.3 \pm 4.4\%$ of all ants present on cards at which they were found, respectively. Less dominant were *Pheidole oceanica* ($72.4 \pm 5.4\%$), *Pheidole umbonata* ($58.8 \pm 4.3\%$), *Nylanderia vaga* ($42.2 \pm 4.1\%$) and *Odontomachus simillimus* ($26.4 \pm 7.6\%$). Ants less frequently collected at bait cards included *Nylanderia minutula*, *Pheidole* Mt. Lata, *Pheidole sexspinosa*, *Technomyrmex vitiensis*, *Tapinoma melanocephalum*, *Tetramorium bicarinatum*, *Tetramorium simillimum*, and *Tetramorium pacificum*.

Binary logistic regression performed to assess the dominance of *Anoplolepis gracilipes*, *Nylanderia vaga*, *Pheidole megacephala*, *Pheidole oceanica*, *Pheidole sexspinosa*, and *Pheidole umbonata* at bait cards (Table 4) indicated a significant level of dominance by *P. megacephala* or *A. gracilipes* in all interactions. Where *P. megacephala* and *A. gracilipes* were absent, pairwise comparisons among the other four species indicated that *P. oceanica* was dominant over *N. vaga* and *P. sexspinosa* while *P. umbonata* was dominant over *P. oceanica*, *N. vaga*, and *P. sexspinosa*. *Pheidole sexspinosa* failed to dominate any interactions.

Table 3. Ant species co-occurrence matrix. Pairs of species found together on at least one survey site are indicated by "1" whereas "0" indicates no co-occurrence. Numbers at the top of the columns represent the number of sites where ant species (directly below) were detected. Numbers at the bottom of the columns indicate the total number of co-occurring species. Ant species codes are explained in Table 1 and Figures 4–15.

No. sites	1	1	1	1	3	1	1	2	2	2	2	2	2	4	5	3	7	3	4	9	4	6	5
	PHML	CAEM	CEBI	ECIN	PALO	CAOB	VOLL	PSST	STME	HYPV	ANGR	TEIN	SOPA	VODE	ANOC	PHME	VOPA	TESI	HYPO	TELA	CARD	CAFL	
PHML	---	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
CAEM	0	---	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0
CEBI	0	0	---	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	0	1	1
ECIN	0	0	0	---	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
PALO	0	1	0	0	---	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	1	1	1
CAOB	0	0	0	0	0	---	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0
VOLL	0	0	0	0	0	1	---	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0
PSST	0	0	0	1	0	0	0	---	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0
STME	0	0	0	0	0	0	0	0	---	0	1	0	0	1	1	0	0	0	0	0	0	0	0
HYPV	0	0	0	0	0	0	0	0	0	---	0	0	1	0	0	0	0	1	0	0	0	0	0
ANGR	0	0	0	0	0	0	0	0	1	0	---	0	0	1	1	0	0	0	0	0	1	1	0
TEIN	0	0	0	0	0	1	1	0	0	0	---	0	1	0	0	0	0	0	0	0	0	0	0
SOPA	0	0	0	0	0	1	1	0	0	1	0	---	1	0	0	0	0	0	0	0	0	0	0
VODE	1	0	0	0	0	0	0	0	1	0	1	0	0	---	1	0	0	0	1	0	0	1	1
ANOC	0	0	0	0	0	0	0	0	1	0	1	0	0	1	---	0	0	0	1	1	1	0	0
PHME	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	---	1	1	0	1	1	1	1
VOPA	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1	---	1	1	1	1	0	1
TESI	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	1	1	---	0	1	1	1	1
HYPO	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	1	1	0	---	0	1	1	1
TELA	0	0	1	0	1	0	0	0	0	1	0	0	0	1	1	1	1	1	0	---	0	1	1
CARD	0	1	0	0	1	0	0	0	0	0	1	0	0	0	1	1	0	1	1	1	---	0	0
CAFL	0	0	1	0	1	0	0	0	0	0	0	0	0	1	0	1	1	1	1	1	1	0	---
TEBI	0	0	0	0	0	0	0	0	1	1	1	0	1	1	1	0	0	0	1	0	0	0	1
PONE	0	0	0	0	0	0	0	0	1	0	1	0	1	1	1	1	1	0	1	1	1	1	0
MOFL	0	0	0	0	1	0	0	0	1	0	1	0	0	1	1	1	0	1	1	1	1	1	1
SYAU	0	0	0	1	1	0	0	1	0	0	0	1	0	1	0	1	1	1	1	0	1	1	1
VOSA	0	0	1	0	0	1	1	0	1	1	1	1	1	0	1	1	1	1	0	1	1	1	1
POIN	0	0	0	1	0	1	1	1	0	1	0	1	1	1	1	0	0	0	1	1	0	1	1
TAME	0	1	0	0	1	0	0	0	1	0	0	0	1	1	1	1	1	1	1	1	1	1	1
ODSI	0	0	0	1	0	1	1	1	0	1	0	1	1	0	0	0	1	1	1	0	1	1	1
CAAT	0	1	1	0	1	0	0	0	0	1	1	0	1	0	1	1	1	1	1	1	1	1	1
STGO	0	0	0	1	0	1	1	1	1	0	1	1	1	1	1	1	0	0	0	1	1	1	1
STEG	0	1	1	0	1	0	0	0	0	1	1	1	1	0	1	1	1	1	0	1	1	1	1
ROST	0	0	1	0	0	1	1	0	1	1	0	1	1	1	0	1	1	1	1	1	1	1	1
PHOC	0	0	0	1	0	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1
PHSE	1	0	0	1	0	1	1	1	1	1	1	1	1	1	1	0	1	0	1	1	1	1	1
TEVI	0	0	1	1	0	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1
TETO	0	1	0	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
PHUM	1	0	0	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
TEPA	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1
CACH	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
NYMI	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
STRO	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
NYVA	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Total	4	11	15	15	17	17	17	17	19	19	20	20	24	24	24	25	25	26	26	27	28	29	29

