



# Elevated dominance of extrafloral nectary-bearing plants is associated with increased abundances of an invasive ant and reduced native ant richness

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## ABSTRACT

**Aim** Invasive ants can have substantial and detrimental effects on co-occurring community members, especially other ants. However, the ecological factors that promote both their population growth and their negative influences remain elusive. Opportunistic associations between invasive ants and extrafloral nectary (EFN)-bearing plants are common and may fuel population expansion and subsequent impacts of invasive ants on native communities. We examined three predictions of this hypothesis, compared ant assemblages between invaded and uninvaded sites and assessed the extent of this species in Samoa.

**Location** The Samoan Archipelago (six islands and 35 sites).

**Methods** We surveyed abundances of the invasive ant *Anoplolepis gracilipes*, other ant species and EFN-bearing plants.

**Results** *Anoplolepis gracilipes* was significantly more widely distributed in 2006 than in 1962, suggesting that the invasion of *A. gracilipes* in Samoa has progressed. Furthermore, (non-*A. gracilipes*) ant assemblages differed significantly between invaded and uninvaded sites. *Anoplolepis gracilipes* workers were found more frequently at nectaries than other plant parts, suggesting that nectar resources were important to this species. There was a strong, positive relationship between the dominance of EFN-bearing plants in the community and *A. gracilipes* abundance on plants, a relationship that co-occurring ants did not display. High abundances of *A. gracilipes* at sites dominated by EFN-bearing plants were associated with low species richness of native plant-visiting ant species. *Anoplolepis gracilipes* did not display any significant relationships with the diversity of other non-native ants.

**Main conclusions** Together, these data suggest that EFN-bearing plants may promote negative impacts of *A. gracilipes* on co-occurring ants across broad spatial scales. This study underscores the potential importance of positive interactions in the dynamics of species invasions. Furthermore, they suggest that conservation managers may benefit from explicit considerations of potential positive interactions in predicting the identities of problematic invaders or the outcomes of species invasions.

## Keywords

*Anoplolepis gracilipes*, ant communities, ant invasions, extrafloral nectar, island communities, mutualism.

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## INTRODUCTION

The introduction of invasive species to novel habitats poses a major threat to global biodiversity and the maintenance of

ecosystem processes (Walker & Steffen, 1997; Mack *et al.*, 2000; Reaser *et al.*, 2007). Invasions have fundamentally altered community structure across marine, freshwater and terrestrial habitats and have led to significant declines in populations of

native species (Sakai *et al.*, 2001; Callaway & Moran, 2006; Snyder & Allendorf, 2006). Tropical oceanic islands, which are characterized by high levels of endemism, are particularly vulnerable (Fritts & Rodda, 1998; Myers *et al.*, 2000; Reaser *et al.*, 2007). Among insect groups, invasive ants have had especially strong effects on native island communities, causing broad-scale changes in island ecosystems, altering community dynamics across multiple trophic levels and ultimately leading to the dissolution of important ecosystem processes (Holway *et al.*, 2002; O'Dowd *et al.*, 2003). One factor that may contribute to these negative effects is the propensity of invasive ants to associate facultatively with carbohydrate-excreting plants and arthropods, thus displacing native ants in mutualistic associations (Lach, 2003; Ness & Bronstein, 2004).

Native ant species appear particularly vulnerable to the impacts of invasive ants (Holway *et al.*, 2002). For example, Hoffmann *et al.* (1999) found that the invasive ant *Pheidole megacephala* was associated with the reductions of 50 to > 95% in the abundance of co-occurring ants across invaded sites. Such negative effects may occur through direct interactions with native ants, such as increased levels of aggression (e.g. Rowles & O'Dowd, 2007) and usurpation of nesting sites (Fluker & Beardsley, 1970). Invasive ant species may also affect native ant populations indirectly. For example, invaders may depress prey populations or restrict access to carbohydrate resources, such as extrafloral nectar and hemipteran honeydew (Ness & Bronstein, 2004). As a result of the strong ecological consequences of ant invasions, it is important to identify factors that contribute to their progression.

Empirically, invasions have often been observed to include a lag phase in which the invader is not abundant enough to negatively influence co-occurring species (Mack *et al.*, 2000; Simberloff and Gibbons 2004). The transition from this lag phase to an exponential growth phase marks a critical step in species invasions, one that often leads to the most extreme negative consequences for native communities. For example, when yellow crazy ants (*Anoplolepis gracilipes*: Formicinae) were introduced to Christmas Island, they remained at low population densities during a lag phase that lasted > 70 years (O'Dowd *et al.*, 2003). In the 1990s, this species began displaying invasive characteristics. Within c. 10 years, *A. gracilipes* had killed up to one-third of the island's endemic red land crabs (*Gecarcoidea natalis*). Furthermore, *A. gracilipes* actively tended scale insects, and correlative evidence suggests that the combination of increased carbohydrate resources for the ants and population expansion of scale insects led to the death of native canopy trees (O'Dowd *et al.*, 2003). The transition out of a benign lag phase is an important component of the process of invasion; however, the ecological factors that promote this transition remain unclear.

For invasive ants, mutualisms with carbohydrate-excreting plants or arthropods can potentially provide a constant resource to 'fuel' the growth of ant populations. Several authors have suggested that these mutualistic associations

structure ant communities, especially in the tropics (Davidson *et al.*, 2003; Heil & McKey, 2003; Lach, 2003; Bluthgen & Stork, 2007). The carbohydrates provided by honeydew-excreting insects and extrafloral nectary (EFN)-bearing plants are predicted to be more important for invasive ants than native ants in many systems (Holway *et al.*, 2002; Ness & Bronstein, 2004; Styrsky & Eubanks, 2007). For example, Lach (2007) showed that invasive Argentine ants (*Linepithema humile*) were more responsive to native honeydew-excreting scale insects than were co-occurring ant species. Additionally, we have found that experimental increases in nectar levels led to higher forager recruitment and numerical dominance of the invasive ant, *A. gracilipes*, whereas co-occurring non-invasive ants did not respond to changing nectar availability (Johnson *et al.*, unpublished data). However, few experiments or broad-scale geographical surveys have explored whether carbohydrate subsidies drive invasive ant abundances or impacts (but see Eubanks, 2001; Kaplan & Eubanks, 2005).

