

# Geological age, ecosystem development, and local resource constraints on arthropod community structure in the Hawaiian Islands

DANIEL S. GRUNER\*

Department of Zoology and Ecology, Evolution and Conservation Biology Program, University of Hawai'i at Mānoa, Honolulu, Hawai'i, USA

Received 22 August 2005; accepted for publication 20 June 2006

An ongoing debate in evolutionary ecology concerns the relative role of contemporary vs. historical processes in determining local species richness and community structure. At sites along a 4 Mya geological chronosequence on Hawai'i, Moloka'i and Kaua'i, numerous extrinsic factors can be held constant, but ecosystem fertility and nutrient availability are low, both very young and very old sites, peaking at intermediate geological age across islands. Thus, contemporary resource traits are similar among sites with different biogeographical legacies, and these opposing gradients allowed a test of their relative importance for arboreal arthropod community structure. Pyrethrum knock-down was used to sample arboreal arthropods from *Metrosideros polymorpha* (Myrtaceae), the dominant tree throughout the Hawaiian Islands. Arthropod abundances and sample-based species richness peaked at more productive, intermediate-aged sites, but did not correlate with geological age. The proportions of individuals and biomass in trophic groups and in different taxonomic orders differed widely across sites, but proportions of species in trophic groups were more regular than the chance expectation. Species richness in local communities did not accumulate or pack more tightly with increasing geological age to the oldest island. Intermediate-aged islands may be contemporary peaks of richness, mediated by ecosystem development and senescence. Although historical and evolutionary processes generate diversity at broad scales, local communities converged in trophic structure and composition, and ecosystem resource availability constrained arthropod numbers and richness at local scales. © 2007 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2007, 90, 551–570.

**ADDITIONAL KEYWORDS:** canopy arthropod community structure – evolutionary lineage – geological chronosequence – mesic forest ecosystems – *Metrosideros polymorpha* – nutrient availability – productivity – species diversity and richness – trophic structure.

## INTRODUCTION

The richness of regional species pools can constrain species diversity and community structure observed at local scales (Cornell & Lawton, 1992; Ricklefs & Schluter, 1993; Hillebrand & Blenckner, 2002). Species-rich tropical arthropod communities, often showing high proportions of unique species and non-asymptotic species accumulation curves (Novotný & Basset, 2000; Stirling & Wilsey, 2001; Basset *et al.*, 2003), appear to exemplify the case for the contin-

gency of local biotic diversity on extrinsic biogeographical, historical, and evolutionary processes. Although intrinsic biotic interactions and abiotic perturbations are thought to limit or reduce the diversity of local communities, local richness can increase only by speciation and dispersal occurring on these larger scales of time and space. Long temporal and spatial scales pose particularly difficult obstacles for studying local communities in a historical context (Pickett, 1989). Thus, there have been few studies of the relative influence of intrinsic ecological and extrinsic historical or evolutionary processes in shaping contemporary community structure, most of which have examined restricted clades within diverse larger communities (McPeck & Brown, 2000;

\*Current address: Bodega Marine Laboratory, University of California-Davis, PO Box 247, Bodega Bay, CA 94923-0247, USA. E-mail: dsgruner@ucdavis.edu

Pärtel, 2002; Stephens & Wiens, 2003; Gillespie, 2004).

Early studies proposed that the geological age of a region may be a major determinant of species richness (Wallace, 1878; Willis, 1922; Fischer, 1960). The fossil record generally indicates positive trends of species accumulation over millennial scales, interrupted only periodically by sudden extinction events (Signor, 1990). On remote oceanic islands, most of the diversity is generated *in situ*, a result of local diversification from a small pool of colonist taxa (Zimmerman, 1970; Cowie, 1995; Whittaker, 1998). Thus, the time available for speciation may impose controls on species richness comparable to the size of islands or their distance from source pools (Wagner, 1991; Paulay, 1994; Price, 2004), and this pattern is supported by macroecological data for insect communities over Quaternary time scales (Birks, 1980; Leather, 1986). Within local communities, colonizing or evolving species might fill previously 'vacant' niches (Compton, Lawton & Rashbrook, 1989), or niches may contract, thus expanding deterministic limits on local diversity over time (May, 2001). However, host range expansion and speciation of arthropods on islands can be extremely rapid (Strong, 1974; Mendelson & Shaw, 2005). To better test the influence of geological time, well-constrained gradients of ecosystem age over long geological timeframes are needed in community-level studies (Borges & Brown, 1999).

At local scales, the quality (e.g. nutrients) and quantity of resources (e.g. productivity) are thought to influence species richness patterns (Huston, 1994). Although decades of intensive research have yielded no consensus, studies of terrestrial animal richness have shown more monotonic positive relationships with productivity than any other single pattern (Rosenzweig & Abramsky, 1993; Abrams, 1995; Waide *et al.*, 1999; Mittelbach *et al.*, 2001). However, this generalization is cast into doubt by differing scales, taxonomic emphasis and resolution, and varying directness of productivity measures or surrogate indices (Groner & Novoplansky, 2003; Whittaker & Heegaard, 2003). Controlled, comparative studies of terrestrial invertebrate diversity, using direct measures of mass production or nutrient availability at local scales, are notably rare.

The Hawaiian archipelago generates as the Pacific plate passes north-westerly over a stationary hot-spot of upwelling basaltic lava (Carson & Clague, 1995); thus, the main high islands represent a discrete geological time series from older, northernmost Kaua'i to the southernmost, volcanically active Hawai'i. Previous teams have identified sites on different islands sharing similar climatic, geochemical, and organismic features, and have used these sites to understand ecosystem development over geological time scales

(Vitousek, 2004). These 'natural experiments' can also be used to disentangle historical and evolutionary effects on local community structure from those occurring in response to contemporary ecosystem fluxes and species interactions (Price & Elliot-Fisk, 2004).

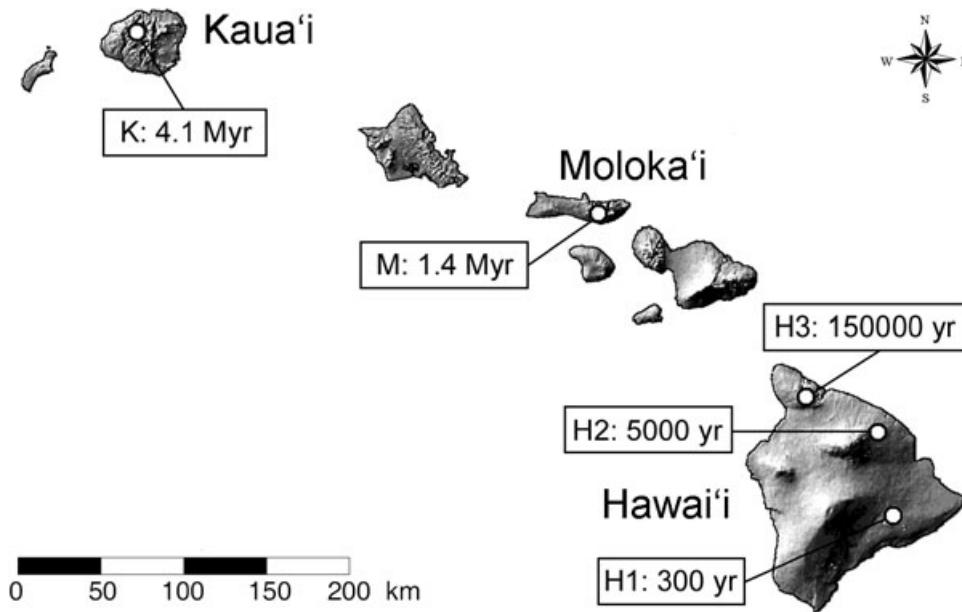
The present study used five sites from a well-constrained chronosequence in montane mesic forest (Fig. 1; Crews *et al.*, 1995). These sites share the same dominant canopy species [*Metrosideros polymorpha* Gaudichaud-Beaupré (Myrtaceae)], and similar topographic position, elevation, average annual temperature and precipitation, land use history (Crews *et al.*, 1995; Gruner & Polhemus, 2003), and soils were derived from volcanic ash (tephra) on the original shield surface (Lockwood *et al.*, 1988). Sites vary in two major, contrasting ways. First, the sites span four orders of magnitude in age of the surficial substrate (300–4.1 Mya). Ecosystems and communities on older sites have had more time for development, colonization, speciation, and niche partitioning, which together may explain the increasing floristic richness on older islands at biogeographical scales (Price, 2004). Second, recently formed soils are deficient in fixed, biologically available nitrogen, whereas the oldest soils on Kaua'i are leached and deficient in mobile phosphorus. Thus, net primary productivity, soil and foliar nutrient levels, and rates of nutrient cycling follow unimodal patterns on a semilog scale, peaking at sites of intermediate age on Hawai'i and Moloka'i (Vitousek, 2004).