Table 3. Continued.

No. sites	8	16	12	13	4	9	18	23	8	15	10	16	28	22	26	20	34	19	21	36	29	39	
	TEBI	PONE	MOFL	SYAU	VOSA	POIN	TAME	ODSI	CAAT	STGO	STEG	ROST	PHOC	PHSE	TEVI	TETO	PHUM	TEPA	CACH	NYMI	STRO	NYVA	
PHML	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	1
CAEM	0	0	0	0	0	0	1	0	1	0	1	0	0	0	0	1	0	0	1	1	1	1	1
CEBI	0	0	0	0	1	0	0	0	1	0	1	1	0	0	1	0	0	1	1	1	1	1	1
ECIN	0	0	0	1	0	1	0	1	0	1	0	0	1	1	1	1	1	1	1	1	1	1	1
PALO	0	0	1	1	0	0	1	0	1	0	1	0	0	0	0	1	0	1	1	1	1	1	1
CAOB	0	0	0	0	1	1	0	1	0	1	0	1	1	1	1	0	1	1	1	1	1	1	1
VOLL	0	0	0	0	1	1	0	1	0	1	0	1	1	1	1	0	1	1	1	1	1	1	1
PSST	0	0	0	1	0	1	0	1	0	1	0	0	1	0	1	1	1	1	1	1	1	1	1
STME	1	1	1	0	0	0	1	0	0	1	0	1	1	1	1	1	1	1	1	1	1	1	1
HYPV	1	0	0	0	1	1	0	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1
ANGR	1	1	1	0	1	0	0	0	1	1	1	0	0	1	0	1	1	1	1	1	1	1	1
TEIN	0	0	0	0	1	1	0	1	0	1	1	1	1	0	1	1	1	1	1	1	1	1	1
SOPA	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
VODE	1	1	1	1	0	1	1	0	0	1	0	1	1	1	1	1	1	1	1	1	1	1	1
ANOC	1	1	1	0	1	0	1	0	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1
PHME	0	1	1	1	1	0	1	0	1	0	1	1	1	0	1	1	1	1	1	1	1	1	1
VOVA	0	1	0	1	1	0	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1
TESI	0	0	1	1	1	1	1	1	1	0	1	1	1	0	1	1	1	1	1	1	1	1	1
HYPO	1	1	1	1	0	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1
TELA	0	1	1	0	1	0	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
CARD	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
CAFL	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
TEBI	---	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
PONE	1	---	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
MOFL	1	1	---	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
SYAU	1	1	1	---	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
VOSA	1	0	1	0	---	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
POIN	1	1	0	1	1	---	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
TAME	1	1	1	1	0	1	---	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
ODSI	1	1	1	1	1	1	1	---	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
CAAT	1	1	1	1	1	1	1	1	---	1	1	1	1	1	1	1	1	1	1	1	1	1	1
STGO	1	1	1	1	1	1	1	1	1	---	1	1	1	1	1	1	1	1	1	1	1	1	1
STEG	1	1	1	1	1	1	1	1	1	1	---	1	1	1	1	1	1	1	1	1	1	1	1
ROST	1	1	1	1	1	1	1	1	1	1	1	---	1	1	1	1	1	1	1	1	1	1	1
PHOC	1	1	1	1	1	1	1	1	1	1	1	1	---	1	1	1	1	1	1	1	1	1	1
PHSE	1	1	1	1	1	1	1	1	1	1	1	1	1	---	1	1	1	1	1	1	1	1	1
TEVI	1	1	1	1	1	1	1	1	1	1	1	1	1	1	---	1	1	1	1	1	1	1	1
TETO	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	---	1	1	1	1	1	1	1
PHUM	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	---	1	1	1	1	1	1
TEPA	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	---	1	1	1	1	1
CACH	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	---	1	1	1	1
NYMI	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	---	1	1	1
STRO	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	---	1	1
NYVA	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	---
Total	29	30	31	31	32	32	33	33	35	35	35	36	38	38	39	39	40	40	42	42	42	42	43