In this study, we investigated the potential for EFN-bearing plants to promote the invasion of the yellow crazy ant, *A. gracilipes*, in the Samoan Archipelago. Although *A. gracilipes* was first recorded in Samoa in 1925, the species was present only near ports and plantations at very low abundances (Emery, 1925 cited in Wilson & Taylor, 1967). Recent evidence suggests that their populations may be expanding in Samoa. Lester & Tavite (2004) collected *A. gracilipes* in pitfall traps around the port of Apia (Upolu). They found that *A. gracilipes* reached abundances of 191–1060 per trap within 24 h. However, to assess the progression of the *A. gracilipes* invasion, it is critical to understand the abundance and dominance *A. gracilipes* across a broad geographical range and quantify the current composition of ant assemblages across both *A. gracilipes*-invaded and uninvaded sites. Importantly, ants have access to a variety of carbohydrate-excreting plant species in Samoa, which could provide resources for *A. gracilipes* population growth. These species include four native EFN-bearing plants: *Hibiscus tiliaceus* (Malvaceae), *Ipomea pres-caprae* (Convolvulaceae), *Erythrina fusca* (Fabaceae) and *Morinda citrifolia* (Rubiaceae) and one non-native EFN-bearing plant, *Clerodendrum fragrans* (Lamiaceae).

In this study, we addressed the following specific questions: (1) Has the *A. gracilipes* invasion progressed in Samoa? Wilson & Taylor (1967) assessed ant assemblages in Samoa in 1962. We predicted that *A. gracilipes* would be more widespread in our (2006) survey, indicating that the *A. gracilipes* invasion has progressed over the past c. 40 years; (2) Do ant assemblages differ in invaded vs. uninvaded sites? We expected *A. gracilipes* presence to lead to an overall simplification of co-occurring ant assemblages; (3) Are *A. gracilipes* foragers more abundant at extrafloral nectaries than other plant parts? Ants may visit EFN-bearing plants to forage for invertebrates, nectar or other resources. Additionally, plants can alter local biotic and abiotic conditions, by providing shade and shelter from wind and natural enemies. Predominance of ants at nectaries (relative to other plant parts) would be consistent with a primary role for

extrafloral nectar in attracting ants to plants. (4) Does the dominance of EFN-bearing plants across communities correlate with the abundance and/or composition of local plant-visiting ant assemblages? If resources provided by EFN-bearing plants are important factors in ant population growth generally, then the abundances of all ant species should be higher at sites with greater dominance of EFN-bearing plants. However, if extrafloral nectar is more important to some ants (e.g. *A. gracilipes*) than it is to others, then high proportions of EFN-bearing plants per site should lead to numerical dominance of one or a few ant species. We expect these differences to be apparent both on EFN-bearing plants and, more generally, at non-EFN-plant locations, e.g. on other plants and on the ground. Finally, we asked: (5) Is the diversity or abundance of plant-visiting ants lower at sites with high abundances of *A. gracilipes*? If populations of *A. gracilipes* reach high abundances at high nectar levels, and this numerical dominance is associated with a reduced diversity or abundance of other ant species, then patterns would support the hypothesis that opportunistic associations between *A. gracilipes* and native EFN-bearing plants: (i) promote the *A. gracilipes* invasion of island communities and (ii) reduce the biodiversity and abundance of other ants, suggesting a need for future experimental tests.

## METHODS

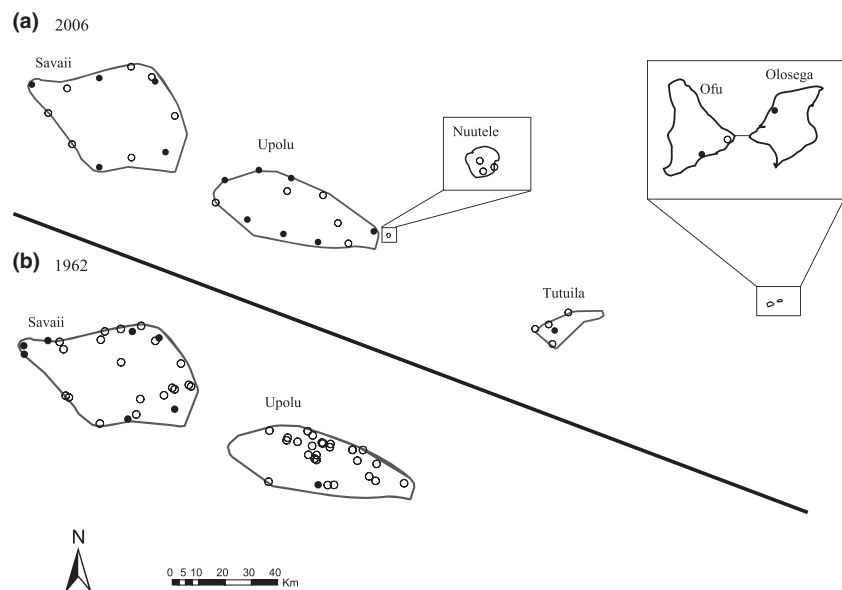
### Survey sites

In July 2006, we surveyed 35 sites spanning the political entities of Independent and American Samoa and including the islands of Upolu, Savaii, Nuutele, Tutuila, Ofu and Olosega (Fig. 1, Appendix S1). On the large islands of Upolu (1115 km<sup>2</sup>) and Savaii (1700 km<sup>2</sup>), sites were located every 15 km around the perimeter of the island. On the small islet of Nuutele, with no

villages, we surveyed three sites. In Tutuila (140 km<sup>2</sup>), we conducted surveys at five sites. We also conducted two surveys on the small island of Ofu and one on its neighbouring island, Olosega (together, Ofu and Olosega are 9 km<sup>2</sup>) (Fig. 1, Appendix S1).