A standardized sampling regime of canopy arthropod communities from the same tree species along the age gradient allowed a test of two alternative hypotheses: (1) if local resources constrain community structure, then arthropod abundance, biomass,  $\alpha$ -richness, and diversity should correlate with nutrient availability and net primary productivity, revealing a humped relationship with log substrate age ('resource hypothesis'). Alternatively, (2) if accumulated speciation and biogeographical effects determine community structure, then local arthropod variables (particularly,  $\alpha$ -richness) should increase with geological age ('time hypothesis'), as observed for the Hawaiian flora (Wagner, 1991; Price, 2004). Another prediction of the time hypothesis is that local communities should be more similar within islands than among islands, regardless of differences in resource availability (Crews *et al.*, 1995). The present study provides uncommonly well-resolved quantitative analyses of local community-wide invertebrate diversity in a standardized protocol across a geological chronosequence.

## MATERIAL AND METHODS

### ARTHROPOD SAMPLING

Arthropods were sampled from *M. polymorpha* at five sites in June, October, and November of 1997 using



**Figure 1.** Location and surficial substrate age of the five arthropod sampling sites along a Hawaiian mesic chronosequence. From youngest to oldest, the sites are Volcano (H1, Hawaii Volcanoes National Park, Hawai'i Island); Laupāhoehoe Flow (H2, Laupāhoehoe Forest Reserve, Hawai'i Island); Kohala (H3, Kohala Forest Reserve, Hawai'i Island); Moloka'i (M, Kamakou Preserve); and Kaua'i (K, Nāpali-Kona Forest Reserve). Coordinates, descriptions and site-level data are provided elsewhere (Crews *et al.*, 1995; Vitousek *et al.*, 1995; Vitousek *et al.*, 1997; Herbert & Fownes, 1999; Gruner & Polhemus, 2003; Gruner, 2004a).

pyrethrum knockdown (Fig. 1). Pyrethrum knockdown fogging is a promising technique for comparative ecological studies (Stork & Hammond, 1997; Gering, Crist & Veech, 2003). The method is underutilized in community ecology, most likely stymied by the daunting magnitude and taxonomic complexity of samples and datasets. However, the arthropod fauna from Hawaiian *Metrosideros* is well characterized (Swezey, 1954; Gagné, 1979; Stein, 1983; Gruner, 2004a) compared to continental tropical forests at similar latitudes, and perhaps an order of magnitude less rich. Although fogging has been criticized for undersampling fauna from epiphytes (Yanoviak, Nadkarni & Gering, 2003), bromeliads and araceous epiphytes are naturally absent in the Hawaiian Islands and epiphytic bryophytes and pterophytes were locally uncommon in these mesic forests.

Individual trees were fogged with a Curtis Dyna-Fog Golden Eagle fogger with pyrenone 100 (1% pyrethrins, 5% piperonyl butoxide, and 94% isoparaffinic petroleum) until the entire crown was saturated for 10 s. Flowering trees or those growing on slopes were avoided, and selected trees, generally of modal size within habitats, were dispersed spatially to eliminate carryover effects of the fog. Trees were sampled during daylight hours in good weather conditions only (no precipitation or wind). On average, we obtained samples from ten *M. polymorpha* trees at each of four

sites, with one individual of *Metrosideros waialealae* (Rock) Rock from Moloka'i later excluded. Weather conditions restricted sample size at the Laupāhoehoe site ( $N = 8$ ), and most of these trees were located adjacent to the chronosequence site on thin tephra over 'a'ā basalt. However, foliar nutrients (Vitousek, Turner & Kitayama, 1995), tree stature and forest structure (D. S. Gruner, personal observ.) were very similar among these adjacent sites.

Arthropods were allowed to drop for one hour onto 3–6 collection trays (1.5 m<sup>2</sup>) arrayed to subsample all horizontal canopy zones (e.g. near bole) and cardinal directions. The number of sampling trays, consisting of white sheets suspended 0.75 m above the forest floor on polyvinyl chloride frames, varied in proportion to crown spread ( $r = 0.667$ , d.f. = 42,  $P < 0.0005$ ). Arthropods were collected immediately into 70% ethanol and later sorted, counted, and identified to taxonomic species or morphospecies (Gruner, 2004a). Length was measured with an ocular micrometer on alcohol-preserved specimens to the nearest millimeter class. Dry biomass estimates were calculated with taxon-specific regression equations on length (Gruner, 2003).

Arthropods were assigned to feeding guilds and aggregated into one of five trophic groups: carnivores, detritivores, herbivores, and tourists, or undetermined. Feeding guilds were assigned based on

personal observation and morphological evidence, literature review, and communication with systematists. Carnivores included all parasitoids, spiders, and other predators; detritivores comprised saprophagous arthropods, dead-wood borers, and grazers of litter, fungi, and microbes; herbivores consisted of sap feeders, foliage chewers, and adult gall-formers; tourists included species known to be incidental or non-feeding on *Metrosideros*, or with highly omnivorous feeding habits. Known tourists were excluded from analyses, whereas species with undetermined functional roles (mostly mites) were retained as separate from tourists and included in analyses of aggregate arthropod variables. Specimens data were managed using the *Biota* database software (Colwell, 1997), and vouchers reside at the Bernicre P. Bishop Museum, Honolulu and the Smithsonian, Washington, DC.

#### ABUNDANCE AND BIOMASS

Arthropod abundance and biomass variables were averaged over all trays for each tree expressed relative to total tray area. Site comparisons were made within taxonomic orders, trophic groups, and for all arthropods combined. To examine among-site differences in arthropod numbers, one-way analysis of variance with multiple comparisons was used (Tukey's HSD, joint  $\alpha = 0.05$ ; all *F*-test d.f. = 4,43). Both abundance and biomass variables were natural log-transformed to meet statistical assumptions.

Pearson correlations of site means of arthropod trophic level abundance and biomass were tested against the  $\log_{10}$  of substrate age and selected ecosystem resource and habitat variables reported previously from these sites. Variables were selected to minimize collinearity and were hypothesized to influence arthropod population dynamics or diversity. From Herbert & Fownes (1999), total NPP, the input rate of *N* in leaf litter (both in units  $\text{g}^1 \text{m}^{-2} \text{years}^{-1}$ ), and leaf area index (LAI,  $\text{m}^2 \text{m}^{-2}$ ), were used. Foliar phosphorus concentrations (%P per  $\text{g}^{-1}$  dry mass) were taken from Vitousek *et al.* (1995), and mean tree height (m), stem basal area ( $\text{m}^2$ ), and canopy volume ( $\text{m}^3$ ) from Gruner & Polhemus (2003). The simultaneous error rate of these 144 tests was not controlled, but it was assumed that 5–10% of individual tests yielded spurious results. Variables were classified into resource variables (NPP, N litterfall rate, foliar P) and habitat variables (LAI, tree height, basal area, canopy volume), and these general categories were inspected for patterns of correlations at  $\alpha = 0.10$ . The arcsine square root transformation was used to normalize percentage canopy cover before averaging, and natural log transformations for tree height, basal area, and canopy volume.

#### SPECIES RICHNESS AND DIVERSITY

Several studies have suggested a nonrandom constancy for predator–prey species ratios and guild proportionality across sites or through time (Evans & Murdoch, 1968; Moran & Southwood, 1982; Jeffries & Lawton, 1985; but see Wilson, 1996). Thus, the proportionality of species richness was examined within taxonomic orders and trophic groups across chronosequence sites. Orders with few species or with spotty distributions across sites were aggregated into more inclusive categories for analysis (Class Malacostraca: Isopoda and Amphipoda; all others: Orders Blattodea, Collembola, Neuroptera, Thysanoptera, and all Class Myriapoda). Contingency table analyses tested the null hypotheses of no differences among sites in the proportions of species in the different orders and trophic groups. Because of the possibility that proportions might differ less among sites than expected under the null hypothesis (Fisher, 1936; Edwards, 1986), two-sided alternative hypotheses were tested. Unusually small values of the  $\chi^2$  statistic (i.e.  $P > 0.95$ ) were taken as evidence against the null hypothesis, and indicated community structure more similar than expected by chance.

Direct comparison of observed richness among sites was not appropriate because sampling effort (the total number of trees and trays) differed among sites, and species number per unit effort is expected to be non-linear (Gotelli & Colwell, 2001). Because the observed species richness usually underestimates true richness, richness for each site was estimated by extrapolation (Colwell & Coddington, 1994). The second-order jackknife, which is a robust nonparametric, incidence-based estimator, was used following the selection criteria of Brose, Martinez & Williams (2003). Individual tray samples for each site were shuffled and sampled randomly 100 times without replacement to produce smoothed species accumulation curves. Fisher's  $\alpha$ , a scalar diversity index that controls for abundance and sampling effects (Magurran, 1988; Rosenzweig, 1995; Hubbell, 2001), was also calculated using the EstimateS software package (Colwell, 2004). Jackknife and Fisher's  $\alpha$  estimates from each site were rarefied to the smallest shared sample size of total trays at all sites (i.e. sample-based rarefaction; Gotelli & Colwell, 2001), and also compared with curves rescaled to total arthropod abundance (i.e. individual-based rarefaction).

As with abundance and biomass variables, site means of richness and diversity were analysed for correlations with substrate age, resource and habitat variables.

