

COMPOSITIONAL AND FUNCTIONAL STABILITY OF ARTHROPOD COMMUNITIES IN THE FACE OF ANT INVASIONS

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Abstract. There is a general consensus that the diversity of a biotic community can have an influence on its stability, but the strength, ubiquity, and relative importance of this effect is less clear. In the context of biological invasions, diversity has usually been studied in terms of its effect on a community's invasibility, but diversity may also influence stability by affecting the magnitude of compositional or functional changes experienced by a community upon invasion. We examined the impacts of invasive ants on arthropod communities at five natural area sites in the Hawaiian Islands, and assessed whether differences among sites in community diversity and density variables were related to measures of stability. Ant invasion was usually associated with significant changes in overall community composition, as measured by Bray-Curtis distances, particularly among endemic subsets of the communities. Changes in mean species richness were also strong at three of the five sites. Among sites, diversity was negatively related to stability as measured by resistance to overall compositional change, but this effect could not be separated from the strong negative effect of invasive ant density on compositional stability. When compositional stability was measured as proportional change in richness, the best predictor of stability among endemic community subsets was endemic richness, with richer communities losing proportionately more species than species-poor communities. This effect was highly significant even after controlling for differences in invasive ant density and suggested that communities that had already lost many endemic species were resistant to further species loss upon ant invasion, while more intact communities remained vulnerable to species loss. Communities underwent strong but idiosyncratic functional shifts in association with ant invasion, both in terms of trophic structure and total arthropod biomass. There were no apparent relationships, however, between functional stability and community diversity or density measures. Instead, invasive ant density was the best among-site predictor of the magnitude of functional change. Overall, diversity appeared to be a poor predictor of stability in the face of ant invasion in these communities, possibly because any actual diversity effects were overshadowed by community-specific factors and variation in the magnitude of the ant-mediated perturbation.

Key words: *Argentine ant; arthropod communities; big-headed ant; biological invasions; diversity; Hawaii; invasive ants; Linepithema humile; Pheidole megacephala; stability.*

INTRODUCTION

The relationship between a community's diversity and its stability has been the topic of much research aimed at understanding the functioning of ecosystems and the importance of preserving biological diversity. The maintenance of a community's functional stability in the face of perturbations has many practical implications, potentially affecting the ecosystem services that humans rely upon (Hooper et al. 2005). In addition, the compositional stability of biological communities can be a direct indicator of whether conservation goals, such as species preservation, are likely to be met. The influence

of diversity on the stability of communities undergoing biological invasions has as yet received relatively little attention in this debate. It is therefore unclear whether diversity plays a role in how a community responds to invasion (as opposed to whether it becomes invaded in the first place), and if so, how important this influence is relative to other factors that affect community properties and species persistence.

In spite of a long, vigorously contested and ongoing debate, there is a consensus emerging that the diversity of a biotic community can have an influence on its stability (MacArthur 1955, Elton 1958, Hurd et al. 1971, May 1972, Pimm 1984, Naeem et al. 1994, Tilman and Downing 1994, Huston 1997, Wardle 2001, Hooper et al. 2005). The strength and nature of this relationship, however, is variable, and depends in part on which communities are examined and which measures of stability are considered (Srivastava and Vellend 2005). Many empirical diversity-stability studies have focused

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on grassland communities (e.g., McNaughton 1977, Tilman and Downing 1994, Sankaran and McNaughton 1999, Lyons and Schwartz 2001, Foster et al. 2002, Zavaleta and Hulvey 2004), but other communities with broader taxonomic scope, including multitrophic experiments in micro- and mesocosms, have also been investigated (Hurd et al. 1971, Naeem et al. 1994, McGrady-Steed et al. 1997). A common finding has been that compositional stability, a community's resistance to changes in species identities and abundances upon perturbation, is negatively related to diversity (McNaughton 1977, Tilman 1996, Foster et al. 2002). On the other hand, a community's functional stability (the ability to resist changes in such aggregate properties or processes as biomass, productivity, rates of decomposition or nutrient cycling, and invasibility) has often been found to be enhanced by greater diversity (McNaughton 1977, Naeem et al. 1994, 2000, Tilman 1996, Levine 2000), although some of these conclusions have been disputed (Huston 1997, Doak et al. 1998, Wardle 2001).

The diversity–stability question is relevant to the study of biological invasions because factors that influence the stability of a community in the face of species invasion may help predict the magnitude of the impact that will be incurred. Impact on a recipient community can be measured both in terms of compositional change and functional change. Understanding compositional change is important because it may be the mechanism by which aggregate functional properties, such as productivity or trophic structure, are stabilized, if compositional change is compensatory (McNaughton 1977, Tilman 1996). This mechanism could therefore be very relevant to conservation, where maintenance of ecosystem function is highly valued. But with today's rapid pace of species introductions, community compositional change may also signal losses or declines of endemic species. This biodiversity loss is generally regarded as a cause for concern, even if introduced species maintain community or ecosystem function through compensation (Schwartz et al. 2000, Srivastava and Vellend 2005).

The use of biological invasions as natural experiments can in turn provide insight into the diversity–stability question. Most studies of community stability have examined responses to such perturbations as disturbance (fire, grazing, manual), nutrient addition, and drought (Srivastava and Vellend 2005). Yet the addition of new species originating from distant biogeographic regions is an increasingly common perturbation to communities worldwide (Mack et al. 2000). While a number of studies have investigated the effects of diversity on the likelihood of successful species invasion (i.e., invasibility [Levine 2000, Naeem et al. 2000, Lyons and Schwartz 2001, Foster et al. 2002, Kennedy et al. 2002, Zavaleta and Hulvey 2004]), an equally important but relatively unexplored question concerns how diversity might influence the magnitude of changes that a community

experiences upon invasion. If we apply the “insurance hypothesis” (McCann 2000) to biological invasions, for instance, we might predict that functional stability should be enhanced in diverse communities because of the greater likelihood of possessing species that are resistant to competition or predation from new invaders, or that can take advantage of resources made available in the course of new invasions.

Part of the debate regarding the linkage between diversity and stability concerns the strength of this influence relative to other factors that clearly affect community and ecosystem processes (Huston 1997, Srivastava and Vellend 2005). In this context, observational studies of actual biological invasions, while usually more poorly suited than manipulative experiments for isolating and measuring the exact role of diversity, may nevertheless accurately depict the importance of diversity in comparison to other intrinsic and extrinsic factors that simultaneously influence stability. In the present study, we investigated the compositional and functional stability of arthropod communities at five sites in the Hawaiian Islands that were being invaded by one of two aggressive ant species, the Argentine ant (*Linepithema humile*) and the big-headed ant (*Pheidole megacephala*). We measured total compositional change as well as changes in richness in these communities, and we evaluated functional stability in terms of changes in total arthropod biomass and shifts in trophic structure. Last, we assessed whether differences among sites in community diversity and density variables were related to these measures of stability, and whether any such relationships might be useful for predicting the magnitude of impacts arising from similar invasions.

METHODS

Study sites

Five middle to high elevation mesic shrubland or savannah ecosystem sites were chosen on the islands of Maui and Hawaii, such that each represented a homogeneous habitat undergoing invasion by an expanding unicolonial population of invasive ants. Pre-existing data on ant population spread over time and/or historical distributional maps were available for four of the five sites (Krushelnycky et al. 2005; C. Farmer, unpublished data), and the fifth was monitored closely for over a year prior to initial sampling, with the population continuing to expand over the following two years. Surrounding areas, while sometimes harboring several ant species that form small colonies (*Cardiocondyla kagutsuchi* and *Hypoponera opaciceps*), were uninvaded by any dominant, unicolonial invasive ants (i.e., species that form large, continuous expanses of cooperating nests). The five sites were all located in natural areas supporting mostly native vegetation. Habitat homogeneity within each site was judged by consistency of vegetative community type and species composition, as well as by the lack of apparent changes in substrate

type or levels of disturbance. There were differences between sites, however, in substrate age, annual rainfall, and vegetative type and composition, and hence arthropod density and diversity.