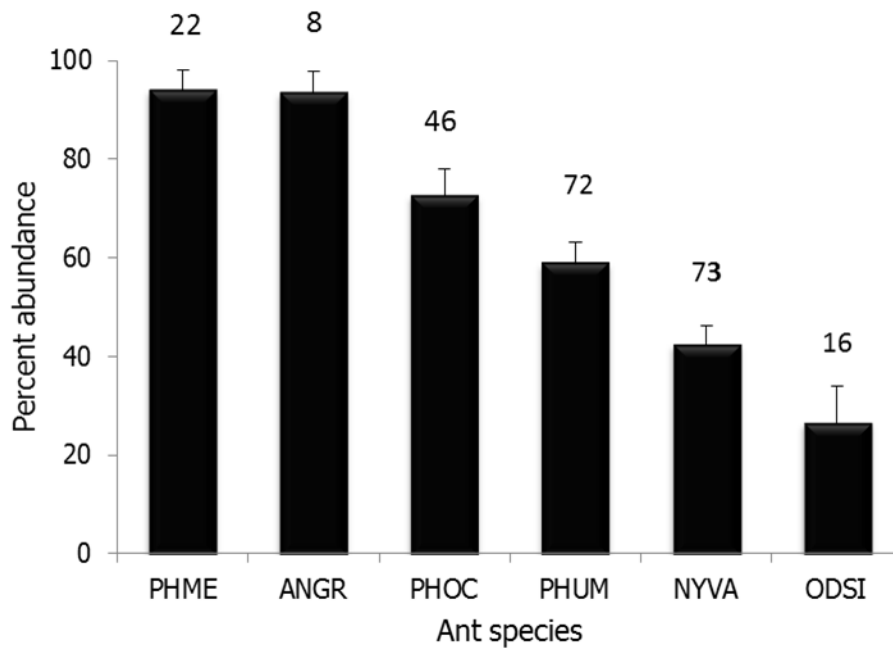


Figure 20. Mean (\pm SEM) percent abundance of the six most commonly recorded species at bait cards. ANGR = *Anoplolepis gracilipes*; PHME = *Pheidole megacephala*; PHOC = *Pheidole oceanica*; PHUM = *Pheidole umbonata*; NYVA = *Nylanderia vaga*; ODSI = *Odontomachus simillimus*. The number above each bar indicates the number of bait cards at which the ant species were detected.