To assess the contribution of evolutionary accumulation to species composition, the species-genus ratio was calculated for native arthropods at each site (Simberloff, 1970). Genera are a reasonable proxy for

unique lineages and colonization events in Hawaiian arthropods (Zimmerman, 1948; J. P. Price and D. S. Gruner, unpubl. data), so these ratios assess the average extent that coexisting evolutionary lineages have diversified or persisted within, or invaded, local communities. This measure does not rely on diversification *in situ*, but examines the extent that related species within lineages *accumulate* at sites over time. To control for sampling effort and to generate estimates of variability, rarefaction curves were calculated for 100 randomly selected native species within genera for each site. Monte Carlo simulations were run for 1000 iterations using EcoSim software (Gotelli & Entsminger, 2002).

#### DIVERSITY PARTITIONS

The sampling design at multiple, nested spatial scales allowed analysis of the  $\alpha$ ,  $\beta$ , and  $\gamma$  components of species diversity (Lande, 1996; Loreau, 2000; Crist *et al.*, 2003). The additive model of diversity partitioning treats the sum of  $\alpha$  and  $\beta$  diversities at any scale as the  $\alpha$  diversity of the next larger scale (Lande, 1996; Crist *et al.*, 2003). In the knockdown sampling design, average within-sample diversity of collection trays represented point diversity: the spatial scale most likely to capture individual biotic interactions and the physical constraints of the habitat (Whittaker, Willis & Field, 2001). The average  $\beta$  diversity was quantified at three scales: (1) within trees; (2) among trees; and (3) among sites across the region (i.e.  $\gamma$  diversity, *sensu* Cody, 1975). Within- and among-tree  $\beta$  diversity depicted community-level patterns, whereas  $\gamma$  diversity measured broad-scale, evolutionary, biogeographical and historical effects (Gering, Crist & Veech, 2003).

Diversity partitions were calculated using the program PARTITION, which used an individual-based Monte Carlo randomization procedure and two-tailed test to distinguish patterns from null expectations (Crist *et al.*, 2003; Veech & Crist, 2003); in each analysis, 1000 iterations were used. Partitions were calculated separately on the basis of individual sites using two levels of  $\beta$  diversity ( $\beta$  diversity within and among trees), and for the region as a whole adding a third level of  $\beta$  diversity (among sites =  $\beta_3$  =  $\gamma$  diversity). To isolate potential evolutionary explanations, native and introduced species also were analysed separately. In addition, the relative contributions of common and rare species, defined as > 0.5% of total abundance and < 0.05%, respectively (Gering, Crist & Veech, 2003), and individual trophic levels (detritivores, herbivores and carnivores), were analysed.

#### COMPOSITIONAL COMPARISONS

The compositional similarity of sites was examined with hierarchical clustering in PC-ORD (McCune &

Mefford, 1999). Pairwise distances were calculated using the Sørensen index, relativized to site totals to control for sampling intensity and to focus the analysis on proportions of species rather than absolute abundance. The group average linkage method was used and the resulting dendrogram was scaled using Wishart's objective function (McCune & Grace, 2002). Separate analyses examined the total community (excluding tourists) and native species only (excluding tourists and introduced species).

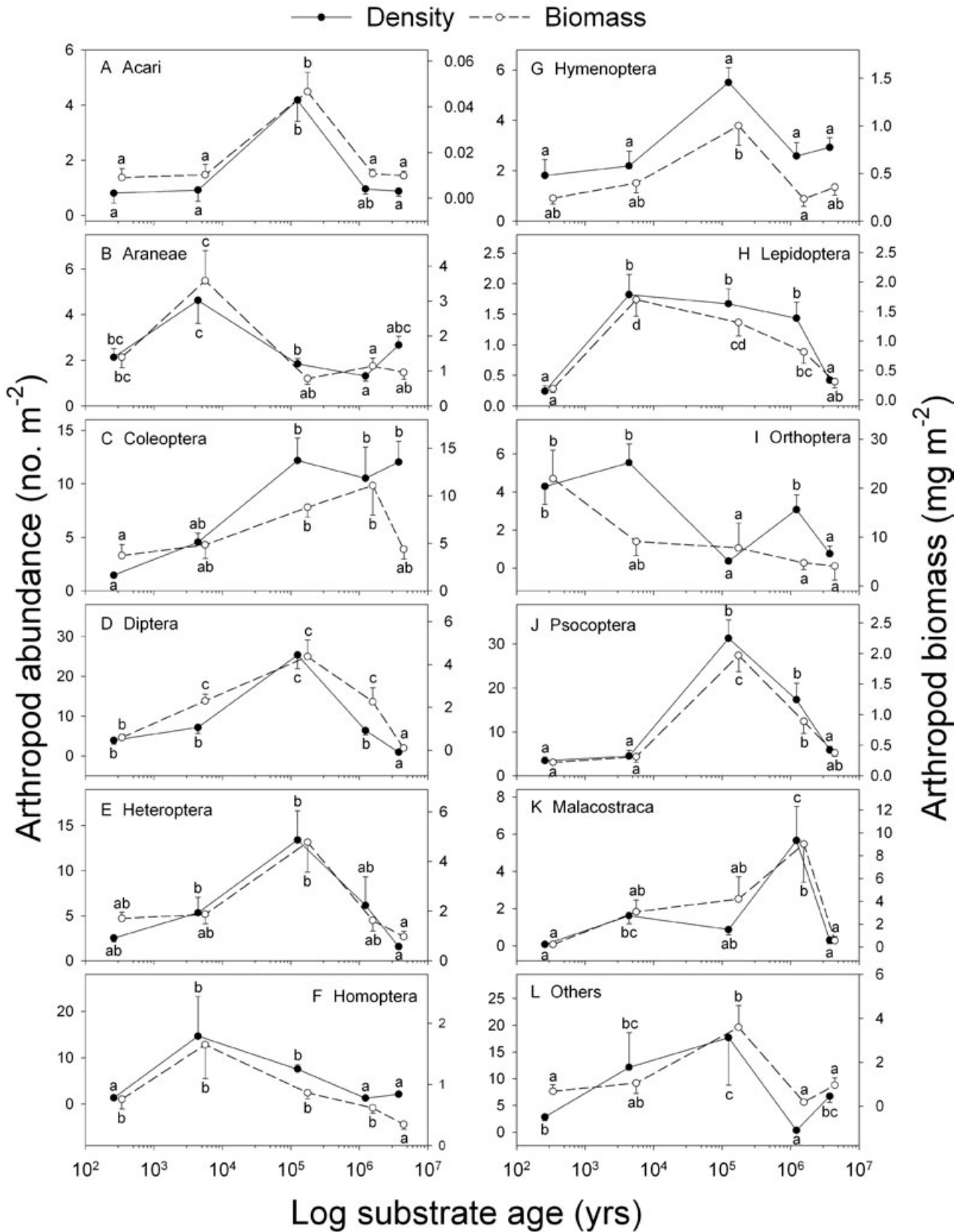
## RESULTS

#### ARTHROPOD ABUNDANCE AND BIOMASS

In total, 17 029 arthropods in 612 species, 119 families, and 19 orders were collected in samples from *M. polymorpha* canopies at the five sites. Known incidentals and nonfeeding or nectarivorous species (e.g. bees, adult moths) were excluded from this analysis, leaving 16 635 individuals from 574 species. Of the 574 species retained, 423 species were considered native to the Hawaiian Islands (all but one endemic), 89 species were introduced historically, and 62 species were of obscure origin (including 22 mite morphospecies). The complete taxonomic list is provided elsewhere (Gruner, 2004a).

Abundance and biomass differed among sites for all analysed orders, although not all in the same way (Fig. 2). Diptera, Heteroptera, Homoptera, Lepidoptera, and Psocoptera abundance and biomass were high at two or more intermediate-aged sites, with lower numbers at the age gradient endpoints. Several orders had high values only at one intermediate-aged site: Araneae at Laupāhoehoe (H2: 5000 years ago), Acari and Hymenoptera at Kohala (H3: 150 000 years ago), and Malacostraca at Moloka'i (M: 1.4 Mya) [the latter reflecting a large population of *Platorchestia* nr. *lanipo* (Amphipoda)]. Coleoptera biomass also was highest on Moloka'i and much lower at the oldest site, Kaua'i (K: 4.1 Mya), but Coleoptera abundance was high on Kaua'i, Kohala, and Moloka'i. Orthoptera showed a very different pattern, especially in biomass, with levels generally decreasing from Volcano, the youngest site (H1: 300 years ago).

Arthropod abundance and biomass, in total and within different trophic levels, differed widely across sites, but in no case were they linearly related to log substrate age (Fig. 3, Table 1). Total arthropod abundance followed a unimodal pattern along the mesic chronosequence, peaking at H3, whereas total biomass was similar across sites, but was lower only at the oldest site. Detritivores accounted for the largest trophic fraction, measured both by abundance and biomass, and their trends were similar to those for all arthropods. Herbivores showed a unimodal relationship with geological age for both abundance and



**Figure 2.** Site means ( $\pm$  standard error) of ordinal arthropod abundance (●) and biomass (○) on a logarithmic scale of geological age (Fig. 1). Orders: A, Acari; B, Araneae; C, Coleoptera; D, Diptera; E, Heteroptera; F, Homoptera; G, Hymenoptera; H, Lepidoptera (larvae only); I, Orthoptera; J, Psocoptera; K, Malacostraca (Isopoda + Amphipoda); L, all others (Blattodea, Collembola, Neuroptera, Thysanoptera, and all Myriapoda). Unique letters indicate significant differences within response variables (Tukey's HSD; all  $F$ -test degrees of freedom = 4,43).