### Survey methodology

All surveys were conducted between 10 and 16 h and thus were focused on diurnally active ants. At each site, we first used a metre tape to delineate a 100-m-long belt transect that was 2 m wide. Every 5 m along each transect, we examined all herbaceous and woody plants within an area of 0.5 × 2 m and recorded the total number of plants. For each site, we calculated the percentage of plants that were EFN bearing. We recorded four native EFN-bearing plants: *Hibiscus tiliaceus* (Malvaceae), *Ipomea pres-caprae* (Convolvulaceae), *Erythrina fusca* (Fabaceae) and *M. citrifolia* (Rubiaceae) and one non-native, EFN-bearing plant, *Clerodendrum fragrans*. This plant was only found at one site (Taputimu, in Tutuila). We recorded the number and identity of ants on each plant, and on plants bearing extrafloral nectaries; we recorded ant location (numbers on nectary bodies vs. numbers on other parts of the plant). Finally, we assessed the activity of ground foragers using 10 × 10 cm cards placed on the ground (Abbott, 2006) < 5 cm from the centre of the belt transect and on non-EFN-bearing plants. We collected type specimens at each site for every ant species recorded. All ants were later identified in the laboratory using Wilson & Taylor (1967), Shattuck (1999) and Andersen (2000). We then determined the geographical origin of each ant species using Wilson & Taylor (1967), Andersen (2000) and Wetterer & Vargo (2005). Species were categorized as native if they were reported as native to Samoa and/or the islands of the South Pacific Ocean.



**Figure 1** Map of sites surveyed in (a) 2006 (the current study) and (b) 1962 (Wilson & Taylor, 1967). Sites invaded by *Anoplolepis gracilipes* are represented by filled symbols and *A. gracilipes*-uninvaded sites are depicted with empty symbols. Note that Wilson and Taylor did not visit Nuutele, Tutuila, Ofu or Olosega.

## Data analysis

### (1) Has the *A. gracilipes* invasion progressed in Samoa?

Wilson & Taylor (1967) assessed the distribution of ant species, including *A. gracilipes* (under previous name, *Anoplolepis longipes*), in Samoa in 1962. They surveyed 55 sites on the two major islands of Savaii and Upolu and observed *A. gracilipes* at eight sites (Fig. 1). We compared results from our survey of *A. gracilipes* incidence on these two islands with their account using a Fisher's exact test to test for differences in the proportion of *A. gracilipes*-invaded sites between the two surveys [Proc Freq; SAS, version 9.1 (SAS Institute 2003)]. While the two surveys did not overlap completely, many sites were shared (Fig. 1). To the extent that both the earlier survey and our survey represent unbiased sampling across the two islands, one would expect no differences between the surveys if indeed the invasion had not progressed. Wilson & Taylor (1967) also reported other accounts of *A. gracilipes* incidence from the literature. However, we only used data from their direct observations, as that 'snapshot' of ant abundances was most comparable to our survey.

### (2) Do Ant assemblages differ in invaded vs. uninvaded sites?

To test for the differences in ant species composition between *A. gracilipes*-invaded and uninvaded sites, we conducted a two-way analysis of similarities (ANOSIM), with Bray–Curtis distance measures and 9999 iterations, using PRIMER, version 6.1.10 (Clarke & Gorley, 2007). This procedure detects differences in species assemblages between two or more groups (Clarke *et al.*, 2006). We included the factors of invasion status (*A. gracilipes*-invaded or uninvaded) and island. As this analysis requires replicates within each combination of invasion status and island, we only included sites from Savaii and Upolu (12 invaded and 12 uninvaded sites). *Anoplolepis gracilipes* workers were excluded from the data. Significantly greater variation between invaded vs. uninvaded sites relative to within invaded/uninvaded sites would indicate that the community composition of non-*A. gracilipes* ants differs with the presence/absence of *A. gracilipes*. We used screen plots to determine the number of axes that maximized the amount of information presented in the ordination and minimized its stress (McCune & Grace, 2002).

Next we used PRIMER v. 6.1.10 (Clarke & Gorley, 2007) to construct non-metric multi-dimensional scaling plots, using Bray–Curtis distances and 9999 iterations. To determine how individual ant species contributed to differences between invaded and uninvaded sites, we used SIMPER (PRIMER v. 6.1.10, Clarke & Gorley, 2007).

Finally, we used ANOVA with the independent factor of *A. gracilipes* invasion status to test for differences between invaded and uninvaded sites in the abundances of all ants and the proportion of native ants per plant. Density of all plants per site was used as a covariate in these analyses. As with many response variables in this study, residuals were non-normally distributed, and normality could not be obtained through

transformations. Therefore, randomization tests were used to evaluate differences among treatments (Manly, 1991). Randomization tests determine *P*-values by comparing an observed test statistic (e.g. *F*-ratio from ANOVA) to a distribution of the test statistic that is expected under the null hypothesis. To create the expected distribution, the response variable values from treatments being compared are pooled, permuted and randomly assigned to the treatments for 9999 iterations. We used randomization test equivalents of ANOVA by embedding Proc GLM code within a SAS randomization test macro programme (Cassell, 2002).

### (3) Are *A. gracilipes* foragers more abundant at extrafloral nectaries than other plant parts?

To test the prediction that there would be more *A. gracilipes* workers on nectaries than any other part of the plant, we used ANOVA [Proc GLM; SAS version 9.1 (SAS Institute 2003)]. The independent factors were location (two levels: nectaries vs. stems, branches, leaves or fruit) and site (15 levels), and the response variable was the number of *A. gracilipes* workers per plant. Plants without extrafloral nectaries were excluded, resulting in a total of 240 plants in the analysis. As above, we used the Cassell (2002) randomization procedure because residuals violated the assumption of a normal distribution.

### (4) Do the levels of extrafloral nectar resources across communities correlate with the abundance and/or composition of local ant assemblages?