The five sites were as follows. (1) The Puu O Ili site, at 2360 m elevation on the west slope of Haleakala volcano, Maui, in Haleakala National Park, supports a fairly dense shrubland. (2) The Kalahaku site, at 2800 m elevation, also in Haleakala National Park, is upslope from Puu O Ili and is characterized by a much more sparse shrub canopy and large expanses of bunchgrass and bare cinder groundcover. The substrate at both sites is between approximately 140 000 and 360 000 years old (Bergmanis et al. 2000, Sherrod et al. 2006). (3) The Ahumoa site, at 1880 m on the southwestern slope of Mauna Kea, Hawaii Island, is relatively open shrubland with dense grass and herb ground cover on top of a 14 000–65 000 year-old substrate (Wolfe and Morris 1996). (4) The Pohakuloa site, at 2060 m elevation at the base of the south slope of Mauna Kea, Hawaii Island, is situated on substrate dating from the Holocene to Pleistocene (Wolfe and Morris 1996) and supports a savannah vegetation community. (5) The Huluhulu site, located at 2040 m elevation in a 1500–3000 year-old *pahoehoe* lava flow (Wolfe and Morris 1996) in the saddle area between Mauna Kea and Mauna Loa, Hawaii Island, is characterized by relatively early successional open shrubland within mostly bare rock groundcover. The Ahumoa site is being invaded by the big-headed ant (*P. megacephala*), while the other four sites are all being invaded by the Argentine ant (*L. humile*). These two species are among the most dominant invasive ants worldwide, and are primarily generalist predators and scavengers, but can also engage in extensive tending of honeydew-producing Hemiptera (Holway et al. 2002a).

Sampling design

As in most studies examining the impacts of invasive ants on arthropod communities, we assessed ant effects by comparing arthropod communities in invaded areas with adjacent uninvaded areas. Ethical concerns prohibited the experimental introduction of ants into randomly assigned treatment plots. However, our sites were carefully selected so as to minimize confounding factors that might be associated with static ant distributional boundaries, habitat gradients, or with invasions from habitat edges (e.g., Heterick 1997, Human and Gordon 1997, Bolger et al. 2000). The ant population boundaries at our sites therefore marked the extents to which ants had invaded to date, and did not appear to represent abiotic limits that might also affect other arthropods.

At each site, we mapped the ant population boundary at points spaced at haphazard intervals of roughly 40–100 m. From each point, we measured behind the ant boundary a distance of 100–175 m; distances were greater at sites with faster rates of ant spread, and at the

two Haleakala National Park sites on Maui we measured 50–100 m behind experimental treatment areas located on the ant population boundaries (which were designed to slow outward ant spread). At each of five such locations at each site, we randomly selected a compass bearing, and walked to the nearest habitat patch that contained all of the dominant shrub or tree species at the site. We defined these as the two to four most common shrub or tree species at a site; four of the five sites had only two or three common species and all of these were used, while at the higher diversity Puu O Ili site we limited sampling to four of the most common species. At each of these patches, we installed a 5 × 5 m sampling plot that contained all of these dominant shrub or tree species as well as some of the intervening grassland or bare ground habitat. Each of these five plots was then matched by a control sampling plot located 120–175 m in front of the expanding ant population boundary. Control habitat patches were again chosen to include all of the dominant shrub or tree species at the site, and the exact position of each control plot within the patch was chosen so that the vegetative cover matched as closely as possible that of the invaded plot situated across the ant boundary. Percent covers of dominant shrub or tree species in control plots deviated from those in matched invaded plots by less than 15%. Based on recent rates of outward spread at the five sites, plots were estimated to have been invaded for at least four years.

We employed three standardized sampling techniques, which should have targeted the majority of species likely to interact with ants in these habitat types, to quantify arthropod densities in each plot. First, we placed three pitfall traps (300 mL, 80 mm mouth diameter plastic cups half-filled with a 50:50 propylene glycol:water solution as preservative), separated by at least 2 m, in each plot, with one randomly chosen trap baited around the rim with blended fish and the other two unbaited. These traps were left open for two weeks. Second, in each plot we collected leaf litter from three different areas, mixed it together and removed 1 L of litter, and placed this in a Berlese funnel extractor for 24 hours. Third, in each plot we beat the two dominant shrub or small tree species that supported the highest arthropod richnesses at the site (Krushelnycky 2007). These plant species were: Ahumoa site, *Dubautia linearis*, *Dodonea viscosa*; Pohakuloa site, *Myoporum sandwicensis*, *Che-nopodium oahuensis*; Huluhulu site, *Leptocophylla tameiameiae*, *Vaccinium reticulatum*; Puu O Ili site, *L. tameiameiae*, *Sophora chrysophylla*; Kalahaku site, *L. tameiameiae*, *Dubautia menziesii*. Each plant species received five beats, spread among multiple individual plants in the plot if possible, and all arthropods were collected onto a 1 × 1 m beating sheet and aspirated.

Because examining species-level variables, such as diversity and richness, and determining arthropod species identities were priorities of this study, the laborious specimen identification process made seasonal

or multiyear sampling at all of the sites unfeasible. Instead, we sampled on one occasion at each site, during summer when arthropod abundances and diversities should have been highest. Sampling occurred from 22 August to 7 September 2002 for the Ahumoa site; from 20 August to 5 September 2002 for the Pohakuloa site; from 14 June to 28 June 2003 for the Kalahaku site; from 6 July to 20 July 2003 for Puu O Ili site; and from 15 August to 30 August 2003 for the Huluhulu site. Because 2002 and 2003 experienced similar weather, we don't believe that our sampling in two different years was likely to have a strong effect on our analyses of among-site patterns. For example, rainfall data at a pair of rain gauges located near our study sites (Haleakala RS 338 on Maui and Halepohaku 111 on Hawaii Island) indicate that annual rainfall totals varied by less than 24% from 2001 to 2003 in both areas (data *available online*).²

Arthropod identification

A total of 104 146 arthropods were collected at the five study sites. With the exception of Acari (mites), Pseudococcidae (mealybugs), parasitic Hymenoptera, and immature individuals of a number of taxa, all individual arthropods were identified as one of 323 species or morphospecies. The vast majority of morphospecies were identified to genus. These taxonomic identifications were made with the help of many systematists, taxonomists, and other specialists (see *Acknowledgments*), allowing confidence that nearly all represent unique species-level taxa; in a very few cases of uncertainty, a conservative approach was taken and taxa were grouped. All taxa are therefore referred to hereafter as species. The species were assigned as either endemic, introduced to the Hawaiian Islands, or of unknown provenance according to Nishida (2002), other literature and the knowledge of specialists in cases of new species or new records for the islands. Representative specimens are deposited at the Bernice P. Bishop Museum, the Essig Museum of Entomology, the University of Hawaii Insect Museum, and the Haleakala National Park Insect Collection.

For the purpose of characterizing community composition in each plot, immatures of many taxa could be matched to adults, though for others, only determination of genus, family, or sometimes order could be made definitively. In most of the latter cases, immatures within a known taxon were assigned to species according to the relative abundances of adults within that taxon. For example, if three species of *Nysius* seed bugs (Hemiptera: Lygaeidae) occurred in a plot, numbers of immature *Nysius* in that plot were allocated to these three species according to the proportional representation of the adults in that plot. In the few cases where immatures could be identified only to an order or to a family with

many species (e.g., some Lepidoptera, Coleoptera, and Araneae), these individuals were excluded from analyses that examined community composition. The unidentified Acari, Pseudococcidae, and parasitic Hymenoptera were each treated as a single species of unknown provenance.

We assigned each arthropod species to one of four broad trophic groups based on reports in the literature, information from specialists and personal observations. These were carnivores (predators and parasitoids), herbivores (chewers, sap feeders, mesophyll feeders, seed feeders, gall formers, and others), detritivores (scavengers, fungivores, and other feeders on dead organic matter), and unknown (almost exclusively Acari). Some taxa were difficult to assign unambiguously to one trophic category; in such cases, we chose the category that best represented the predominant trophic role of the taxon. There were few species, aside from invasive ants, that could be classified as omnivores according to the definition of using both plant and prey resources (Coll and Guershon 2002). These species were excluded from analyses that examined trophic structure. For each species we also estimated mean biomass, in milligrams dry mass, from mean body length measurements of adults and immatures, using regression relationships of biomass on length (reported in Gruner 2003). The mean length value for each species took into account the relative frequencies of adults and immatures captured at each site.