**Table 1.** Pearson correlation statistics ( $r$ ) among site-level means of ecological and arthropod community variables

	Time	Resources			Habitat			
	Parental material age (log)	NPP†	Litter N†	Foliar P‡	LAI†	Height§	Basal area§	Crown volume§
<b>Abundance</b>								
Total	0.209	0.470	0.863*	0.916**	-0.221	-0.305	-0.028	-0.260
Detritivores	0.332	0.486	0.741	0.815*	-0.311	-0.360	-0.164	-0.454
Herbivores	-0.016	0.353	0.966**	0.979**	-0.074	-0.181	0.204	0.103
Carnivores	0.107	0.515	0.920**	0.952**	-0.096	-0.256	0.064	-0.139
<b>Biomass</b>								
Total	-0.401	0.713	0.753	0.676	0.594	0.143	0.211	0.230
Detritivores	-0.704	0.486	0.271	0.132	0.875*	0.504	0.143	0.437
Herbivores	0.013	0.444	0.955**	0.972**	-0.061	-0.184	0.113	-0.012
Carnivores	-0.016	0.776	0.050	0.005	0.737	-0.302	0.675	0.189
<b>Richness</b>								
Total	0.291	0.763	0.860*	0.910**	0.004	-0.511	0.271	-0.223
Detritivores	-0.141	0.804	0.846*	0.804	0.551	-0.276	0.704	0.354
Herbivores	0.653	0.742	0.618	0.725	-0.207	-0.829*	0.326	-0.452
Carnivores	0.328	0.517	0.774	0.846*	-0.28	-0.384	-0.102	-0.418
<b>Diversity</b>								
Total	0.323	0.951**	0.688	0.726	0.246	-0.620	0.493	-0.179
Detritivores	0.197	0.857*	0.769	0.783	0.334	-0.587	0.733	0.111
Herbivores	0.544	0.859*	0.170	0.244	0.083	-0.633	0.120	-0.595
Carnivores	0.389	0.764	0.830*	0.894**	-0.037	-0.629	0.367	-0.230

Abundance and biomass values were standardized by capture tray area ( $m^2$ ); species richness values are nonparametric second-order jackknife estimators rarified to the smallest shared sample size of total trays at all sites; species diversity estimates are the Fisher's  $\alpha$  index rarified to the smallest shared sample size of total trays at all sites.

†Data from Herbert & Fownes (1999); NPP, net primary productivity ( $g^1 m^{-2} years^{-1}$ ); Litter N, annual flux of mass nitrogen in litterfall ( $g^1 m^{-2} years^{-1}$ ); LAI, leaf area index ( $m^2 m^{-2}$ ).

‡Data from Vitousek *et al.* (1995); foliar P, percent phosphorus by dry mass.

§Data from Gruner & Polhemus (2003); average tree height (m); average tree basal area ( $m^2$ ); average crown volume ( $m^3$ ).

\* $P = 0.10$ ; \*\* $P = 0.05$ .

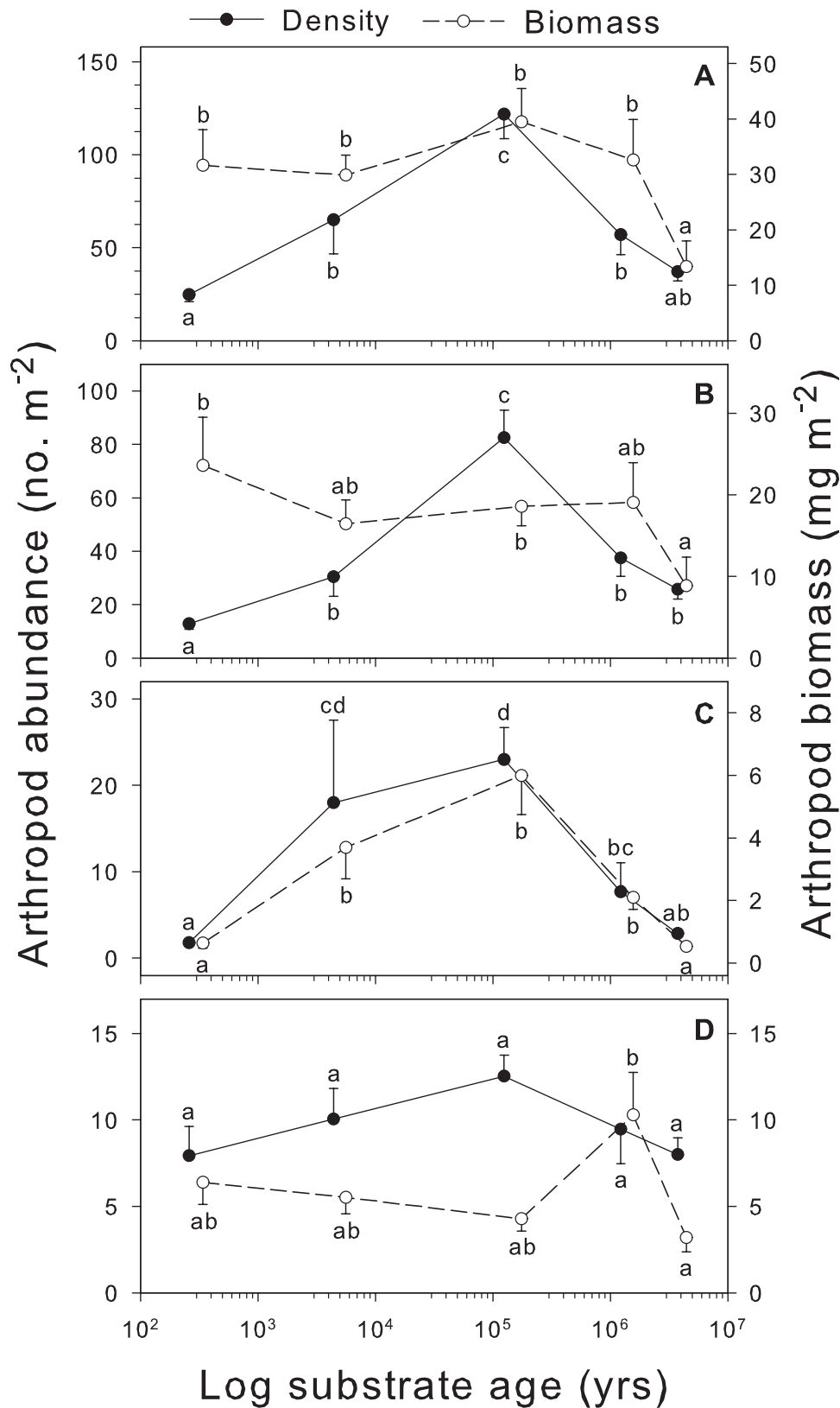
biomass. Carnivore biomass was higher on Moloka'i than elsewhere; carnivores were more abundant at intermediate-aged sites, but this difference was not statistically significant ( $F_{4,43} = 2.07$ ,  $P = 0.105$ ).

Most correlations of arthropod variables with resource and habitat variables across the five sites were not significant (Table 1). Arthropod abundances were strongly, positively related to nutrient status variables, with all trophic levels correlated with percent foliar P and the input rate of N in leaf litter

(except detritivores with N litter rate,  $r = 0.741$ ,  $P = 0.152$ ). Biomass was unrelated to all habitat and most resource variables, with only herbivore biomass correlated to N cycling and foliar P, and detritivore biomass weakly related to LAI.

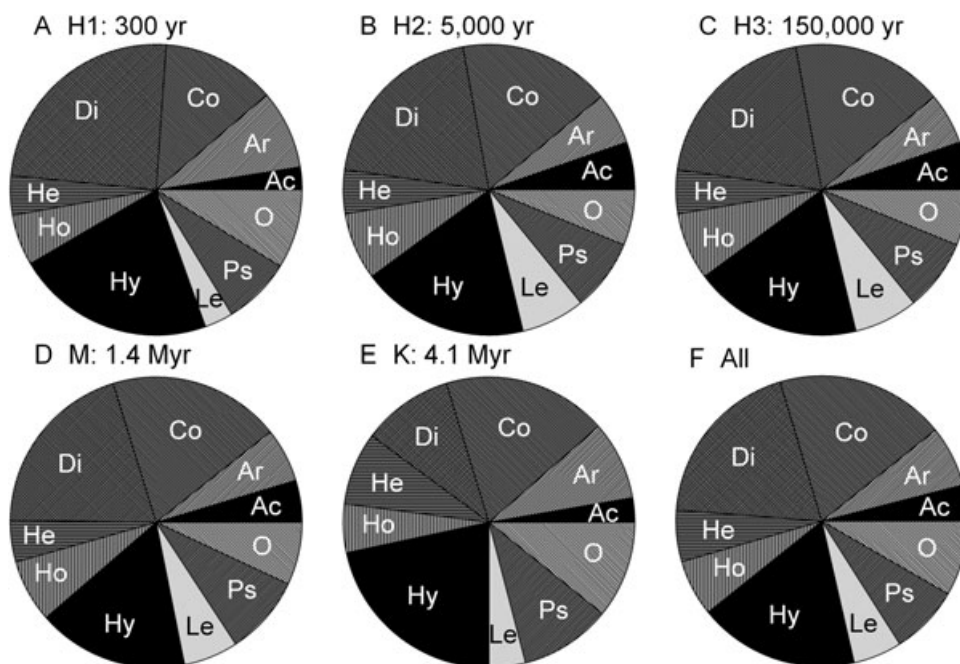
#### ARTHROPOD SPECIES DIVERSITY

Proportions of species in different orders did not differ significantly among sites (Fig. 4;  $\chi^2 = 34.566$ ,



**Figure 3.** Site means ( $\pm$  standard error) of trophic abundance ( $\bullet$ ) and biomass ( $\circ$ ) on a logarithmic scale of geological age (Fig. 1). Trophic groups: A, all; B, detritivores; C, herbivores; D, carnivores. Unique letters indicate significant differences within response variables (Tukey's HSD; all  $F$ -test degrees of freedom = 4,43).