We tested the prediction that the abundance of plant-visiting ants increases as the proportion of EFN-bearing plants per site increases using ANCOVA [Proc GLM; SAS version 9.1 (SAS Institute 2003)]. This indirect estimate of extrafloral nectar provides a conservative test: as EFN-bearing plant species may differ from each other in nectar production, any observed correlation between the proportion of EFN-bearing plants and ants likely indicates a strong EFN-ant signal. The independent factors were the percentage of EFN-bearing plants per site, ant type (*A. gracilipes*, other non-native ants or native ants) and their interaction. The response variable was ant abundance per site, and the analysis was conducted separately for *A. gracilipes*-invaded and uninvaded sites ( $n = 15$  and  $n = 20$  respectively). Total plant density per site was used as a covariate in these analyses. A significant interaction for ant type  $\times$  percentage EFN-bearing plants would indicate that different categories of ants exhibit different associations with EFN-bearing plants; we predicted that *A. gracilipes* would demonstrate the strongest positive association. We then used multiple regression analysis (Proc REG; SAS version 9.1) to examine the slope of the relationship between the percentage of EFN-bearing plants and total plant density per site and the individual abundances of (i) *A. gracilipes*, (ii) other non-native ants or (iii) native ants. Species that occurred in five or fewer sites or were represented by five or fewer individuals were excluded from this analysis, resulting in a total of 10 individual regressions. Therefore, we



used a Bonferroni-corrected  $\alpha$  of 0.0005 to determine significance. For (ii) and (iii), we pooled all native and non-native ants, respectively, and examined these relationships separately for the invaded vs. uninvaded sites. We embedded ANCOVA and regressions in a randomization procedure (as described above).

Plants bearing EFN can be considered as a resource, and dominant ants sometimes exclude co-occurring species from resources (Andersen, 1992). We therefore tested whether patterns of ant abundance on EFN-bearing plants reflect abundances at a site generally. Preliminary regressions examined whether dominance of EFN-bearing plants had similar relationships to the proportion of the ant community comprised *A. gracilipes* (i) at 'resource locations', that is, on EFN-bearing plants and (ii) at 'non-resource locations', that is, on the ground and on non-EFN-bearing plants. At both location types, the proportion of *A. gracilipes* was significantly higher when EFN-bearing plants were numerically dominant (resource locations:  $\beta = 1.23$ ,  $P = 0.0017$ ; non-resource locations:  $\beta = 0.58$ ,  $P = 0.0471$ ). Consequently, while we restrict our conclusions to plant-visiting ants, our measures of ant abundances on all plants (EFN bearing + non-EFN bearing) are likely indicative of general, site-level patterns.

(5) *Is the diversity or abundance of co-occurring ants lower at sites with high abundances of A. gracilipes?*

We predicted that the diversity of co-occurring, plant-visiting ants would be negatively related to *A. gracilipes* abundance across the subset of invaded sites. To test this prediction, we first calculated species richness, the Shannon–Weiner diversity index ( $H$ ) and evenness ( $J$ ) (Begon *et al.*, 2006) for: (i) all ants, excluding *A. gracilipes*, (ii) other non-native ants and (iii) native ants. We then used multiple regression analysis (following methods for question 2) to examine the relationships between the abundance of *A. gracilipes* and richness,  $H$  or  $J$  for each of the two categories of co-occurring ant species ( $n = 35$  sites). The abundances of *A. gracilipes*, richness,  $H$  and  $J$  values were all log-transformed. Again, we used the randomization procedure described above to conduct statistical tests due to residuals with significantly non-normal distributions. Finally, we used a Bonferroni-corrected  $\alpha$  of 0.00625 to determine statistical significance, because a total of eight tests were conducted.

## RESULTS

### (1) Has the *A. gracilipes* invasion progressed in Samoa?

We surveyed 24 sites and observed *A. gracilipes* at 12 sites on the islands of Savaii and Upolu. In contrast, Wilson & Taylor (1967) found *A. gracilipes* in 8 of 55 sites in their 1962 survey of the same two islands. The incidence of *A. gracilipes* was significantly higher in our 2006 survey (Fisher's exact test,  $P = 0.0016$ , Fig. 1). This pattern was the strongest on the island of Upolu (Fig. 1).

### (2) Do Ant assemblages differ in invaded vs. uninvaded sites?

We recorded a total of 21 species of plant-visiting ants during our survey of 35 sites across six islands (Appendix S2). Ten species were native to Samoa and/or the islands of the South Pacific Ocean, while the remaining eleven (including *A. gracilipes*) were non-native. Two species were only present in sites that were uninvaded by *A. gracilipes*: the native species *Vollenhovia samoensis* was only observed in one uninvaded site, while the non-native *Plagiolepis alluaudi* was only present in four uninvaded sites. Additionally, the native species *Tetraponera guineense* and the non-native species *Monomorium destructor* were both only observed at one invaded site. The absolute abundance of individuals observed in invaded sites ( $14.17 \pm 1.73$ ) was significantly higher than that of uninvaded sites ( $8.6 \pm 0.15$ , randomization ANCOVA, *A. gracilipes* invasion status:  $P = 0.0137$ , plant density:  $P = 0.6736$ ). Native ants represented 22% ( $\pm 2.5\%$ ) of the individuals at *A. gracilipes*-uninvaded sites, compared with 14% ( $\pm 3.0\%$ ) at *A. gracilipes*-invaded sites (*A. gracilipes* invasion status:  $P = 0.0730$ , plant density:  $P = 0.8505$ ). At invaded sites, *A. gracilipes* workers comprised 60% ( $\pm 1.20\%$ ) of all individuals.