Table 4. Results of binary logistic regression analyses testing for dominance between pairs of ant species at bait cards. Mean (\pm SEM) values represent the probability that ant species A was dominant over ant species B (n represents the number of interactions compared). Dashed lines indicate that species pairs did not coexist on the same sites. A significant level of dominance was detected for all pairs analyzed. ANGR = *Anoplolepis gracilipes*; PHME = *Pheidole megacephala*; NYVA = *Nylanderia vaga*; PHOC = *Pheidole oceanica*; PHSE = *Pheidole sexspinosa*; PHUM = *Pheidole umbonata*.

Species		n	Mean (\pm SEM)
A	B		
ANGR	PHME	---	---
ANGR	NYVA	8	1.000 (0.000)
ANGR	PHOC	---	---
ANGR	PHSE	8	0.996 (0.981–0.999)
ANGR	PHUM	8	0.996 (0.987–0.999)
PHME	NYVA	25	0.965 (0.956–0.972)
PHME	PHOC	4	insufficient data ¹

PHME	PHSE	---	---
PHME	PHUM	8	0.998 (0.978–1.000)
NYVA	PHOC	79	0.144 (0.125–0.166)
NYVA	PHSE	39	0.608 (0.547–0.665)
NYVA	PHUM	88	0.130 (0.115–0.147)
PHOC	PHSE	33	0.886 (0.863–0.905)
PHOC	PHUM	91	0.432 (0.412–0.452)
PHSE	PHUM	47	0.082 (0.068–0.098)

¹ A minimum of 8 comparisons required for analysis

DISCUSSION

Community Composition

Our results indicate that the National Park of American Samoa supports a diverse ant fauna comprised of at least 44 species from 23 genera. Ant species richness within the park is exemplified by the fact that the park represents only about 2% of the land area of the Samoan Archipelago but supports nearly 65% of all ant species known from the archipelago (Wetterer and Vargo 2003). Many species were widespread throughout the park; 40 species were detected on the Tutuila unit and 32 species were found on the Ta'ū unit. Like most islands in the Pacific Basin, the ant fauna of NPSA is comprised of an assemblage of native and non-native species.

Many of the 23 species that comprise the native ant fauna of NPSA are found throughout the Indo-Pacific region. Natural ranges of ant species are generally poorly understood, but distributions of species such as *Strumigenys godeffroyi*, *Technomyrmex vitiensis*, *Pheidole oceanica* and *Tetramorium pacificum* currently include islands of the western Pacific region such as Australia, New Caledonia, Vanuatu and Fiji, as well as much of Polynesia (Wetterer and Vargo 2003). In contrast, several species have more localized distributions, with *Camponotus chloroticus* and *Vollenhovia pacifica* endemic to the Samoan Archipelago, and *Vollenhovia samoensis* endemic to the Samoan Archipelago and Tonga (Wetterer and Vargo 2003).

An additional species, first collected in this study, was only found on the summit of Mt. Lata, and may be restricted to Ta'ū. This ant, here referred to as *Pheidole* Mt. Lata, was only collected in summit scrub habitat at about 966 m elevation (Figure 21). Because the summit of Mt. Lata is the most isolated location in American Samoa and distant from human disturbance, this ant likely represents an undescribed species rather than one known from elsewhere but not yet reported from the Samoan Archipelago. *Pheidole* is an extremely diverse genus of ants with over 900 described species worldwide (Wilson 2003) and has diversified on Pacific islands (Sarnat and Morneau 2011). Two other species of *Pheidole* are known only from the island of Upolu, Samoa (Wilson and Taylor 1967), but have not been reported in American Samoa (Wetterer and Vargo 2003, this report). Our finding of *P.* Mt. Lata supports Wetterer and Vargo's (2003) conjecture that remote places in American Samoa, such as the summits of Mt. Lata and Mt. Matafao on Tutuila, may harbor previously unrecognized ant species. While we did not find this species at other sites on Ta'ū, its range may also include habitat at lower elevations.



Figure 21. Major worker of *Pheidole* Mt. Lata.