Compositional and functional change

All samples collected in each plot were pooled to produce a single multivariate dataset of species abundances for that plot. Arthropod community compositional "change" associated with ant invasion was estimated from the differences in community composition (excluding the invading ants themselves) between invaded and uninvaded plots at each site. This differs from manipulative experiments in which change is typically measured before and after a manipulation, i.e., across time rather than across space. Our approach reflects the limitations imposed by our study of a "natural experiment" (Diamond 1986), in which we could not manipulate the treatment ourselves. Hereafter, we use terminology such as community composition change as shorthand for compositional differences between adjacent invaded and uninvaded areas; similarly, our measure of community resistance to compositional change (see *Among-site patterns in stability*), with which we assess stability and make comparisons to other diversity-stability studies, refers to the magnitude of compositional differences between invaded and uninvaded areas at a site.

Overall compositional differences between plots were assessed using Bray-Curtis distances calculated with species abundance data that were log-transformed and standardized by plot abundance totals. Transformation and standardization have the effect of giving more

² (<http://www.wrcc.dri.edu/CLIMATEDATA.html>)

equitable weight to all species by reducing the influence of the most abundant species, and placing emphasis on differences in proportional representation of species between plots rather than their absolute abundance differences (McCune and Grace 2002). Multi-response permutation procedures (MRPP) were used to estimate whether the compositions in invaded plots were significantly different from those of uninvaded plots at each site, based on inter-plot Bray-Curtis distances. MRPP is a nonparametric permutation method that can test the probability of a difference between groups of multivariate data against the null hypothesis of no difference between the groups (Mielke and Berry 2001). In addition to calculating the test statistic (T), MRPP provides an estimate of the effect size (A), the “chance-corrected within-group agreement.” A scores equal 1 when all species identities and abundances are identical within groups, equal 0 when within-group agreement is random, and are negative when within-group agreement is less than that expected by chance. A scores for significantly different groups are often below 0.1 in community ecology, and higher values indicate stronger differences (McCune and Grace 2002). We also used Mann-Whitney U tests to evaluate differences in species richness, percentage of species in the community that were endemic, and percentage of individuals in the community that were endemic, between invaded and uninvaded plots at each site.

Changes in arthropod community composition resulting from ant invasion may be indicative of shifts in aggregate properties, such as total community biomass and trophic structure, that mediate community function. We compared arthropod biomass in invaded plots with uninvaded plots at each site using Mann-Whitney U tests, for total community biomass as well as for biomass of each of the four trophic groups specified above (excluding invasive ants). We also compared trophic structure between invaded and uninvaded plots at each site using MRPP, whereby overall trophic compositional change was assessed according to trophic-based Bray-Curtis distances between plots. For this analysis, Bray-Curtis distances were calculated by treating each of the four trophic groups as a species and using total biomass for each trophic group in each plot in place of species abundance data. We again used log-transformed data that were then standardized by plot totals, placing emphasis on changes in the proportional contributions of the trophic groups to total community biomass.

Among-site patterns in stability

Most of the variation in diversity in this study system existed across sites, rather than among plots within sites. We therefore chose to assess relationships between diversity and stability by looking at patterns among sites, using mean values of the replicate plots at each site. This approach was also the most compatible with the goal of evaluating the importance of diversity for

predicting variation in impact arising from similar invasions at new sites.

Compositional stability at each site was assessed in two ways. The first was the community's resistance to overall compositional change (RCC; Sankaran and McNaughton 1999, Foster et al. 2002), which was measured by the mean Bray-Curtis similarity between invaded and uninvaded plots, and was calculated as 1 minus the mean of all 25 pairwise Bray-Curtis distances between invaded plots and uninvaded plots at a site. RCC was therefore positively scaled with compositional stability. The second measure, proportional change in richness, was more narrowly focused than RCC but was more relevant to the issue of biodiversity preservation. Proportional change in richness at each site was calculated as the mean richness in invaded plots minus the mean richness in uninvaded plots, divided by the mean richness in uninvaded plots (the reference condition). Because proportional change in richness could be either positive or negative, this measure could scale either positively or negatively with stability.

Functional stability of the arthropod communities was assessed as the resistance to trophic structure change (RTC), and with an index of total community biomass deviation. RTC, like RCC, was the mean Bray-Curtis similarity between invaded and uninvaded plots, and was calculated as 1 minus the mean of all 25 pairwise trophic Bray-Curtis distances between invaded and uninvaded plots at each site. Biomass deviation was calculated as the absolute value of $\ln(\text{mean total community biomass in invaded plots divided by mean total community biomass in uninvaded plots})$. Thus it measured the relative degree of departure, either positive or negative, of biomass in invaded plots (including invasive ants) from biomass in uninvaded reference plots. RTC was positively scaled with functional stability, while biomass deviation was negatively scaled with functional stability.

To determine whether the two measures of compositional stability were related to among-site differences in arthropod community diversity, we calculated Pearson correlations between each stability measure and diversity (H'), as well as the two component parts of diversity, richness and evenness ($H'/\ln[\text{richness}]$), because each component may differentially contribute to stability (Foster et al. 2002). In addition to arthropod diversity, the density of invasive ants at each site could be expected to influence stability, as could total arthropod density. Correlations between compositional stability and ant and arthropod density were therefore also calculated. Finally, we calculated intercorrelations between all of these potential explanatory variables. For each functional stability measure (RTC and biomass stability), we calculated Pearson correlation coefficients with diversity (H'), richness and evenness, as well as with ant biomass and total community biomass to account for their potential influences on stability. We

TABLE 1. Results of multi-response permutation procedures (MRPP) analysis on differences in overall arthropod community composition between invaded and uninvaded plots at each site.

Site	Entire			Endemic			Introduced		
	<i>A</i>	<i>T</i>	<i>P</i>	<i>A</i>	<i>T</i>	<i>P</i>	<i>A</i>	<i>T</i>	<i>P</i>
Ahumoa	0.073	-4.10	0.002	0.094	-2.67	0.020	0.066	-3.33	0.003
Pohakuloa	0.033	-2.32	0.018	0.066	-1.83	0.056	0.017	-1.13	0.128
Huluhulu	0.113	-4.46	0.002	0.070	-2.76	0.008	0.114	-4.18	0.002
Kalahaku	0.097	-4.34	0.001	0.184	-5.24	0.001	-0.023	1.14	0.880
Puu O Ili	0.093	-4.08	0.002	0.146	-3.99	0.005	0.056	-2.28	0.023

Notes: Community composition differences were measured as Bray-Curtis distances using log-transformed, relativized abundance data. Presented are the chance-corrected within-group agreement (*A*, a measure of effect size), the test statistic for the analysis (*T*), and the *P* value for each test for entire arthropod communities, as well as endemic and introduced community subsets of the communities.

also calculated Pearson correlations among all of these potential explanatory variables.

Arthropod density values were log transformed to improve linearity, while the other variables matched statistical assumptions equally well or better when untransformed. Arthropod diversity, richness, evenness, log arthropod density, and arthropod biomass values used in among-site correlation models were the means of the five uninvaded plots at each site, while ant density and biomass values were the means of the five invaded plots at each site. Where multicollinearity was low (as judged by variance inflation factors near 1 [Kutner et al. 2005]), two variables were sometimes simultaneously included in multiple regression models (Minitab regression procedure [Minitab, State College, Pennsylvania, USA]) in order to assess the unique contribution of each to community stability. For all of the analyses in this study, sample size was limited to either five replicate plots or five replicate sites, and thus statistical power was low; we therefore used a more lenient α level of 0.10 when considering potential statistical significance. We also did not adjust α for groups of multiple tests because we felt such a correction would be overly conservative (Gotelli and Ellison 2004). Instead, we focused on general trends and assumed that up to 10% of comparisons within groups of related tests may falsely reject the null hypothesis (however, *P* values are provided for all statistical tests). All univariate statistical analyses were conducted in Minitab (Ryan et al. 2005), and all multivariate analyses were conducted in PC-ORD (McCune and Mefford 2006).