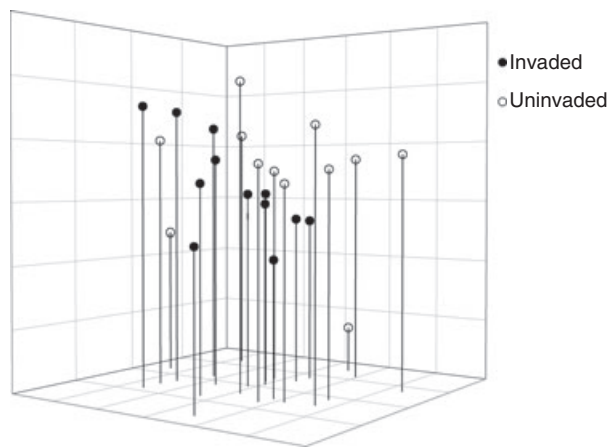
The composition of non-*A. gracilipes* ant assemblages differed between *A. gracilipes*-invaded and uninvaded sites on the large islands of Upolu and Savaii (two-way crossed ANOSIM, Global  $r = 0.171$ ,  $P = 0.037$ ; Fig. 2). However, islands did not significantly differ in species composition ( $r = 0.039$ ,  $P = 0.139$ ). Eight ant species contributed to more than 90% of the dissimilarity between *A. gracilipes*-invaded and uninvaded sites, and six of these had decreased abundances in *A. gracilipes*-invaded sites, relative to uninvaded sites (SIMPER, Table 1).

### (3) Are *A. gracilipes* foragers more abundant at extrafloral nectaries than other plant parts?

There were more *A. gracilipes* workers on nectaries than on the stems and leaves of the five species of EFN-bearing plants (ANOVA, location:  $P < 0.00001$ , site:  $P < 0.00001$ , location  $\times$  site:  $P = 0.3333$ ). This pattern was present even though nectaries typically made up  $< 1\%$  of the total plant surface area. For example, active nectary bodies comprised on average 0.34% ( $\pm 0.04\%$  SE) of the surface area of five *M. citrifolia* plants measured on Savaii. Thus, ant abundance would be expected to be higher on stems and leaves if ants were randomly distributed on the plant.

### (4) Do the levels of extrafloral nectar resources across communities correlate with the abundance and/or composition of local ant assemblages?

At *A. gracilipes*-invaded sites, the total abundance of all ants on plants was four times greater at sites with high proportions of EFN-bearing plants than at sites with no EFN-bearing plants (linear regression,  $r = 0.65$ ,  $P = 0.0094$ ). *Anoplolepis gracilipes*



**Figure 2** Ordination plot comparing non-*Anoplolepis gracilipes* ant species composition between *A. gracilipes*-invaded sites (filled circles,  $n = 12$  sites) and uninvaded sites (open circles,  $n = 12$  sites) in Savaii and Upolu. This plot was created using non-metric multidimensional scaling (NMDS) with Bray–Curtis distance measures and 9999 iterations. *Anoplolepis gracilipes* invasion status significantly contributed to the differences between sites (two-way crossed ANOSIM, global  $r = 0.171$ ,  $P = 0.037$ ); however, the island on which sites were located did not (global  $r = 0.039$ ,  $P = 0.139$ ). The NMDS had a 3-D stress value of 0.08 (PRIMER v.6).

and other ants displayed different relationships with extrafloral nectar availability, as evidenced by a significant interaction between ant type and the proportion of EFN-bearing plants (ANCOVA, ant type,  $P = 0.3869$ , percentage EFN-bearing plants per site,  $P = 0.0214$ , and ant type  $\times$  percentage EFN-bearing plants per site,  $P = 0.0036$ ) at *A. gracilipes*-invaded sites. *Anoplolepis gracilipes* displayed a strong, positive relationship with the proportion of EFN-bearing plants per site (Table 2; Fig. 3a). However, after Bonferroni correction, there were no significant relationships between the percentage of EFN-bearing plants and the abundances of either native or other (non-*A. gracilipes*) non-native ants, across both *A. gra-*

*cilipes*-invaded and uninvaded sites (Table 2, Fig. 3b,c). Plant density was not significantly correlated with abundances of any ant species (Table 2).

### (5) Is the diversity or abundance of co-occurring ants lower at sites with high abundances of *A. gracilipes*?

Within invaded sites, higher *A. gracilipes* abundances were associated with a lower diversity of plant-visiting native ants (Fig. 4a, Table 3), although this effect was not significant after Bonferroni corrections were applied. Decomposing the native ant diversity indices into species richness and evenness, while both were negatively correlated with *A. gracilipes* abundances, we found that this effect was only significant for species richness (Fig. 4b,c, Table 3). In contrast, *A. gracilipes* abundances were not significantly related to the diversity, richness and evenness of other non-native ants, nor were they related to abundances of either native or other non-native ants (Table 3).

One common non-native ant species (*Paratrechina longicornis*) reached high abundances at some sites; abundances were occasionally even higher than those of *A. gracilipes* (Appendix S2). Therefore, the negative association between *A. gracilipes* and other ants could conceivably be driven by *P. longicornis* if it positively co-varied with *A. gracilipes*. However, there was no significant relationship between *P. longicornis* and the diversity of native ants (multiple regression,  $r^2 = 0.15$ , *P. longicornis*:  $\beta = 0.1401$ ,  $P = 0.3239$ , plant density:  $\beta = 0.0050$ ,  $P = 0.1722$ ), or between the abundances of *A. gracilipes* and *P. longicornis* (multiple regression,  $r^2 = 0.62$ , *A. gracilipes*:  $\beta = -0.0288$ ,  $P = 0.8548$ , plant density:  $\beta = -0.0189$ ,  $P = 0.0042$ ). These patterns suggest that native ant diversity is related to the abundance of *A. gracilipes* but not of *P. longicornis*.

## DISCUSSION

Invasive ants readily associate with EFN-bearing plants in their introduced ranges (Lach, 2003; Ness & Bronstein, 2004). These

**Table 1** Summary of differences in the abundances of the non-*Anoplolepis gracilipes* ant species that contributed to c. 90% of the dissimilarity between *A. gracilipes*-invaded vs. uninvaded sites. Only sites from Savaii and Upolu were used in this analysis.