**Figure 4.** Distributions of ordinal species richness at chronosequence sites: A, H1; Volcano; B, H2; Laupāhoehoe; C, H3; Kohala; D, M, Moloka'i; E, K, Kaua'i; F, all sites combined. Ac, Acari; Ar, Araneae; Co, Coleoptera; Di, Diptera; He, Heteroptera; Ho, Homoptera; Hy, Hymenoptera; Le, Lepidoptera; Ps, Psocoptera; O, all others, including Blattodea, Collembola, Malacostraca, Myriapoda, Neuroptera, Orthoptera, Thysanoptera.

d.f. = 36,  $P = 0.537$ ). Diptera, Hymenoptera, and Coleoptera had the most species overall, and relative taxonomic proportions generally were similar across sites. However, there were fewer species of flies on Kaua'i, and of beetles at H1. Trophic structure showed marked constancy in proportions of species distributed within broadly defined feeding groups (Fig. 5), differing among sites significantly less than expected by chance (with undetermined species:  $\chi^2 = 6.885$ , d.f. = 16,  $P = 0.975$ ,  $1 - P = 0.025$ ; without undetermined species:  $\chi^2 = 4.549$ , d.f. = 12,  $P = 0.971$ ,  $1 - P = 0.029$ ).

Overall and trophic-level diversity measures did not correlate linearly with most resource and habitat variables (Table 1). Species richness for several groups were weakly correlated with N cycling rates and foliar P. Herbivore species richness was negatively related to average tree height. Relative diversities (Fisher's  $\alpha$ ) of both detritivores and herbivores, and for all arthropods combined, were positively associated with NPP, and carnivore diversity was positively related to nutrient variables.

Sample-based rarefactions of the second-order jackknife estimator showed higher site-level richness for H3, M, and H2 (Fig. 6A). The sites on chronosequence endpoints, H1 and K, had a lower richness than more productive sites. Individual-based rarefaction, however, showed similar richness trajectories as a

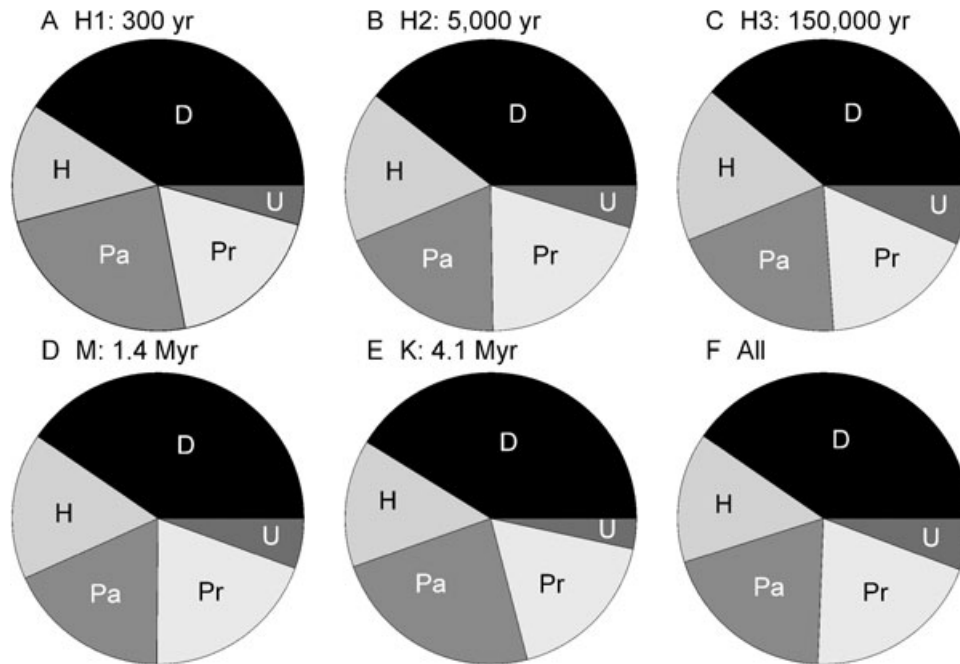
**Table 2.** Species to genus ratios for native species (S) and genera (G) from chronosequence sites

Site	Observed		Rarefaction	
	Number of G	S/G	Number of G	S/G $\pm$ SD
Volcano (H1)	66	1.71	59.7	1.66 $\pm$ 0.016
Laupāhoehoe (H2)	74	1.80	60.5	1.64 $\pm$ 0.024
Kohala (H3)	82	1.89	60.7	1.65 $\pm$ 0.028
Moloka'i (M)	78	2.08	57.2	1.75 $\pm$ 0.028
Kaua'i (K)	65	1.79	59.0	1.68 $\pm$ 0.019

The total measured native genera and ratios are given, followed by estimates obtained by rarefaction to the common baseline of 100 native species ( $\pm$  standard deviation).

function of accumulating abundance across all sites (Fig. 6B).

The total observed richness of native genera mirrored results for abundance and species richness, with a unimodal pattern peaking at H3 (Table 2). However, the ratio of species to genera was greatest on Moloka'i. M remained the highest after rarefaction to the common level of 100 native species; all other sites were comparable at slightly lower values.



**Figure 5.** Distributions of species richness within trophic groups at chronosequence sites: A, H1; Volcano; B, H2, Laupāhoehoe; C, H3; Kohala; D, M, Molokaʻi; E, K, Kauaʻi; F, all sites combined. D, detritivores; H, herbivores; Pa, parasitoids; Pr, predators; U, unassigned.

#### DIVERSITY PARTITIONS

Species diversity partitioned similarly across sites, with the largest fraction found in the among-tree components (Fig. 7A;  $\beta_2$  range = 57.3–66.1%). This  $\beta_2$  component was significantly larger than expected by null models, and the within-tree partitions were significantly smaller than random expectation in all but one case (Kohala  $\beta_1$ : 15.4%,  $P = 0.936$ ;  $\alpha_1$  range = 13.3–20.3%;  $\beta_1$  range = 15.4–23.1%). Within trees at H1, H2, and M sites, variation across trays explained more diversity on average than typical  $\alpha$ -diversity on single trays, whereas these levels were comparable on Kauaʻi, and  $\alpha_1$  was higher at H3. Partitions of native species diversity were similar to the totals, with most of the turnover occurring among trees ( $\beta_2$  range = 58.5–62.8%).

Regional scale analysis showed that the greatest fraction of richness was found among sites, the top hierarchical level of diversity in this study ( $\beta_3 = \gamma$ ; Fig. 7B). For the total community excluding only tourists, all diversity components within sites showed significantly fewer species than expected by chance but species turnover among sites ( $\gamma$ -diversity) was greater than expected. Restricted analyses on native taxa and species defined as rare mirrored this pattern, whereas the partitions of introduced species and common species showed larger fractions explained by  $\alpha$ -diversity. Regional diversity was the smallest fraction of richness for introduced taxa ( $\beta_3 = 4.3\%$ ), presumably

because many of these species were widely distributed. The  $\gamma$ -diversity partition was greater for common species ( $\beta_3 = 39.5\%$ ) because this category included some native species endemic to one island or restricted to one site. All levels of  $\beta$ -diversity of introduced species were significantly greater than expected by chance.