RESULTS

Compositional and functional change

MRPP analyses of inter-plot Bray-Curtis distances indicated that, within sites, arthropod community compositions of invaded plots were usually significantly different from those of uninvaded plots (Table 1). This was true for the entire communities and endemic subsets of the communities, and to a lesser extent for the introduced subsets of the communities. Values of the chance-corrected within-group agreement (*A*), a measure of effect size, varied among sites and community

subsets, but were highest for endemic community subsets at the two Maui sites, Kalahaku and Puu O Ili (Table 1). Ant invasion was often associated with declines in endemic, introduced and overall arthropod species richnesses (Table 2, Appendix A). Changes in richness were most pronounced among endemic community subsets at the Kalahaku, Puu O Ili, and Huluhulu sites. Invasive ants were also sometimes associated with reductions in the percentage of endemic species and the percentage of endemic individuals in communities (Table 2). The reductions in proportional representation of endemic individuals appeared to be especially severe when invasive ants were included in totals for invaded plots (Table 2). Although these latter shifts may be biased by the fact that ants may have a higher rate of capture, on average, than other arthropods, it is probably nevertheless true that the shifts were substantially larger when ants themselves were counted.

Ant invaded plots were only sometimes different from uninvaded plots in overall community trophic structure (excluding the invasive ants themselves), as assessed by MRPP analysis of inter-plot trophic-based Bray-Curtis distances (Table 3). Shifts in the relative representations of log biomass among the four trophic groups considered were strongest at the Puu O Ili site, followed by the Huluhulu and Kalahaku sites (Table 3). There was less evidence of such shifts at the Ahumoa and Pohakuloa sites. Examination of the percent change in biomass for each of the four trophic groups highlights the nature of these trophic shifts (Fig. 1a-d). For the Huluhulu, Kalahaku, and Puu Oili sites, trophic changes were marked by substantial decreases in both carnivore and herbivore biomass in invaded plots, while the opposite was true at the Ahumoa site, although not all of these changes were statistically significant. At the Puu O Ili site, there was also a large increase in detritivore biomass in invaded plots. Biomass of arthropods of unknown trophic identity, represented almost exclusively by mites (Acari), increased substantially at the Ahumoa and Puu O Ili sites. Other trophic shifts were less dramatic, and no trophic group exhibited completely consistent invasion-associated changes across all study sites. This was also true for total community biomass, which increased at some sites and decreased at others (Fig. 1e). Inclusion

TABLE 2. Effects of ant invasion on species richness and endemic composition in the arthropod communities at each of the five study sites.

Site	Species richness									Endemic composition				
	Entire			Endemic‡			Introduced‡			Endemic species (%)§		Endemic individuals (%)§		
	Uninv.	Inv.	Change (%)	Uninv.	Inv.	Change (%)	Uninv.	Inv.	Change (%)	Uninv.	Inv.	Uninv.	Inv.	Inv. with ants#
Ahumoa	43.0	41.8	-2.8	8.6	9.2	7.0	28.2	27.6	-2.1	23.4	25.0	23.2	29.2	7.2
Pohakuloa	49.6	46.8	-5.6	11.4	10.0	-12.3	30.8	30.8	0	27.0	24.5	83.7	87.1	84.5
Huluhulu	43.0	31.4*	-27.0	14.4	9.8*	-31.9	22.2	16.2*	-27.0	39.3	37.7	(32.9)¶	(17.9)¶	(15.0)¶
Kalahaku	40.8	27.4*	-32.8	19.4	9.2*	-52.6	16.0	14.0	-12.5	54.8	39.7*	61.0	25.2†	12.3
Puu O Ili	48.6	39.0*	-19.8	18.6	8.6*	-53.8	23.6	25.6	8.5	44.1	25.2	59.1	26.9	8.1

Notes: All data exclude the invasive ants themselves, except where noted below, and all data presented are the means of five uninvaded (uninv.) and invaded (inv.) plots at each site. Percentage change indicates the difference in mean values between uninvaded and invaded plots, relative to the uninvaded condition. Species richness data are given for the entire arthropod communities as well as the endemic and introduced subsets of the communities. For Mann-Whitney *U* tests comparing invaded plots with uninvaded plots at a site, significance is indicated as follows: * $P \leq 0.05$; † $P \leq 0.10$.

‡ Endemic and introduced richnesses do not add up to entire richnesses because a small percentage of species at each site were of unknown provenance.

§ Calculated as the percentage among combined endemic and introduced species or individuals, i.e., excluding species and individuals of unknown provenance.

Percentages when including the invasive ants themselves. These numbers may be biased relative to percentages in uninvaded plots because invasive ants may be captured at higher rates than other arthropod species, on average. Mann-Whitney *U* tests were not performed with these data.

¶ Percentages in parentheses exclude *Xenylla auka*, an endemic springtail (Collembola: Hypogastruridae) that was very abundant at Pohakuloa site.

of invasive ants among the total invaded communities often had little qualitative effect on these results (Fig. 1e), because although invasive ants were usually very numerous, they are relatively small and thus usually did not contribute greatly to total community biomass.

Among-site patterns in stability

Examination of among-site patterns revealed that the relationship between compositional stability and diversity was contingent on how stability was assessed and on which part of the arthropod communities was considered. There appeared to be a dependence of RCC on *H'* for entire communities and possibly for endemic community subsets (Fig. 2). The simple linear regressions indicate a statistically significant negative relationship between RCC and *H'* for entire communities, a marginally significant negative relationship for endemic community subsets, and no relationship for introduced community subsets. Of the components that form *H'*, evenness appeared to be more important than richness for entire communities, whereas richness and evenness appeared to contribute relatively equally (but not statistically significantly) to the relationship of diversity with RCC for endemic subsets (Table 4). In both cases, communities with lower evenness (higher dominance by fewer species) were more resistant to compositional change, and among endemic community subsets, lower richness was also related to greater compositional stability.

For both the entire and endemic community data sets, however, RCC was most strongly correlated with ant density (Table 4): sites with higher ant densities experienced greater compositional change. Moreover,

moderate to strong intercorrelations between diversity and ant density for both data sets ($r = 0.909, P = 0.032$ for entire communities; $r = 0.795, P = 0.108$ for endemic subsets; see Appendix B) made it difficult to separate and quantify the unique contributions of diversity to RCC. Inclusion of both ant density and *H'* as explanatory variables in multiple regression models, for example, resulted in instability of estimated coefficients and high variance inflation factors. Diversity was further correlated with log arthropod density, and log arthropod density was marginally correlated with ant density, at least among entire communities (Appendix B). These last relationships may have been the primary reason that log arthropod density was marginally positively correlated with RCC among entire communities (Table 4). Although it was expected that arthropod richness would correlate positively with log arthropod

TABLE 3. Results of MRPP analyses of differences in overall community trophic structure between invaded and uninvaded plots at each site.

Site	<i>A</i>	<i>T</i>	<i>P</i>
Ahumoa	0.048	-0.74	0.187
Pohakuloa	-0.044	0.78	0.778
Huluhulu	0.118	-1.80	0.057
Kalahaku	0.084	-1.59	0.072
Puu O Ili	0.274	-3.81	0.008

Notes: Differences in trophic structure were measured as interplot Bray-Curtis distances using log-transformed, relativized biomass data for each of four trophic groups: carnivores, herbivores, detritivores, and unknown (primarily Acari). Presented are the chance-corrected within-group agreement (*A*, a measure of effect size), the test statistic for the analysis (*T*), and the *P* value for each test.