This study also revealed that exotic ants are firmly established throughout the park, including in the most intact habitats and in areas most distant from human disturbance. Overall, 43% of all ant species we collected are considered exotic to the Samoan Archipelago (Wetterer and Vargo 2003). Exotic ants are widespread in the park, and all 39 sites surveyed contained at least one exotic species. *Nylanderia vaga* was particularly widespread, being the only species collected at every site. Species such as *Strumigenys rogeri* (29 sites), *Tapinoma melanocephalum* (18 sites) and *Monomorium floricola* (12 sites) were also commonly found. Exotic ants were most prevalent at a site on the northern tip of Sauma Ridge on Tutuila, where 8 of 10 species were exotic, and they were least prevalent at a site on the northern edge of Luatele Crater on Ta'ū, where only 2 of 16 species were exotic. Because exotic ants are generally associated with human disturbance, it was assumed that the proportion of exotic ants would be greater on Tutuila (40%) than Ta'ū (26%). Ports, roads and human settlements are the most likely avenue for the introduction of exotic ants into forest habitats. Because some species may have penetrated native habitats very quickly, it is difficult to distinguish between those that have been present for a long time versus those that have recently invaded. Most of the exotic species found in our study occur throughout much of the Pacific Basin (Wilson and Taylor 1967, Huddleston and Fluker 1968, Morrison 1997, Wetterer and Vargo 2003).

Our collection of *Strumigenys eggersi* indicates that exotic species are continually becoming established in NPSA, American Samoa, and the Pacific region. *Strumigenys eggersi* is a small, litter-dwelling ant thought to be native to Central or South America (Deyrup *et al.* 2000) and our detection represents the first record of its occurrence in the Pacific Basin. The presence of this ant at 12 sites on the Tutuila and Ta'ū units of the park suggests that it may have been present in American Samoa for many years but overlooked due to its cryptic habits.

The specific role that most ant species play in ecosystem dynamics is unknown, but ants are often categorized into functional groups based on taxonomic status and broad knowledge of their behavior and interactions with other ant species (Anderson 1997, King *et al.* 1998, Narendra *et al.* 2011). On Pacific islands, the most dominant species are often members of the “generalized Myrmicinae”, which in the park includes five species of *Pheidole*. This group of ants, named for the subfamily in which they belong, characteristically recruit rapidly to and dominate ephemeral or high-value food resources. *Pheidole megacephala* is the most successful generalized Myrmicinae in many instances, and is often found in extremely high densities. In contrast, ants in the “opportunist” group are unspecialized “weedy” species that are highly adaptive and capable of occupying a wide range of habitats. Species of *Nylanderia*, *Tapinoma*, *Technomyrmex* and *Tetramorium* are prominent opportunists. Because opportunists are less aggressive than many other species and tend not to dominate habitats, they are often overlooked despite their prevalence. The opportunist group also includes the trap-jaw ant, *Odontomachus simillimus*, the largest and most distinctive species found in NPSA (Figure 22). Unlike many other opportunists, it readily stings humans when agitated. Members of the “cryptic” group also often go unnoticed, primarily because of their small size and habit of living in soil, litter and decaying wood. Cryptic species include *Hypoponera*, *Ponera* and *Strumigenys*. Many cryptic species are specialized predators of small arthropods such as Collembola.



Figure 22. The trap-jaw ant *Odontomachus simillimus* with pupal cases. Note the open, locked mandibles of the individual on the left. Sensory hairs located on the mandibles act as triggers that when contacted initiate rapid closure of the mandibles onto prey.

In contrast to many ant species collected in the park, the impacts of the exotic *Pheidole megacephala* and *Anoplolepis gracilipes* are well documented. These two ants are considered to