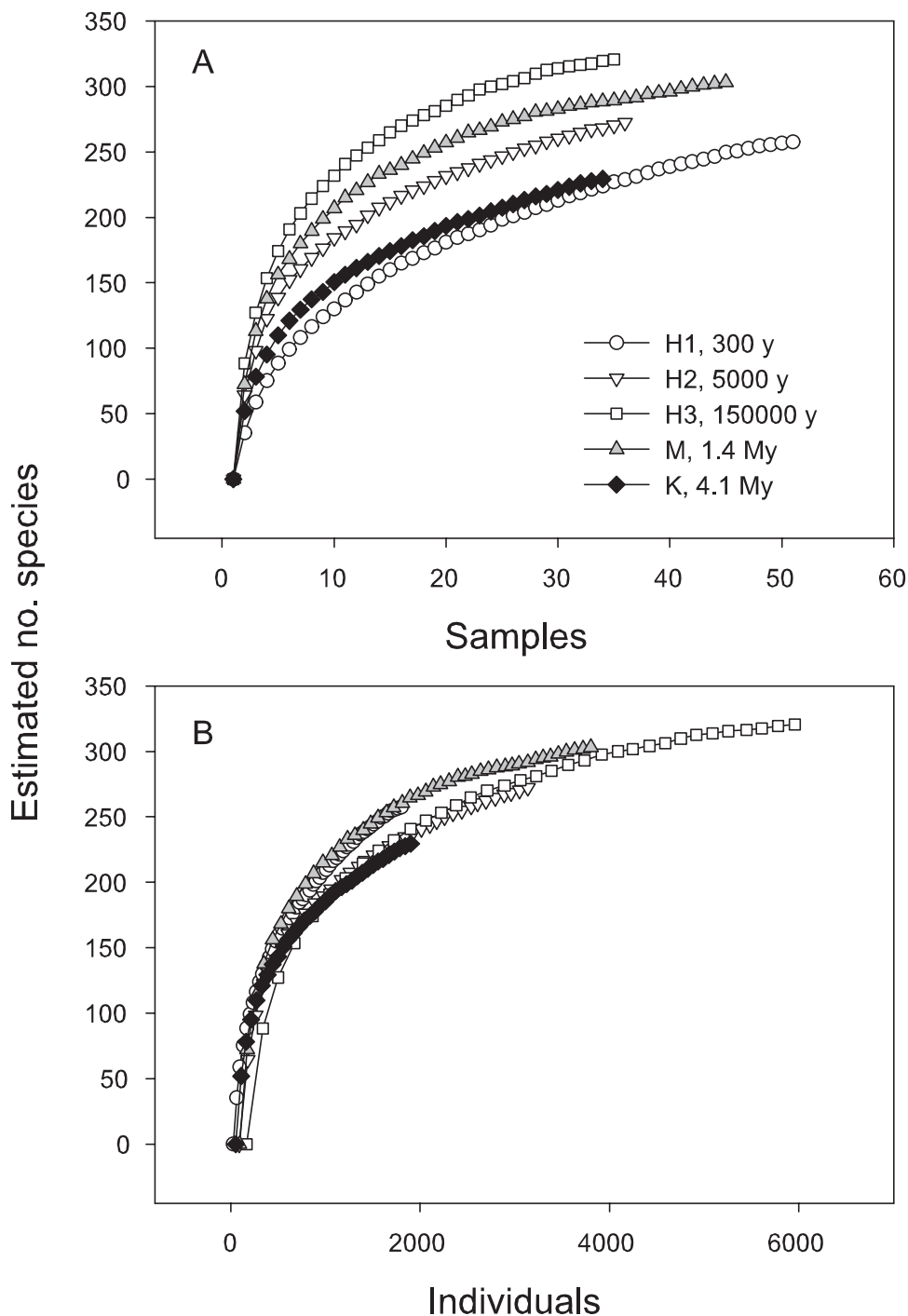
#### HIERARCHICAL CLUSTER ANALYSIS

Cluster analysis for the total community (including recently introduced species) showed the three Hawaiʻi Island sites were most similar, and Molokaʻi was the most unique (Fig. 8A). When all non-indigenous and undetermined species were excluded, the most similar sites were the two youngest and geographically proximate sites, H2 and H1 (Fig. 8B). However, sites on different islands, M and H3, clustered together at the next level, and K was distinct.

## DISCUSSION

#### LOCAL RESOURCES AND COMMUNITY STRUCTURE

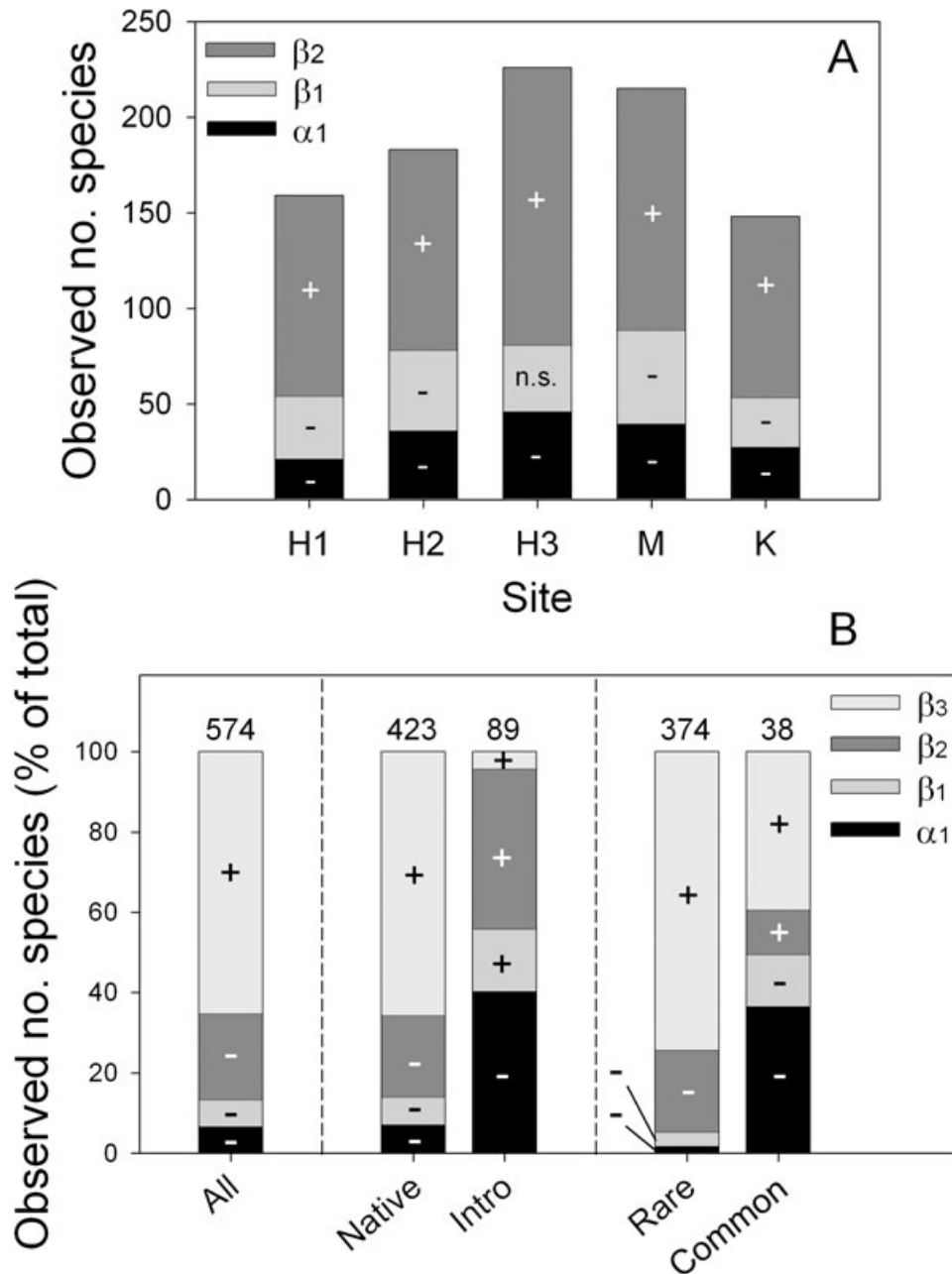
The present study adds to a growing number of examples from terrestrial invertebrate communities showing monotonic increases in diversity with increasing resource availability or productivity (Mittelbach *et al.*, 2001). Abundance, biomass, and total species richness of *Metrosideros* canopy arthropods were generally cor-



**Figure 6.** Sample-based (A) and individual-based (B) rarefaction curves for the five chronosequence sites estimated with the second-order jackknife index. Unshaded symbols represent sites on Hawai'i Island (H1–3), grey triangles show Moloka'i (M), and black diamonds are Kaua'i (K) samples.

related positively with foliar and litter nutrients, and Fisher's  $\alpha$  of herbivores, detritivores, and all arthropods in sum were related positively to net primary productivity (Table 1). However, the strength of these correlative relationships was dependent on the

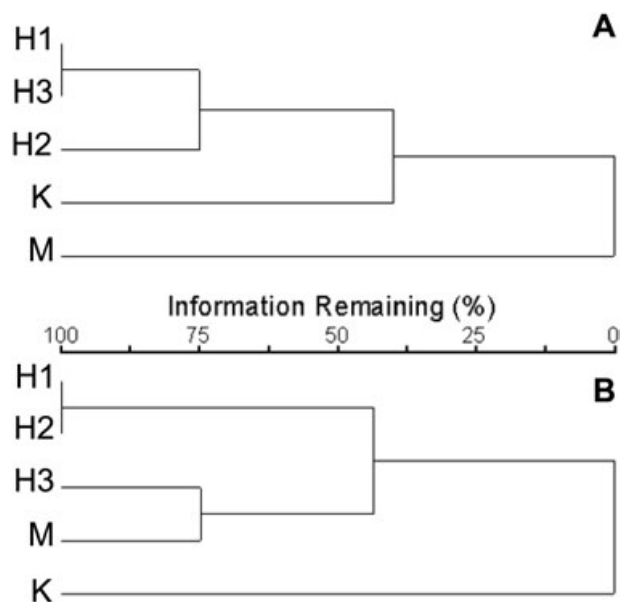
resource variables used (Table 1), highlighting the difficulties in inducing general patterns from studies using different diversity metrics and surrogate measures for productivity or resource availability (Abrams, 1995; Waide *et al.*, 1999; Groner &



**Figure 7.** A, total observed richness of all nontourist arthropods in additive partitions of  $\alpha$  and  $\beta$  components at two spatial scales (samples and trees) within the five chronosequence sites. B, percentage of total observed arthropod species in additive partitions of  $\alpha$  and  $\beta$  components at three spatial scales: samples, trees, and sites. Symbols within plots indicate diversity components larger (+), smaller (-), or not different (n.s.) than null expectations. Partitions in (B) also are shown for native and introduced community subsets, and for all rare (< 0.05% of absolute abundance) and common species (> 0.5%). Numbers above bars indicate the total species count for each comparison.