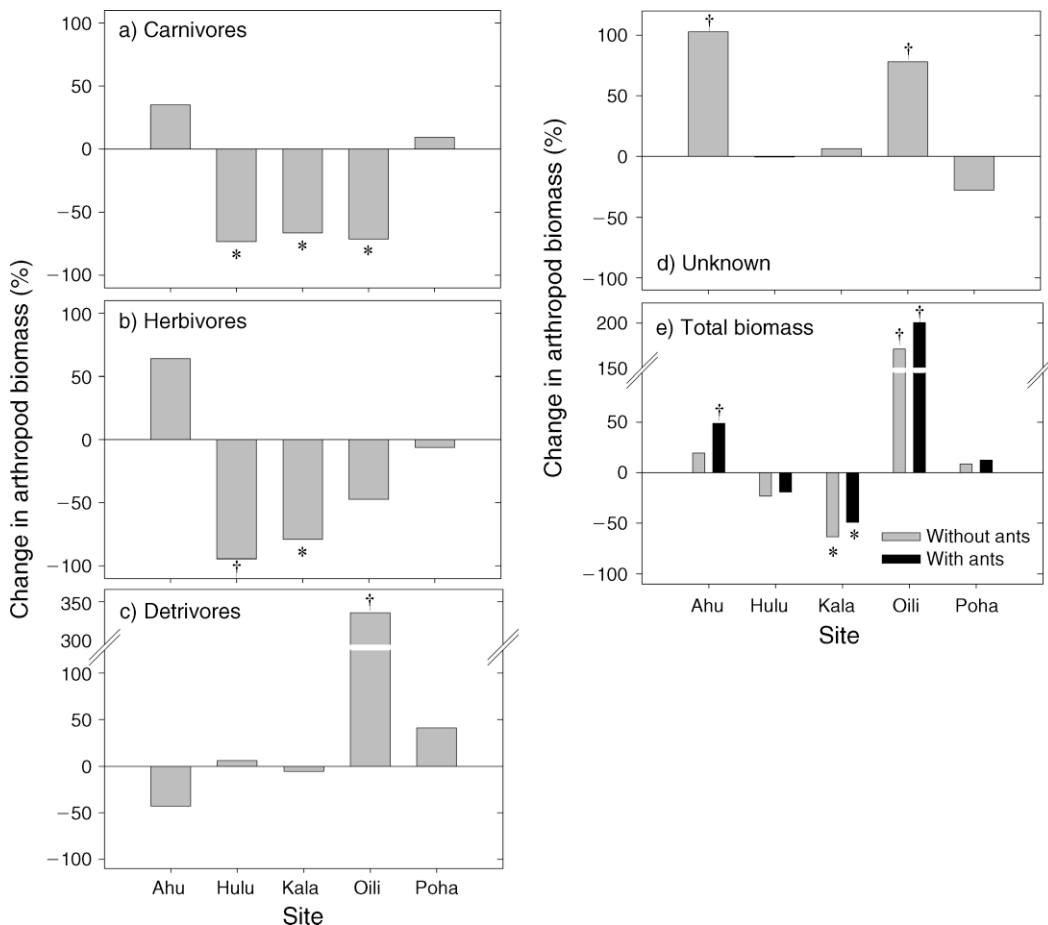


FIG. 1. Percentage change in mean biomass as a result of ant invasion for (a) carnivores, (b) herbivores, (c) detritivores, (d) species of unknown trophic status (represented almost entirely by mites), and (e) the entire arthropod communities at each site. Invasive ants are omnivorous and so were excluded from calculations presented in panels (a)–(d); panel (e) presents changes in total biomass with invasive ants included and excluded. Note breaks in y -axes in panels (c) and (e). Significant differences in biomass between invaded and uninvaded plots at each site (Mann-Whitney U) are indicated above or below the corresponding bar: * $P \leq 0.05$; † $P \leq 0.10$. Abbreviations for sites are as follows: Ahu = Ahumoa, Hulu = Huluhulu, Kala = Kalahaku, Oili = Puu O Ili, Poha = Pohakuloa.

density (e.g., Siemann 1998, Martinko et al. 2006, Gruner 2007), this pattern was strong only among introduced community subsets ($r = 0.953$, $P = 0.012$; Appendix B) and was moderate among entire communities ($r = 0.718$, $P = 0.172$; Appendix B).

When compositional stability was measured as proportional change in richness, a somewhat different but clearer picture emerged. Proportional change in richness was not strongly related to any of the variables measured when considering the entire communities, but was strongly correlated with richness among endemic community subsets and with H' among introduced community subsets (Table 4). Most of the proportional change in richness associated with ant invasion was negative for both endemic and introduced community subsets, but trends differed between the two (Fig. 3). For endemic species, sites with high endemic richness lost proportionally many more species than did sites with low endemic richness (Fig. 3a). In contrast, low diversity

introduced community subsets lost more species than did higher diversity subsets (Fig. 3b). Intercorrelation between endemic richness and other potential explanatory variables was not excessively high (Appendix B), allowing multiple regression to estimate the unique contribution of richness to compositional stability. Even after accounting for ant density (the strongest non-diversity correlate of stability), endemic richness was still highly significantly related to proportional change in endemic richness (Table 5). A similar multiple regression model found that, after accounting for the effect of ant density, introduced H' was marginally significantly related to proportional change in introduced richness (Table 5).

There was little evidence of among-site relationships between functional stability and community diversity. Resistance to overall trophic compositional change (RTC) was not strongly related to community diversity (H'), richness or evenness, and was also not strongly

related to ant biomass or total community biomass (Table 6). The second measure of functional stability, biomass deviation, appeared to be moderately positively related to H' , and this (nonsignificant) relationship appeared to be driven more by evenness than by richness (Table 6). These tentative trends could be interpreted to indicate that communities with greater species dominance (lower evenness) change less in total biomass as they incorporate invading ants. However, biomass deviation was most strongly related to ant biomass (Table 6): community biomass changed proportionally more at sites invaded by more ants. Because ant biomass was intercorrelated with H' ($r = 0.942$, $P = 0.017$; Appendix C), it was again not possible to determine the unique effect, if any, of diversity on community biomass deviation using multiple regression. It should also be noted that while the calculation of community biomass deviation included ants among the total invaded communities, the correlation between biomass deviation and ant biomass was not heavily influenced by ant biomass itself. This was because ants typically made up only a small part of total invaded community biomass, and ant biomass was therefore not correlated with total invaded community biomass ($r = 0.127$, $P = 0.839$). More importantly, the large total community biomass changes that corresponded with higher ant biomasses were not all positive: at the two sites with the highest ant biomasses and the greatest biomass deviations, total community biomass increased at one (Puu O Ili) and decreased at the other (Kalahaku) (Fig. 1e).

DISCUSSION

The study of biological invasions, like other natural experiments (Diamond 1986), often imposes certain limitations. One difficulty in assessing the effects of ant invasion through comparative sampling across invasion fronts is that each individual invasion becomes the unit of replication when examining broad-scale patterns. Because large numbers of suitable invasion sites can be difficult to find, the resultant sample size may be small. It is also usually not possible to control for multiple factors that may covary among sites. Finally, the comparative observational approach typically holds lower inferential power, relative to true manipulative experiments, regarding the causation of measured effects. For instance, arthropod community differences between invaded and uninvaded areas at our sites could have resulted from undetected changes in habitat that were distinct from, and correlated with, ant presence. But the use of ongoing biological invasions as natural experiments has certain advantages over small-scale manipulative experiments (Diamond 1986), in our case providing a more realistic assessment of the breadth, and variation, of community-level effects. Moreover, our inference of the causal role of ants in this study system was greatly strengthened because (1) we carefully chose study sites that were free from apparent systematic differences between adjacent invaded and uninvaded