Species	Mean $\pm$ SE abundance (uninvaded)	Mean $\pm$ SE abundance (invaded)	Difference (%)	Contribution to dissimilarity (%)
<b>Non-native</b>				
<i>Monomorium floricola</i>	3.40 $\pm$ 0.70	1.61 $\pm$ 0.41	-53	32.7
<i>Paratrechina longicornis</i>	2.08 $\pm$ 0.59	2.61 $\pm$ 1.01	+27	25.01
<i>Monomorium pharoensis</i>	0.80 $\pm$ 0.27	0.65 $\pm$ 0.25	-19	10.78
<i>Tetramorium simillimum</i>	0.77 $\pm$ 0.32	0.36 $\pm$ 0.08	-53	8.69
<b>Native</b>				
<i>Tetramorium tonganum</i>	0.41 $\pm$ 0.33	0	-100	4.47
<i>Solenopsis papuana</i>	0.24 $\pm$ 0.24	0.18 $\pm$ 0.13	-25	4.03
<i>Pheidole sexspinoso</i>	0.27 $\pm$ 0.24	0.11 $\pm$ 0.11	-59	3.37
<i>Camponotus chloroticus</i>	0.13 $\pm$ 0.08	0.24 $\pm$ 0.18	+85	2.32

interactions may provide fuel for the growth of invasive ant populations, and thereby mediate the negative influences of invasive ants on other species, especially co-occurring ant species. We examined this hypothesis using surveys of the invasive ant, *A. gracilipes*, co-occurring ants and EFN-bearing plants in the Samoan Archipelago. We found that *A. gracilipes* workers were more abundant on extrafloral nectaries than other plant parts. In addition, overall ant abundance was higher at sites with higher proportions of EFN-bearing plants, with stronger positive associations for *A. gracilipes* than for other ant species. Furthermore, the species richness of plant-visiting native ants was lower at sites with high *A. gracilipes* abundance. These correlative data indicate that negative influences of *A. gracilipes* on co-occurring ants may be mediated by the amount of available extrafloral nectar resources.

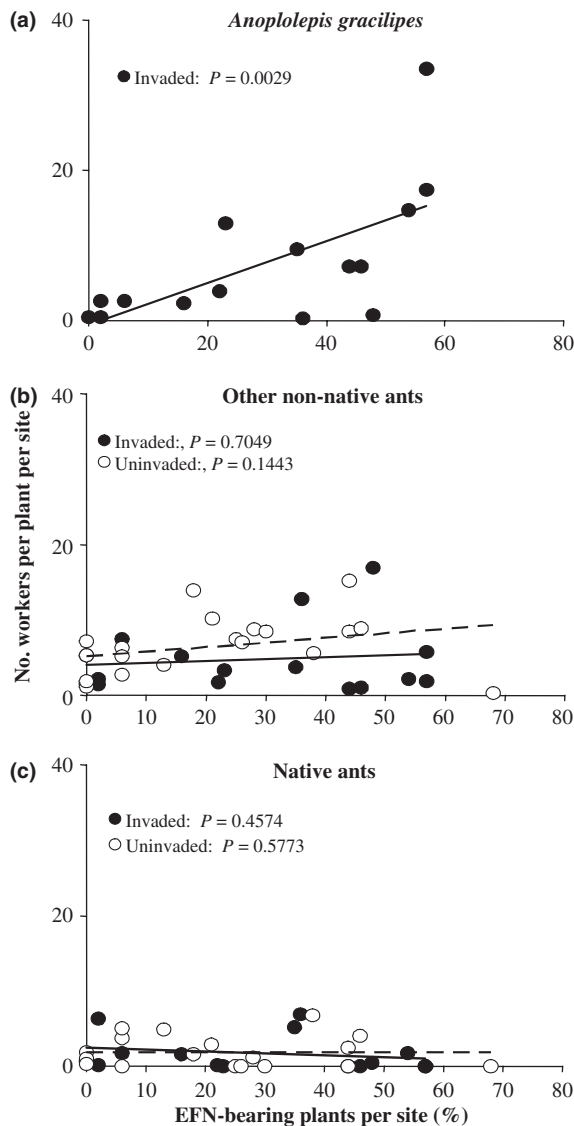
If extrafloral nectar resources are valuable to invasive ants (including *A. gracilipes*), then we predicted that workers should spend more time at nectaries than on the stems and leaves of EFN-bearing plants. If, however, *A. gracilipes* workers are randomly distributed across all parts of the plants, then it is less likely that nectar is responsible for the presence of *A. gracilipes* on EFN-bearing plants. Our finding that *A. gracilipes* was more abundant at nectaries than other plant parts supported the prediction that extrafloral nectar is important to this species. Moreover, in prior work, we manipulated nectar availability and showed that increasing nectar levels altered ant recruitment, tending and foraging behaviours, most strongly for the invasive species, *A. gracilipes* (Johnson *et al.*, unpublished data). Similarly, Lach (2007) demonstrated that *L. humile* (the Argentine ant) was more likely to forage on floral nectar of *Protea nitida* if native honeydew-excreting

arthropods were found on the plants, a response that native ants did not display. In another study, she showed that *A. gracilipes* was not only more likely to be found on floral nectaries, but also collected much more floral nectar than other non-native ants (including *L. humile*; Lach, 2005). Taken together, these data suggest that carbohydrate-rich resources may be particularly important for invasive ants. Furthermore, the importance of nectar resources to *A. gracilipes* provides a possible explanation for the patchy distribution of this species across the Samoan Archipelago. In a similar broad-scale investigation, Eubanks (2001) found patchy distributions of the red imported fire ant (*Solenopsis invicta*) in agricultural systems of the South-eastern United States. He suggested that the presence of ant-tended aphids explained much of this variation – a supposition that was later supported by manipulative experiments (Eubanks, 2001; Kaplan & Eubanks, 2005).