Novoplansky, 2003). Moreover, elevated abundances at more productive sites (Fig. 3) appeared to drive the increased richness on a sample-standardized basis (Fig. 6A). Site differences in richness disappeared when samples were re-scaled to total abundances using individual-based rarefaction (Fig. 6B). In an

experimental companion study in low productivity volcanic savannah, fertilization increased arthropod abundance and species density on *M. polymorpha*, but abundance-corrected richness did not change or even decreased (Gruner, 2004b; Gruner, Taylor & Forkner, 2005; Gruner & Taylor, 2006). In both studies, rich-



**Figure 8.** Hierarchical cluster analysis of similarity among sites for all nontourist species (A) and native species only (B). Sites are coded as in Figure 1: Volcano (H1), Laupahoehoe (H2), Kohala (H3), Moloka'i (M), Kaua'i (K). Distances were calculated using the relative Sørensen index and sorted by the group average linking method (McCune & Grace, 2002).

ness was tied ultimately to local abundance, perhaps driven by faster organismal growth rates with higher resource fluxes (De Angelis, 1980), higher quality of enriched plant tissues (Sterner & Elser, 2003), or by the increased range and variability of resource supply. Productivity also may increase diversity by allowing locally rare species to invade, persist or coexist in larger local populations or in metacommunities linked by dispersal (Fig. 7B; Preston, 1962; Siemann, 1998; Srivastava & Lawton, 1998; Mouquet & Loreau, 2002). This latter component of  $\beta$ -diversity may include mobile generalist taxa that are using multiple hosts or plant species, in addition to *M. polymorpha*, for food or space.

Cluster analyses of native species composition also supported the resource hypothesis: H3 was more similar to Moloka'i than to other sites closer in geographical proximity on the same island (Fig. 8B). This pattern also has been reported for plants on the chronosequence, with communities at intermediate-aged, productive sites sharing the most similar composition (Crews *et al.*, 1995) despite a monotonic increase in local plant species richness with geological age (Kitayama & Mueller-Dombois, 1995). Although plant species identities and total richness were determined ultimately by differing regional floristic richness and conformed to the time hypothesis (Wagner, 1991;

Price, 2004), quantitative changes in vegetation composition at these sites were influenced more by local soil fertility and forest structure (Crews *et al.*, 1995; Kitayama & Mueller-Dombois, 1995). Island-by-island regional pools of invertebrate diversity in the Hawaiian Islands are well understood only for select, well-studied taxa (Nishida, 2002), and biogeographical studies using catalogues and species lists for diversity analyses have been equivocal on the role of geological age (Cowie, 1995; Peck, Wigfull & Nishida, 1999).

#### LOCAL AND REGIONAL PROCESSES

Diversity partitions universally showed less  $\alpha$ -richness but greater  $\gamma$ -richness than predicted from null randomizations (Fig. 7). Interspecific competition may impose limits on local diversity, explaining this finding for  $\alpha$ -richness (Gillespie, 2004); however, intraspecific aggregation behaviour may also depress local diversity by reducing evenness (Veech, Crist & Summerville, 2003). Intraspecific aggregation is well-documented in arthropod communities (Novotný & Basset, 2000), and can arise locally through mating behaviour, habitat selection, patchiness of resources, or as the legacy of oviposition and limited juvenile dispersal (Veech, Crist & Summerville, 2003).

At broad scales, the high observed species turnover among sites and islands is not surprising because many Hawaiian arthropods are endemic to single islands or even single volcanoes (Howarth, 1990; Otte, 1994; Paulay, 1994). In many cases, closely-related sister species are found at distant sites with similar habitats (Carson, 1987; Gillespie, 2004; Gruner, 2004a) such that local composition changes, but functionality does not. Even with large differences in overall abundance and biomass proportions, however, trophic structure of species was strikingly constant among sites (Fig. 5). Numerous community studies have asserted constancy of guild structure or predator to prey ratios (Evans & Murdoch, 1968; Moran & Southwood, 1982; Jeffries & Lawton, 1985; Krüger & McGavin, 2001), but many have not distinguished these claims from null hypotheses or random expectations (Wilson, 1996; but see Jeffries, 2002). In the present case, the ratios of trophic groups were even more regular than expected by chance, despite differing geological history, productivity, taxonomic composition, abundances, and overall richness. However, potential explanations for such constancy remain cryptic. The patterns could implicate predator-prey interactions, competition for enemy-free space, energetic constraints, or common requirements or responses to the environment by feeding guilds (Warren & Gaston, 1992). Presumably, all these processes would again operate at the local scale.

Even with the large contribution of total richness arising at regional scales (Fig. 7B), local  $\alpha$  and  $\beta$  components of diversity and the total site-level richness correlated most strongly to resource variables, rather than to habitat structural variables or the underlying age of the landmass (Fig. 7A, Table 1). However, the species to genus ratio within native genera on *M. polymorpha*, an index of native species accumulation, was elevated only on Moloka'i, but not at productive sites on Hawai'i where richness and diversity were also high (Table 2). Speciation apparently did not continue to expand coexistence of arthropod species over four million years, and was not the sole force generating higher richness at intermediate-aged sites.

#### GEOLOGICAL AGE, SPECIATION, AND SPECIES ACCUMULATION

Although few molecular clock estimates exist for Hawaiian arthropod lineages (Price & Clague, 2002), most of the analysed lineages were present on the current oldest island, Kaua'i (4.0–5.1 Mya) at least as long, often much longer, than on the other islands, and thus have had more opportunity to accumulate species on older islands (Asquith, 1995; Russo, Takezaki & Nei, 1995; Hormiga, Arnedo & Gillespie, 2003; Jordan, Simon & Polhemus, 2003). The predominant diversification pattern empirically identified within lineages follows a stepwise progression from Kaua'i to younger islands (Carson, 1983; Wagner & Funk, 1995; Shaw, 1996; Liebherr & Zimmerman, 2000; Hormiga, Arnedo & Gillespie, 2003; Jordan, Simon & Polhemus, 2003; Gillespie, 2004; Hoch, 2006).

Why then did the time hypothesis fail to describe the patterns in local diversity seen in on *M. polymorpha*? First, lineage age may be linked only loosely to speciation and  $\alpha$ -diversity. Individual lineages may vary in their underlying diversification rates (Sanderson & Donoghue, 1994; Buzas, Collins & Culver, 2002) and in their capacity to diversify by adaptive or non-adaptive mechanisms (Paulay, 1994). The modal diversity of all arthropod lineages in the Hawaiian Islands is only one species per lineage, many of which are widespread species (Zimmerman, 1948; Roderick & Gillespie, 1998; J. P. Price, unpubl. data). Second, physical environmental characteristics may alter speciation rates or catalyse speciation events (Losos & Schluter, 2000). Volcanic activity has always been most vigorous on the youngest, growing islands of the Hawaiian chain (Carson & Clague, 1995). Frequent volcanism destroyed local populations, forcing repeated recolonization, founder episodes, and genetic drift, and possibly accelerating speciation rates relative to older, dormant islands (Carson *et al.*, 1990; Vandergast, Gillespie & Roderick, 2004). A similar scenario of diversification without

adaptation has been proposed for *Enallagma* damselflies on the margins of retreating glaciers in North America (McPeck & Brown, 2000).

Moreover, the balance between speciation and extinction on islands may differ systematically in concordance with ecosystem development over time (Gillespie, 2004). On older islands, erosion and subsidence reduce island area and elevational range even as topographic diversity increases (Price & Elliot-Fisk, 2004). This phase of forest ecosystem decline has been associated with reduction of tree basal area, increasing phosphorus limitation, and decreased litter decomposition rates and activity of microbes (Vitousek, 2004; Wardle, Walker & Bardgett, 2004). The taxon cycle and taxon pulse hypotheses assume irreversible habitat specialization and range restriction over time within diversifying lineages (Wilson, 1961; Erwin, 1981; Liebherr & Hajek, 1990), which may increase vulnerability to extinction in this changing environment. Indeed, the deeply eroded, oldest high island of Kaua'i may be a 'graveyard' for invertebrate diversity (Asquith, 1995), where examples of relictual, presumably ancient endemic lineages survive but are found nowhere else. For example, two monotypic spiders, *Doryonychus raptor* Simon (Tetragnathidae) and *Adelocosa anops* Gertsch (Lycosidae), exhibit bizarre behavioural, ecological and morphological shifts that are unlike any other extant species (Howarth, 1987; Gillespie, 1992), suggesting that the bulk of diversity in these clades, in the form of intermediates and sibling species, has gone extinct (Asquith, 1995; Roderick & Gillespie, 1998).