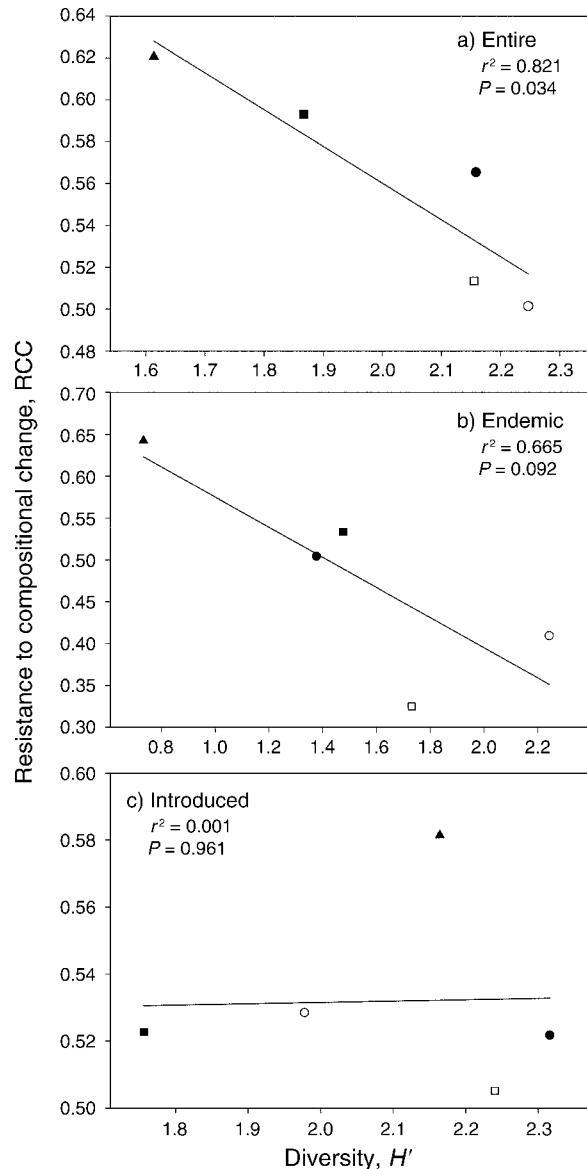


FIG. 2. Among-site relationships between compositional stability, as measured by resistance to compositional change (RCC), and diversity (H') for (a) entire arthropod communities, (b) endemic subsets of communities, and (c) introduced subsets of communities. Least-squares regressions are shown. Symbols indicate sites as follows: solid circles, Ahumoa; solid squares, Huluhulu; open circles, Kalahaku; open squares, Puu O Ili; solid triangles, Pohakuloa.

areas in plant community composition, levels of disturbance, or other edge effects; (2) the degree of total arthropod community compositional change between invaded and uninvaded areas within each site was strongly correlated to ant density at the site, a pattern that is unlikely to have arisen as a result of some unrelated and undetected factor; and (3) before-and-after invasion sampling at two of the sites revealed patterns of compositional change consistent with those between adjacent invaded and uninvaded plots (Kru-

TABLE 4. Among-site relationships, reported as Pearson correlation coefficients, between two community compositional stability measures and diversity and density variables.

Stability measures	Potential correlates‡				
	H'	Richness	Evenness	Ant density	log(arthropod density)
RCC					
Entire	-0.906*	0.356	-0.880*	-0.964**	0.861†
Endemic	-0.815†	-0.729	-0.709	-0.959**	0.615
Introduced	0.031	0.525	-0.344	-0.740	0.632
Proportional change in richness					
Entire	-0.372	0.495	-0.419	-0.355	0.497
Endemic	-0.702	-0.993***	-0.314	-0.561	0.037
Introduced	0.915*	0.454	0.688	0.409	0.215

Notes: See *Methods: Among-site patterns in stability*, for explanation of compositional stability measures (resistance to overall compositional change [RCC] and proportional change in richness). Coefficients are given for the entire arthropod communities as well as the endemic and introduced subsets of the communities.

‡ Except for ant density, which was averaged among invaded plots at each site, all diversity and density variables used the means of uninvaded plots at each site; log(arthropod density) was the log of total density of all arthropods in uninvaded plots.

* $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$; † $P \leq 0.10$.

shelnycky 2007). Consequently, our results suggest that ant invasion was often, but not always, directly or indirectly responsible for substantial changes in the composition, biomass, and trophic structure of arthropod communities in Hawaii. Furthermore, our comparative assessment of multiple sites, which differed from the small-scale constructed-community approach used in many diversity–stability studies, yielded insights into which factors may serve as good predictors of the stability of real arthropod communities undergoing biological invasion.

Compositional change and stability

In the five mesic natural areas studied here, ant invasion was usually associated with significant changes in arthropod community composition. Compositional changes, including both changes in species identities and relative abundances, occurred more consistently within endemic subsets of the communities than within introduced subsets of the communities. These endemic compositional changes were most pronounced at three of the five sites (Huluhulu, Kalahaku, and Puu O Ili) and signaled overall declines rather than increases in endemic biodiversity. Mean plot richness of endemic species, for example, was reduced by 32–54% at these sites. Introduced species at all of the sites were generally less likely to decline and also were more likely to benefit with ant invasion than were endemic species, and this pattern appeared to be consistent between the site invaded by the big-headed ant and those invaded by the Argentine ant (Krushelnycky 2007). Although the reasons for this greater relative vulnerability of endemic species are not known, they likely include an evolutionary history lacking native ants on the part of Hawaiian species (i.e., “evolutionary naiveté”), as well as a higher prevalence of more competitive traits among introduced

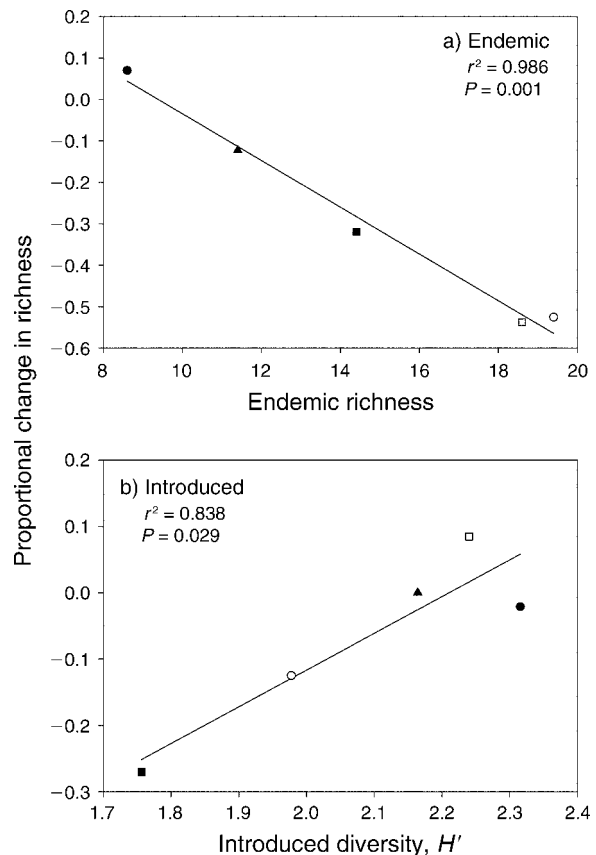


FIG. 3. Among-site relationships between (a) proportional change in endemic richness and endemic richness and (b) proportional change in introduced richness and introduced diversity (H'). Least-squares regressions are shown. Symbols correspond to sites as in Fig. 2.

TABLE 5. Multiple regression analyses of the relationships of proportional change in endemic richness and introduced richness with ant density and community diversity measures.

Predictor	Coefficient	SE	<i>t</i>	<i>P</i>
Proportional change in endemic richness†				
Intercept	0.537	0.061	8.82	0.013
Ant density‡	0.046	0.050	0.93	0.452
Endemic richness‡	-0.059	0.005	-11.64	0.007
Proportional change in introduced richness§				
Intercept	-1.201	0.354	-3.40	0.077
Ant density¶	0.033	0.084	0.39	0.734
Introduced <i>H'</i> ¶	0.531	0.176	3.01	0.095

Note: Ant density per plot was measured in thousands of ants per total sampling effort.

† $R^2 = 0.99$.

‡ Variance inflation factor = 1.6.

§ $R^2 = 0.85$.