be among the 100 worst invasive species worldwide due to their impact on native ecosystems in which they invade (Lowe *et al.* 2000). *Pheidole megacephala* has been found to reduce numbers of both ant and non-ant arthropods in infiltrated habitats (Gillespie and Reimer 1993, Heterick 1997, Hoffmann *et al.* 1999, Vanderwoude *et al.* 2000). Native to Africa, *P. megacephala* is currently found on most tropical and subtropical islands in the Pacific (reviewed by Wetterer 1997) and has likely been in American Samoa since the early 1900s (Wilson and Taylor 1967). Its impact in the park is unknown, but we found it to be highly competitive at baits (see below) and associated with low native ant diversity (the proportion of native ants was 4.3 times higher on sites without *P. megacephala* than on sites with *P. megacephala*). Honeydew-producing aphids, mealybugs and scales (Hemiptera) are common sources of carbohydrates for ants (Way 1963, Styrsky and Eubanks 2007), and habitats supporting these insects are often favored by *P. megacephala*. This rich carbohydrate source may contribute to the high density and dominance of this ant in habitats where these insects are abundant (Beardsley *et al.* 1982, Bach 1991, Campbell 1994). We found *P. megacephala* at several low elevation sites near the village of Vatia at the northern tip of the Tutuila unit as well as at one site above Pago Pago near Fagasa Pass. *Pheidole megacephala* was not detected on the Ta'ū unit, but it has been found in the village of Fiti'uta on the northeast end of the island (U.S. Geological Survey unpublished data). *Pheidole megacephala* generally favors disturbed habitats (Wetterer 1997), and it is unclear whether it will invade relatively intact areas of the park.

Anoplolepis gracilipes also is capable of reducing the diversity of native arthropods (Haines *et al.* 1994, Hill *et al.* 2003, Hoffmann and Saul 2010). This ant's ability to disrupt ecosystem processes and alter forest development through extirpation of the red land crab (*Gecarcoidea natalis*) on Christmas Island in the Indian Ocean has been thoroughly documented (Green *et al.* 1999, O'Dowd *et al.* 2003). *Anoplolepis gracilipes* also attacks seabird chicks and its control is a high priority in several areas of high ecological value, such as Christmas Island (Boland *et al.* 2011) and Johnston Atoll (Stefan Kropidowski, U.S. Fish and Wildlife Service, personal communication). *Anoplolepis gracilipes* was detected at only two coastal sites in the park during our survey. However, its presence at the northern edge of Vatia Bay on the Tutuila unit and near Ma'efu Cove west of Siu Point on the southeast end of the Ta'ū unit indicate that it has the potential to spread in both sections. We also found *A. gracilipes* during our brief survey of coastal habitat on the Ofu unit. However, since *A. gracilipes* has been in American Samoa since at least 1925 (Wilson and Taylor 1967), it may be relatively ineffective at penetrating montane habitats. Like *Pheidole megacephala*, it reaches highest densities in areas with rich carbohydrate sources (Abbott 2005, Abbott 2006) and may be less successful competing with aggressive ants in habitats where carbohydrate resources are scarce. In addition to honeydew-producing insects as sources of carbohydrates, plants containing extrafloral nectaries are also important to ants (Oliveira and Brandão 1991) and could promote the spread of *A. gracilipes* in Samoa (Savage *et al.* 2009, Savage *et al.* 2011). We did not assess the availability of carbohydrate sources at our study sites but limited availability may help explain the distribution of *A. gracilipes* in the park. *Anoplolepis gracilipes* dominates baits, but ant species richness at sites containing *A. gracilipes* was similar to nearby sites lacking this ant. Other studies have shown *A. gracilipes* to coexist with many other ants, particularly smaller species (Hoffmann *et al.* 2014), suggesting that additional research may be needed to understand how habitat conditions may affect coexistence patterns.

The tropical fire ant, *Solenopsis geminata*, first documented in American Samoa on Tutuila in 2002 (Wetterer and Vargo 2003), was not detected during our survey of NPSA. This species is of considerable concern because it forms large colonies, readily stings people and pets, preys

upon native arthropods (Holway *et al.* 2002), negatively impacts the growth and survival of ground nesting seabirds (Plentovich *et al.* 2009), and may pose a threat to hatchling sea turtles (Wetterer 2006). Native to tropical and subtropical regions of the New World, it maintains a near worldwide distribution, including many islands in the Pacific (Wetterer 2011). On Tutuila, this ant is widespread in disturbed habitats. Although *S. geminata* likely displaces less aggressive ants, it appears not to occupy habitat with other aggressive species, such as *Pheidole megacephala* (Wheeler 1910, Wetterer and O'Hara 2002). Therefore, the ability of *S. geminata* to penetrate forest habitat within the park may be inhibited by the existing ant fauna. To our knowledge, *S. geminata* has not been detected on Ta'ū or elsewhere in Manu'a.