We predicted that EFN-bearing plants provide important resources to ant assemblages, leading to higher abundances of ants as the extrafloral nectar levels in the community increase. The finding that *A. gracilipes* was strongly, positively correlated with the dominance of EFN-bearing plants supports this prediction and corresponds with other studies of invasive ants, particularly in the subfamilies Formicinae (e.g. *A. gracilipes*, *P. longicornis*) and Dolichoderinae (e.g. *L. humile*) (Holway *et al.*, 2002; Ness & Bronstein, 2004). For example, *L. humile* only became dominant in the ant community of a South African vineyard after the introduction of honeydew-excreting insects (Addison and Samways 2000). Additionally, *A. gracilipes* have been observed tending honeydew-excreting scale insects in high abundances in both agricultural (Greenslade, 1971) and forested (Abbott & Green, 2007) habitats. Recently, authors have suggested that EFN-

**Table 2** Relationships between the abundances of the most common ant species, and the proportion of EFN-bearing plants per site and the density of all plants per site.  $\beta$  is the partial regression coefficient. The number of *Anoplolepis gracilipes*-invaded/uninvaded sites in which each species was recorded is also presented. Ant species that occurred in five or fewer sites or were represented by five or fewer individuals were excluded from these regression analyses. As 10 separate tests were conducted, we used a Bonferroni-corrected  $\alpha$  of 0.005 to determine significance and bolded significant relationships.

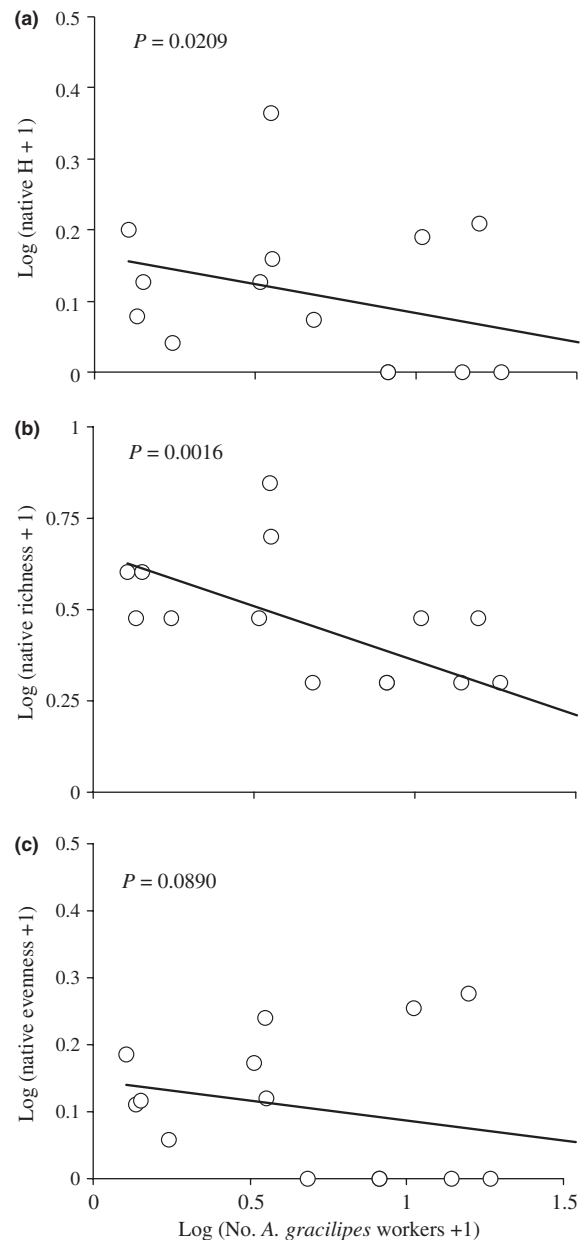
Species	Subfamily	Presence at invaded/ uninvaded sites	Proportion of EFN-bearing plants per site		Plant density		$r^2$
			$\beta$	<i>P</i> -value	$\beta$	<i>P</i> -value	
Non-native							
<i>Anoplolepis gracilipes</i>	Formicinae	15/–	<b>27.33</b>	<b>0.0027</b>	0.1831	0.2251	0.48
<i>Paratrechina longicornis</i>	Formicinae	13/18	1.72	0.0151	–0.05	0.5569	0.14
<i>Paratrechina bourbonica</i>	Formicinae	2/4	–0.34	0.0396	0.02	0.9063	0.33
<i>Monomorium floricola</i>	Myrmicinae	15/18	0.98	0.0071	–0.03	0.9745	0.09
<i>Monomorium pharoensis</i>	Myrmicinae	11/14	1.13	0.6227	0.003	0.4849	0.06
<i>Tetramorium simillimum</i>	Myrmicinae	10/15	–0.61	0.4892	0.003	0.0999	0.03
Native							
<i>Camponotus chloroticus</i>	Formicinae	4/7	0.14	0.0090	–0.005	0.1019	0.06
<i>Tapinoma minutum</i>	Dolichoderinae	3/6	0.06	0.0169	0.03	0.5427	0.31
<i>Solenopsis papuana</i>	Myrmicinae	3/5	–0.62	0.1724	0.007	0.0595	0.07
<i>Tetramorium tonganum</i>	Myrmicinae	3/5	0.30	0.0871	0.004	0.1445	0.01



**Figure 3** Relationship between the percentage of EFN-bearing plants per site and the mean abundance of (a) *Anoplolepis gracilipes*, (b) other non-native ants and (c) native ants ( $n = 15$  invaded sites and  $n = 20$  uninvaded sites).

bearing plants may influence invasive ants in a similar manner to these honeydew-excreting arthropods (Lach, 2003; Ness & Bronstein, 2004). However, to our knowledge, this study is the first to provide evidence that invasive ants positively co-vary with the proportion of EFN-bearing plants in communities, indicating the potential importance of extrafloral nectar to invasion dynamics.

Unlike the abundance of *A. gracilipes*, which displayed a positive linear relationship to EFN-bearing plants, the abundances of other plant-visiting ant species did not vary positively with EFN frequency across sites. These data suggest that by supporting the population growth of the invader, EFN-bearing plants may negatively affect other ants. Consistent with this idea, we found that the species richness of native ants was lower at sites with high abundances of *A. gracilipes*, and that



**Figure 4** Relationship between *Anoplolepis gracilipes* abundance and (a) native ant species diversity (Shannon–Weiner  $H$ ), (b) native ant species richness and (c) native ant species evenness (Shannon–Weiner  $J$ ). Note log transformations of all variables. ( $n = 15$  invaded sites). After Bonferroni correction, only the relationship in (b) remains significant.

the composition of co-occurring ant species significantly differed between *A. gracilipes*-invaded and uninvaded sites. Most of the ant species that contributed to these differences (including three native species) experienced declines in abundance when *A. gracilipes* workers were present. If these dynamics are indeed occurring, then the presence of EFN-bearing plants may serve to reduce the abundance of non-invasive ants and simplify ant assemblages, despite the increased resources provided by the plants.