¶ Variance inflation factor = 1.1.

species (Krushelnycky 2007). The net result at the community level was often a compositional shift towards greater dominance by non-native arthropods, in terms of both proportion of species and proportion of individuals (especially when the invasive ants themselves were counted). All of these trends should raise serious concerns about the persistence of endemic arthropod species in natural areas where ants are invading, and are consistent with numerous earlier assessments of the damaging effects of invasive ants in the Hawaiian Islands (Perkins 1913, Zimmerman 1970, Cole et al. 1992, Gillespie and Reimer 1993, LaPolla et al. 2000) and elsewhere (Lubin 1984, Porter and Savignano 1990, Human and Gordon 1997, Jourdan 1997, Suarez et al. 1998, Hoffmann et al. 1999, Walker 2006).

In contrast to the trends at Kalahaku, Puu O Ili, and Huluhulu sites, however, species richness at the Ahumoa and Pohakuloa sites changed little, regardless of whether the entire communities, or endemic or introduced community subsets were considered. Compositional shifts at these two sites were also smaller; in fact, at the Ahumoa site, endemic richness and percentage of the community represented by endemic species or individuals was actually slightly higher in invaded plots, at least when the invasive ants themselves were not counted. Differences in the magnitude of apparent impacts at the different sites raise the possibility that stability in these communities might be linked in part to intrinsic factors, such as arthropod diversity or arthropod density. Like a

number of studies that examined the diversity–stability relationship in grassland communities (McNaughton 1977, Tilman 1996, Foster et al. 2002), we found a negative relationship between compositional stability, as measured by RCC, and arthropod community diversity, measured by H' , at least among entire communities. This pattern was statistically weaker among endemic subsets of communities, and was clearly absent among introduced subsets of communities, which generally underwent similar degrees of compositional change. But the actual influence of diversity, as well as that of arthropod density, on compositional stability was obscured by a covarying extrinsic factor: the density of invasive ants at each site. The intercorrelations between ant density and arthropod diversity and density measures were probably largely coincidental. Abiotic factors have often been found to be the best predictors of invasive ant success (Holway et al. 2002b, Krushelnycky et al. 2005, Menke and Holway 2006), and the particular abiotic conditions at each of the sites probably played the largest role in determining ant densities. Nevertheless, ant density is the most obvious explanation for the magnitude of compositional change experienced by recipient communities, and not surprisingly, it was strongly negatively correlated with RCC among entire communities and endemic community subsets. This made it impossible to determine what, if any, unique influence arthropod diversity or arthropod density had on RCC.

TABLE 6. Among-site relationships, reported as Pearson correlation coefficients, between two community functional stability measures and diversity and biomass variables.

Stability measures	Potential correlates				
	H'	Richness	Evenness	Ant biomass	Community biomass
RTC	-0.202	0.450	-0.238	-0.018	-0.566
Biomass deviation	0.736	0.068	0.656	0.866†	-0.311

Note: See *Methods: Among-site patterns in stability* for explanation of functional stability measures (resistance to trophic structure change [RTC] and biomass deviation). Except for ant biomass, which was averaged among invaded plots at each site, all diversity and biomass variables used the means of uninvaded plots at each site. Community biomass was the total biomass of all arthropods in uninvaded plots.

† $P \leq 0.10$.

The influence of diversity could be seen more clearly when considering a more specific aspect of compositional stability: proportional change in richness. From a conservation perspective, this measure is a more direct gauge of potential biodiversity loss and is arguably more meaningful than an index of cumulative changes in species relative abundances (i.e., RCC). Both endemic and introduced subsets of the arthropod communities showed strong, but opposing, trends between proportional change in richness and diversity measures: communities lost proportionately more endemic species at sites with higher endemic richness, but lost proportionately more introduced species at sites with lower introduced H' . Moreover, lower inter-correlation between these diversity variables and ant density permitted estimation of the unique influence of each on the observed trends. After controlling for the effects of ant density, proportional change in endemic richness was still very strongly related to endemic richness, and proportional change in introduced richness was marginally significantly related to introduced H' .

While it is not entirely clear why lower diversity introduced community subsets should lose more species to ant invasion than higher diversity subsets, the pattern of species loss among endemic community subsets makes sense in light of differences between sites in prior invasion history and prior species loss. Specifically, it is likely that proportional change in endemic species richness associated with ant invasion was not related so much to endemic richness per se, but rather to the degree to which endemic species had already disappeared from the communities. Sites with low endemic richness, such as Ahumoa and Pohakuloa, were not naturally low, but instead had few endemic species because the most vulnerable among them had already been lost, probably due to the combined pressures of many introduced arthropod species. Upon ant invasion, the persisting endemic species at these sites were relatively resistant, while communities with higher endemic richness remained vulnerable to further species loss. Evidence for this interpretation includes the facts that endemic richness in uninvaded plots was negatively correlated with introduced richness among sites ($r = -0.818$, $P = 0.091$), and that endemic richness in uninvaded plots varied much more among sites (55.7%) than did total community richness (17.7%). Together, these trends suggest an incremental gain of introduced species that has been offset by a similar loss of endemic species. This pattern is exemplified by the fact that the uninvaded plots at the Pohakuloa site possessed very few endemic species in the same taxonomic groups that were found to be most vulnerable to invasive ants, such as beetles, spiders, and other predators (Krushelnycky 2007), while the Ahumoa site had no endemic species in these groups. Indeed, it was surprising to find such low percentages of endemic species among the total *uninvaded* arthropod communi-

ties at these two sites, given that they were located in natural areas dominated by native vegetation.

Endemic richness varied substantially between sites prior to ant invasion, but once invaded by ants, the five sites converged on a remarkably consistent mean of 8–10 endemic species per plot (Table 2). This pattern again suggests an incremental reduction of endemic biodiversity to a small core group of species that can withstand a variety of invaders. It likewise suggests that ants can single-handedly exert an impact equal to that of many non-ant introduced species. The corollary to this conclusion, however, is that a steady accumulation of introduced species, which individually may not be regarded as particularly threatening to endemic biodiversity, may collectively be exerting an impact as strong as that of the worst invaders.

Functional change and stability

Ant invasion was sometimes associated with significant changes in total arthropod biomass and trophic structure, properties that are directly related to community function. One prominent trend was a common lack of compensatory changes between carnivore and herbivore biomass at a site (Fig. 1). Carnivores usually exert strong top-down control on herbivores in terrestrial communities (Shurin et al. 2006, but see Gruner 2004), and so the fact that carnivore biomass and herbivore biomass both tended to decrease in ant-invaded plots at three sites (Huluhulu, Kalahaku, Puu O Ili) suggests that ants often preyed heavily on or effectively displaced both trophic groups. At the Ahumoa site, carnivore and herbivore biomass also shifted in concert, but in this case both tended to increase in invaded plots (although not significantly so). Closer examination of trends at Ahumoa suggests that herbivores increased in invaded plots due to an ant-mediated decrease in spiders on shrubs (Krushelnycky 2007), but that this predator decrease on shrubs was overwhelmed by a larger gain in ground-active predator biomass. Detritivore response to ant invasion was also variable between sites. The largest change occurred at the Puu O Ili site, which saw a dramatic increase in detritivore biomass in invaded plots.

There was therefore no consistent pattern, among sites, in the way trophic structure shifted in association with ant invasion. Instead, trophic changes appeared to be largely community-specific and idiosyncratic, often driven by large changes in biomass of one or several species. For instance at the Kalahaku and Huluhulu sites, decreases in carnivore biomass were due mainly to strong declines in a large, ground-active, and vulnerable endemic wolf spider (*Lycosa* sp.), while at the Ahumoa site the opposite outcome was due mainly to increases in several species of large, ground-active introduced spiders (*Urozelotes rusticus* and *Meriola arcifera*) that were resistant to ant invasion, and perhaps even used ants as an abundant new prey resource. Likewise, the large gains in detritivore biomass at the Puu O Ili site was

dominated by increases in densities of a single introduced isopod species (*Porcellio scaber*), a result that was strikingly similar to one reported from an Argentine ant invasion in California (Human and Gordon 1997). But this isopod did not respond in the same fashion at the Huluhulu site, and a general positive response among isopods has not been a consistent feature of ant invasions elsewhere (Human and Gordon 1997). In fact many arthropod species in the present study system exhibited variable responses between sites (Krushelnicky 2007), underscoring the importance of both compositional differences and context-dependency in explaining variation among communities in trophic changes following ant invasion.