The little fire ant, *Wasmannia auropunctata*, is another exotic species of widespread concern in the Pacific Basin but was not detected during our surveys and appears not to be present in American Samoa (Wetterer and Vargo 2003). Like many other fire ants, *W. auropunctata* is notorious for its painful sting and ability to degrade native ecosystems (Lubin 1984, Wetterer *et al.* 1999). This species is spreading in the Pacific, having become established in New Caledonia (Fabres and Brown 1978), Wallis and Futuna (Gutierrez 1981 in Jourdan 1997), the Solomon Islands (Wetterer 1997), Vanuatu (Rapp 1999), Hawai'i (Conant and Hirayama 2000), and Guam (Raymundo and Miller 2012). Vigilance toward this ant on Tutuila at points of entry is a high priority (Mark Schmaedick, American Samoa Community College, personal communication).

Influence of Vegetation Type and Habitat Structure

Vegetation type and elevation, which varied considerably across the survey areas (Whistler 2002, Liu *et al.* 2011), had little influence on ant species richness. That our measures of habitat structure could not effectively explain ant diversity patterns suggests that the carrying capacity for ant species richness is generally similar among sites in NPSA, regardless of vegetation type and location, at least for the current assemblage of ant species. The proportion of exotic ant species at sites also was similar among vegetation types, except for the single site surveyed in montane scrub that alone was dominated by exotic species (8 of 12 species were exotic). Montane scrub vegetation is characterized by trachyte rock that generally supports stunted vegetation (Whistler 2002) and occupies relatively little area of the park. The extent to which montane scrub influenced ant species composition is obscured by the presence of *Pheidole megacephala*, which may have displaced some native ant species. Despite the overall similarity in ant species richness among all vegetation types, the presence of exotic species was negatively associated with elevation, particularly on Tutuila. As expected, exotic ants are less prevalent at high elevation, possibly due to resistance from native ants (Holway *et al.* 2002), less habitat disturbance (Suarez *et al.* 2001), or cooler and wetter conditions.

Species Co-occurrence Patterns

The degree of ant species co-occurrence increased in proportion to the number of sites occupied by a species, particularly for widespread native species such as *Nylanderia minutula*, *Pheidole umbonata* and *Pheidole oceanica*. The two species detected at the most sites, the exotic *Nylanderia vaga* and *Strumigenys rogeri*, also co-occurred with the greatest number of other species, suggesting that their interactions with native species were generally benign. *Tetramorium pacificum* and *Camponotus chloroticus* were found at intermediate numbers of sites, but they co-occurred with many other species presumably because their habitat requirements were widely shared.

There was little evidence of ant species being entirely excluded from sites by other ant species. Considering that *Pheidole megacephala* excludes native ants from habitats that it invades elsewhere (Hoffmann *et al.* 1999, Vanderwoude *et al.* 2000, Hoffmann 2010), it was surprising that this aggressive species coexisted with 25 other species, only slightly fewer than other ant species occupying a similar number of sites. Furthermore, there was no difference in the number of native and exotic species absent from sites occupied by *P. megacephala* (8 species each), suggesting no vulnerability particular to native species. An exception to that may be the native *Pheidole* species. *Pheidole umbonata*, *P. oceanica*, and *P. sexspinosa* were all relatively common and widespread ant species, but each coexisted with *P. megacephala* at only 2, 1, and 0 sites, respectively. Regardless, the pattern whereby *P. megacephala* co-exists with a generally expected number of other ant species appears to contradict our finding that the ratio of native to exotic ants was much lower on sites occupied by *P. megacephala* compared to sites on which it was absent (3.0 ± 0.2 and 0.6 ± 0.1 , respectively). However, *P. megacephala* was generally found at lower elevation sites on Tutuila which tended to support fewer native species. Additional surveys of ant richness and composition at sites across the range of *P. megacephala* are required to fully identify how *P. megacephala* impacts the structure of ant communities in NPSA.

Interestingly, *Pheidole megacephala* and *Anoplolepis gracilipes* were not detected on the same sites even though they were in relatively close proximity (< 200 m apart in one instance) near Vatia Village. A similar pattern was observed in the Yasawa Islands group, Fiji, where these two species occupied different habitats on the same small island (Ward and Beggs 2007). In Hawaii Volcanoes National Park, mutually exclusive territories were found to exist only a few meters apart indicating that populations avoid occupying the same ground (Wetterer 1998). Mechanisms explaining why populations of these two species rarely overlap are unclear, but may be due to nest site availability or the stage in the invasion cycle (Fluker and Beardsley 1970).