**Table 3** Relationships between non-*Anoplolepis gracilipes* ant abundance and diversity measures and two variables that differed among sites: *A. gracilipes* abundance and plant density. 'Non-native ants' refer to all non-native ants excluding *A. gracilipes*. Ant abundances were log transformed prior to multiple regression analysis. As eight separate tests were conducted, we used a Bonferroni-corrected  $\alpha$  of 0.00625 to determine significance and bolded significant relationships.  $N = 15$  *A. gracilipes*-invaded sites.

Dependent variable	<i>Anoplolepis gracilipes</i> abundance		Plant density		$r^2$
	$\beta$	$P$ -value	$\beta$	$P$ -value	
Native ant					
Abundance	-0.3959	0.0932	0.0096	0.2199	0.22
Diversity ( $H$ )	-0.1603	0.0209	0.0052	0.0311	0.42
Richness	<b>-0.3982</b>	<b>0.0016</b>	0.0066	0.0781	0.58
Evenness ( $J$ )	-0.1240	0.0890	0.0042	0.0886	0.28
Non-native ant					
Abundance	-0.0596	0.7189	-0.0136	0.0325	0.45
Diversity ( $H$ )	0.0422	0.3554	-0.0016	0.2966	0.11
Richness	0.0474	0.3150	-0.0021	0.2067	0.14
Evenness ( $J$ )	-0.0069	0.7909	0.0005	0.6139	0.02

Although most of the prior studies have focused on the ground-foraging (rather than plant-foraging) ant community, a negative association between invasive and native ants has been commonly observed following ant invasions (Holway *et al.*, 2002). For example, Abbott (2006) found that *A. gracilipes* was associated with reduced abundances of co-occurring ants. Similarly, Sarty *et al.* (2007) documented lower species richness of ant communities on islands of Tokelau that were invaded by *A. gracilipes*. Additionally, Lester & Tavite (2004) presented anecdotal evidence that ants foraging for extrafloral nectar in Tokelau were negatively influenced by *A. gracilipes*. Specifically, when *A. gracilipes* were observed visiting EFN, no other ant species occurred on the plant. In contrast, multiple ant species foraged for extrafloral nectar in sites where *A. gracilipes* was absent. These studies, in combination with the data presented here, indicate that *A. gracilipes* may have strong, negative effects on co-occurring ant assemblages – spanning both plant- and ground-foragers. Similar consequences have been found for ant assemblages in locales invaded by the Argentine ant (*L. humile*; Holway *et al.*, 1998; Sanders *et al.*, 2001), the red imported fire ant (*Solenopsis invicta*; Porter & Savignano, 1990) and the big headed ant (*Pheidole megacephala*; Hoffmann *et al.*, 1999). As ants are important to the population dynamics of a variety of plants and animals (Wilson & Hölldobler, 1990), a simplification of ant assemblages caused by ant invasions could lead to cascading declines of species across multiple trophic and taxonomic levels (Sanders *et al.*, 2001; Moya-Laraño & Wise, 2007).

We have examined some alternate explanations for the patterns observed in this study and are able to reject some of them, while others need further testing. First, plant density

could potentially affect ant abundance, independent of the dominance of EFN-bearing plants. Plants can modify local abiotic conditions, provide refuge and housing and often host insect prey. However, these general effects of plant density were apparently relatively unimportant in our system compared with the dominance of EFN-bearing plants. We found no significant relationships between plant density and metrics of *A. gracilipes* abundance. Moreover, our experimental data (Johnson *et al.*, unpublished data) demonstrated that ants, and especially *A. gracilipes*, responded strongly to experimentally manipulated nectar levels. Second, honeydew-excreting insects could also influence ant assemblages (O'Dowd *et al.*, 2003; Styrsky & Eubanks, 2007). However, we found no significant differences in the numbers of ant-tended Hemiptera across sites (Savage, unpublished data). We have also experimentally demonstrated that ants are significantly less likely to tend honeydew-excreting insects when nectar is available (Johnson *et al.*, unpublished data). Finally, other aspects of the environment, such as soil characteristics, resource availability or the availability of nest sites for ants, could also co-vary with both *A. gracilipes* abundance and the frequency of EFN-bearing plants. Manipulative experiments that tease apart the effects of EFN-bearing plants, invasive ants and honeydew-excreting insects, and their interaction on co-occurring ant communities are currently underway to determine the mechanisms leading to the patterns reported here. Additionally, it will be important to ascertain the influence of *A. gracilipes* on other (i.e. non-ant) arthropods and plants.

## CONCLUSIONS

Understanding geographical variation in the abundance and community-level impacts of invasive species will be critical to predict the population expansion of invaders and prevent local extirpation of native species. Importantly, novel positive interactions that include non-native species may alter the effects of invaders on co-occurring community members (Richardson *et al.*, 2000; Stachowicz, 2001; Bruno *et al.*, 2005). In this study, we documented variation in the abundance of the invasive ant, *A. gracilipes*; the abundance of co-occurring ants, and the abundance of EFN-bearing plants across 35 sites and six islands of the Samoan Archipelago. These broad-scale surveys are consistent with the hypothesis that plant-derived, carbohydrate-rich resources can increase both the local abundance of *A. gracilipes* and the negative impacts of this invader on native ant species. These findings suggest that conservation managers may benefit from explicit considerations of potential positive interactions in predicting the identities of problematic invaders or the outcomes of species invasions.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Appendix S1** Latitude and longitude coordinates of survey sites in independent and American Samoa.

**Appendix S2** Density of ants (no. ants/plant/site) at survey sites in Independent and American Samoa, July 2006.

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