In line with this conclusion, there was no strong evidence that community diversity had any relationship with overall trophic structure stability, as measured by RTC. The strongest correlation between RTC and a diversity measure was a positive one with community richness ($r = 0.450$; Table 6). Because statistical power for these correlations was low, it could be argued that this relationship was in fact quite strong and would be statistically significant with a larger sample size. However, there appeared to be a weak negative trend between RTC and evenness, which undermines the interpretation that greater numbers of species in these communities might stabilize them against trophic structure change when ants invade. Another potential critique is that, compared with many experimentally constructed communities, these communities exhibited a relatively narrow range of mean diversities and richnesses (e.g., see x -axes in Figs. 2 and 3; Appendix A) and that greater variation in diversity measures may have revealed a relationship with stability. But these were real arthropod communities existing in fairly dissimilar habitats, suggesting that if diversity did play a role in stabilizing trophic structure, it was relatively weak at these natural scales and in practice may often be overridden by other factors (Huston 1997, Hooper et al. 2005, Srivastava and Vellend 2005), such as the community-specific characteristics noted above.

All of the above trophic shifts characterize the effects of invasive ants on the rest of the arthropod community. Of course invasive ants become integrated members of the communities they invade, and so an accurate accounting of trophic structure in invaded areas would incorporate the ants as well. Invasive ants probably influence arthropod community energy flow as predatory carnivores, scavenging detritivores and herbivores through their consumption of nectar, honeydew and in some cases seeds (Holway et al. 2002a). However, it is unknown how much energy they generally derive from each source (but see Helms et al. 2002), and in fact the relative contributions of each can vary over space and time (Tillberg et al. 2007). A second source of potential bias concerns changes in densities of mites, which were ignored in the specific trophic changes discussed above. Mites were usually very abundant, and this extremely

diverse group is known to include herbivorous, carnivorous and detritivorous species (Borror et al. 1989). These unknown quantities therefore make it difficult to estimate true changes in trophic structure arising from ant invasion, although some trophic shifts were unambiguous: the large gain in detritivore biomass at the Puu O Ili site, for example, would only be strengthened with the inclusion of invasive ants and increasing mite densities. Perhaps more importantly, the use of several broad trophic groups falls far short of capturing the complexity of actual energy flow through a community (Polis and Strong 1996), and can obscure more specific patterns. For instance, the use of plant resources by ants in their consumption of nectar and honeydew could be seen to partially offset the losses in total herbivore biomass that often accompanied their invasion. But in reality this mode of primary productivity use is distinct from those employed by other herbivore guilds, such as the leaf chewers that underwent strong declines at most sites (not shown). This and other changes in guild structure among herbivores and detritivores could affect plant growth (Styrsky and Eubanks 2007), seed survival (Bond and Slingsby 1984, Christian 2001, Carney et al. 2003, Gómez et al. 2003), pollination (Cole et al. 1992, Lach 2005), or rates of decomposition and nutrient cycling.

Changes in total arthropod biomass at a site are also indicative of changes in energy flow through the ecosystem. Overall increases of arthropod biomass in invaded plots, such as at the Ahumoa and Puu O Ili sites, suggests that invasive ants can sometimes induce a more efficient use, or enable a more complete acquisition, of resources by the arthropod community. For example, ants may capture and make available more energy by feeding extensively on carbohydrate-rich insect honeydew, which ultimately derives from plant sap (Helms and Vinson 2002). In contrast, substantial decreases in overall arthropod biomass, such as at the Kalahaku site, suggest that invaded communities may sometimes become less efficient in energy use. The Kalahaku site is situated at approximately 2800 m elevation, and arthropods in the alpine zone of Haleakala are thought to rely at least partly on an allochthonous input of wind-blown food resources (Loope and Medeiros 1994). It is possible that Argentine ants are more poorly adapted to utilize this type of inconsistent resource base than are the large endemic wolf spiders that are displaced.

In general, total arthropod biomass appeared to be less stable to ant invasion as ant biomass increased. But because this instability took the form of both increases and decreases in total arthropod biomass, it was difficult to draw any conclusions about typical effects associated with invasion. There was also a relatively strong (but nonsignificant) tendency for biomass deviation to be greater in higher diversity communities, a trend contrary to that reported from some grassland diversity–stability studies (McNaughton 1977, Tilman and Downing 1994). However, the actual influence of community diversity on

biomass deviation was questionable because diversity was strongly correlated with ant biomass. Thus, if diversity did have an effect on biomass deviation, it was again overshadowed by another variable: the magnitude of the perturbation (i.e., ant biomass). At least one additional study failed to find a stabilizing effect of diversity on the biomass of herbivores and carnivores in a diverse terrestrial arthropod community (Hurd et al. 1971).

Conclusions

By studying multiple ant invasions in a standardized fashion, it was anticipated that general patterns would emerge, and specifically that intrinsic characteristics of arthropod communities, such as diversity, might help predict the degree of impact incurred. The best predictor of compositional stability in the face of ant invasion in these communities, at least among endemic species, was endemic richness. However, endemic richness acted in this case less as a measure of diversity than as an indicator of prior diversity loss. Communities with few remaining endemic species were resistant to further species loss, while communities with more endemic species were vulnerable to large declines in endemic richness when ants invaded. This trend was highly significant irrespective of the density of invading ants, and appeared to be independent of the species of invasive ant involved, suggesting that it will hold in other similar invasions. This pattern may also serve as a central explanation for variation in impact on non-ant arthropods among other invasion localities. It lends support, for example, to the hypothesis that the apparent lack of impact by Argentine ants on non-ant arthropods in a California riparian system could indicate that most of the vulnerable non-ant native species there had already disappeared (Holway 1998). More generally, this pattern may extend to other community types, and may indicate that prior invasion history is of central importance in determining the compositional stability of communities undergoing biological invasions.

Functional stability in these communities, measured as resistance to trophic structure change and total biomass deviation, was not found to be strongly related to any of the intrinsic community factors considered. Although precise trophic shifts were difficult to measure, they appeared to be more idiosyncratic than predictable, and the magnitude of total arthropod biomass deviation was most strongly related to the biomass of invading ants at a site: an extrinsic factor. Even here, though, outcomes were unpredictable, since total arthropod biomass could either increase or decrease upon ant invasion, potentially signaling dramatically different effects on overall ecosystem function. The net shifts in biomass within trophic groups and for entire arthropod communities indicated that overall compositional changes were generally not compensatory. In sum, if there was any stabilizing effect of diversity on commu-

nity function as measured here, it was overshadowed by community-specific factors and the magnitude of the ant-mediated perturbation.

The insurance hypothesis and related ideas state that, when perturbed, diverse communities should be better able to resist changes in function through the possession of a greater diversity and greater redundancy of functional traits (McCann 2000, Loreau et al. 2001). However, the benefits of greater diversity for any given community function often appear to saturate at relatively low levels (Schwartz et al. 2000), and the diversity effect may often be weak in comparison to other factors affecting community properties and processes, particularly across larger spatial scales (Huston 1997, Tilman 1999, Loreau et al. 2001, Hooper et al. 2005, Srivastava and Vellend 2005). These two qualifications could explain why diversity had no detectable influence on measures of functional stability in this study system, where variation in total local richness was relatively low, and where community-specific compositional characteristics appeared to dictate the nature of trophic shifts. Similar conditions in other invasions, when combined with the overriding importance of invader density, may signify that diversity will generally serve as a poor predictor of the magnitude of functional change in real communities undergoing species invasion.

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APPENDIX A

Basic statistics for the arthropod sampling in this study (*Ecological Archives* A018-054-A1).

APPENDIX B

Among-site intercorrelations between all of the potential correlates of compositional stability examined in Table 4 (*Ecological Archives* A018-054-A2).

APPENDIX C

Among-site intercorrelations between all of the potential correlates of functional stability examined in Table 6 (*Ecological Archives* A018-054-A3).