Behavioral Dominance at Baits

Pheidole megacephala and *Anoplolepis gracilipes* were clearly dominant over other ants at baits in pairwise comparisons. Although we did not quantify ant abundance on the study sites, both of these species obtained very high densities that probably contributed to their ability to rapidly locate and numerically dominate bait. In Fiji, Ward and Beggs (2007) also found *P. megacephala* and *A. gracilipes* dominating other ants at baits through interference and exploitative competition. Similarly, Lester *et al.* (2009) found high densities of *A. gracilipes* to dominate food resources on islands of the Tokelau Archipelago, allowing only species with sufficiently different foraging modes to coexist. While we found *P. megacephala* and *A. gracilipes* monopolizing a protein-rich bait, other ant species may have coexisted due to differences in feeding behavior or food abundance.

In the absence of *Pheidole megacephala* and *Anoplolepis gracilipes*, the native *Pheidole oceanica* tended to dominate at bait cards and in pairwise comparisons. *Pheidole oceanica*, the only native species at a New Caledonian study site, outcompeted seven exotic species at bait (Cerdá *et al.* 2012). Similarly, *P. oceanica* recruit quicker to bait than eight other ant species on Rose Atoll at the eastern end of the Samoan Archipelago (U.S. Geological Survey unpublished data).

Conclusion

The National Park of American Samoa supports a diverse assemblage of native and exotic ant species. While exotic ants have deeply penetrated native forest within NPSA, our data suggest that habitats at higher elevation, particularly on Tutuila, support a greater proportion of native species than sites at lower elevation. This pattern is expected since factors that facilitate the incursion of exotic ants into native forest, such as the prevalence of roads, human settlements and other habitat disturbance, are all greater in the lowlands. In contrast, habitat variables such as percent cover of the forest canopy and several understory components did not explain ant community composition patterns. Two exotic ant species notorious worldwide for their ability to invade and disrupt native ecosystems, *Pheidole megacephala* and *Anoplolepis gracilipes*, were found at several low elevations sites on the Tutuila and Ta'ū units of the park, and as expected, displayed behavioral dominance over other ant species. The impact of these aggressive ants on the diversity of native and other ants is unclear because of the potentially confounding influence of elevation. We did not measure the impact of exotic ants on native non-ant arthropods, or on ecosystem processes, such as pollination or nutrient cycling, but some impacts are likely to occur. Identifying whether exotic ants affect park resources that are sensitive to disturbance, or critical to ecosystem function, may be warranted. Ant distribution and community composition are likely dynamic, with major changes expected in the distribution of exotic species over time. Future surveys should continue to track distributions of *P. megacephala* and *A. gracilipes* and monitor for the incursion of *Solenopsis geminata* into the park.

A potential management action for controlling aggressive exotic ants is the application of toxic bait. Bait containing hydramethylnon (e.g., Amdro) has proven effective at eradicating relatively small populations of *P. megacephala* in several instances (Hoffmann and O'Connor 2004, Hoffmann 2010, Plentovich et al. 2011). However, *P. megacephala* likely occupies a considerable amount of habitat in and adjacent to the park, so eradication would be difficult and a long-term endeavor due to the incursion of ants into the park from untreated areas outside the park. *Anoplolepis gracilipes* occupies less area than *P. megacephala* in the park, but has proven to be extremely difficult to eradicate. Unless these two ant species are found to have unacceptable impacts on park resources, the most prudent approach to their management would be to minimize their spread into unoccupied habitats. Ant nests are readily transported in potted plants, loose soil, and wood and other building materials, as well as on vehicles. Preventing ants from colonizing substrates that are moved into the park is therefore critical to minimizing further infestation. Monitoring for *P. megacephala* and *A. gracilipes* around plant nurseries or plant propagation sites, as well as at staging areas and where vehicles are parked, is important. If these ants are detected in these areas, then toxic baits can be used to control their populations and reduce the likelihood that they will be further spread in the park.

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