Community-wide species to genus ratios, adjusted for effort and sample size, suggests Moloka'i had the highest level of species accumulation per lineage (as approximated by genera; Table 2). An elevated ratio could arise from a combination of lower extinction rates and disproportionately high speciation or colonization. A clade of *Tetragnatha* spiders showed a similar unimodal relationship of richness with geological age across the Hawaiian archipelago, with peaks in local richness on Maui, Moloka'i, and O'ahu (Gillespie, 2004). This was interpreted as evidence for a dynamic equilibrium of community assembly, with build-up through speciation and subsequent decline through extinction on older islands. The island group of Moloka'i, Maui, Lana'i, and Kaho'olawe were coalesced for much of their history into one land mass ('Maui Nui'), which once was larger than the current largest island of Hawai'i (Price & Elliot-Fisk, 2004). Repeated sea level fluctuations over the millennia may have periodically isolated and rejoined populations in a similar manner to that proposed for active volcanics on the youngest island (Carson, Lockwood & Craddock, 1990). Volcanism and sea level changes suggest mechanisms for young and intermediate aged

islands to generate diversity, acting as 'cradles' (Chown & Gaston, 2000) or 'crucibles' (Carson *et al.*, 1990) of evolutionary change. Thus, the regional pools of species available to Moloka'i and other islands in the Maui Nui complex are potentially larger than predictable by their current sizes (Price, 2004).

#### ALTERNATIVE HYPOTHESES

The present study provides rare quantitative analyses of local community-wide invertebrate structure and diversity across a well-resolved and tightly constrained geological chronosequence. An alternate approach would be to sample numerous sites from multiple islands, and necessarily sample each site less intensively, with lower taxonomic resolution and non-asymptotic species accumulation curves. This approach would increase site and intrainland replication, but would invite confounding variation in elevation, rainfall, parental substrate chemistry, topography, vegetative structure, and land use history. Sites on standard substrate on the original volcanic shield surface are extremely rare on the eroded high islands of Kaua'i and Moloka'i (Porder, Asner & Vitousek, 2005), and a tephra site at comparable elevation on O'ahu does not exist (Juvik & Juvik, 1998). The present study opted for high precision and taxonomic resolution, on well-characterized sites with tight constraint over extrinsic factors, vs. more extensive sampling on sites that could sacrifice control over these potentially confounding variables.

It remains possible that the diversity patterns of arthropods on *M. polymorpha* are not general to all host plants or habitats across islands. Several spectacular examples of species-rich radiations of arthropods in the Hawaiian Islands have diversified in concert with unrelated host plant lineages (Montgomery, 1975; Gagné, 1997; Polhemus, 2004). If native plant richness is higher within local sites on older main islands (Wagner, 1991; Kitayama & Mueller-Dombois, 1995), it follows that a similar pattern could be expected for phytophagous arthropods associated with these hosts. Thus, a profitable approach to further test the geological time hypothesis would involve sampling fixed areas of representative habitat, irrespective of plant composition, from these sites or on other gradients. However, *M. polymorpha* is the most abundant, widespread, and locally dominant tree species in the islands (Dawson & Stemmerman, 1999). This species hosts the most diverse assemblage of associated arthropods among native plants (Swezey, 1954; Gruner, 2004a), and is also the largest biotic structural resource within local habitats. Although lineages specialized on other host plant taxa were neglected by this study, generalist feeders (e.g. some detritivores and predators) undoubtedly use multiple

plant species and microhabitats within local sites. Thus, the objective of the present study, to detect a community-wide pattern insensitive to individualistic signals of arthropod clades (Gruner & Polhemus, 2003), was well served by using this model system.

A difficulty for interpretation of space-for-time chronosequences is that the prevailing local conditions at sites probably differed over time (Pickett, 1989). Geological and palynological evidence suggest the vegetation of Hawaiian montane forests differed under previous climatic regimes (Gavenda, 1992; Hotchkiss *et al.*, 2000). However, the great elevational range in the main Hawaiian Islands probably allowed gradual altitudinal migration, rather than elimination, of ecotypes within each region. *Metrosideros polymorpha* is the dominant tree in a wide variety of ecosystems in Hawai'i (Dawson & Stemmerman, 1999), and its presence in the islands dates to the early Pleistocene (Wright *et al.*, 2000). Although its distribution may have shifted, this morphologically and physiologically plastic and variable tree probably persisted in comparable abundances under differing climatic regimes.

The observed positive correlations of arthropod abundance and diversity with resource variables suggest causal effects of productivity, but there are several alternative explanations that must be considered. First, these canopy knockdown samples report abundances per unit tray area, when in reality three-dimensional volumes above trays were sampled. Thus, larger or denser crowns may hold higher arthropod numbers. However, only two of 64 correlations of arthropod variables with leaf area index (Herbert & Fownes, 1999), tree basal area, canopy cover, and crown volume were significant at the  $P = 0.10$  level (Table 1). This suggests that sampling difficulties associated with site differences in physical habitat and tree architecture were minor.

Another alternative interpretation is that the differences in arthropod abundance or diversity were caused by differences in predation intensity because passerine birds were less abundant at more productive, intermediate-aged sites (D. S. Gruner, unpubl. observations). Anthropogenic disturbances and related indirect effects have caused the extinction of more than half of the native forest bird fauna in the Hawaiian Islands (Scott, Conant & van Riper, 2001). The Moloka'i and H3 sites, which showed the highest arthropod abundance and total richness in the present study, have sustained the most local bird extinctions in historical times and currently have the lowest population densities of all the compared sites (Scott *et al.*, 1986). Insectivorous birds can depress the abundance and biomass of forest arthropods (Van Bael, Brawn & Robinson, 2003) and, more generally, top predators can change the diversity of prey (Paine, 1966; Schoener & Spiller, 1996). It follows that the decreased

abundance of insectivorous birds could be responsible for higher arthropod numbers and diversity. However, a multiyear field experiment comparing the effects of birds and nutrient resources on *Metrosideros* arthropods at a single site on Hawai'i island found that the quantitative impacts of birds were restricted to arthropod carnivores, especially spiders (Gruner, 2004b; Gruner, 2005). Fertilization broadly increased arthropod numbers and diversity in a manner analogous to the present study (Gruner, Taylor & Forkner, 2005; Gruner & Taylor, 2006); thus, the resource hypothesis is more consistent with experimental data.

#### CONCLUSIONS

Arthropod abundance and diversity patterns within individual lineages were idiosyncratic, but contemporary diversity on balance was not a monotonic function of geological time for the accumulation of species. Arthropod richness and diversity instead were related to local ecosystem resource variables and mediated by arthropod abundance. Although historical and evolutionary processes generate diversity at broad scales, local communities were convergent in coarse structure and composition, and ecosystem resource availability was predictive of arthropod numbers and richness at local scales. However, the effects of geological age on ecosystem productivity and evolutionary change may be tightly linked (Gillespie, 2004). As ecosystems senesce and productivity declines, specialized species may become restricted to narrow ranges in smaller local populations, and become more susceptible to demographic and environmental stochasticity. As such, ecosystem development and resulting local ecological conditions may constrain the balance of speciation and extinction, and thus the emergent evolutionary patterns, in Hawaiian arthropods.

#### ACKNOWLEDGEMENTS

This study would not have been possible without Dan Polhemus, who provided many hours in the field, equipment, and taxonomic expertise. I thank the Division of Forestry and Wildlife of the State of Hawai'i, Hawaii Volcanoes National Park, the Joseph Souza Center at Koke'e State Park, Parker Ranch, and the Nature Conservancy of Hawai'i for legal permits and access to field sites; S. Fretz, L. Santiago, C. Ewing, and J. Liebherr for assistance with field collections; K. Heckmann, L. Wilson, S. McDaniel, and E. McDaniels for laboratory assistance; D. Foote, H. Farrington, and P. Vitousek for logistical assistance; and the Bernice P. Bishop Museum for providing laboratory space, access to collections, and housing of vouchers. I am grateful to K. Arakaki, M. Arnedo, M. Asche, J. Beatty, T. Blackledge, N. Even-

huis, C. Ewing, J. Garb, M. Gates, G. Gibson, R. Gillespie, J. Huber, K. Kaneshiro, B. Kumashiro, J. Liebherr, E. Mockford, S. Montgomery, J. Noyes, D. Percy, D. Polhemus, D. Preston, A. Richardson, G. A. Samuelson, M. Schauff, C. Tauber, and A. Vandergast for providing or verifying arthropod identifications. D. Herbert kindly provided detailed NPP data, J. Veech shared the PARTITION software, and A. Taylor, J. Ewel, J. Chase, R. Kinzie, T. Miller, D. Strong, and an anonymous reviewer improved the manuscript with critical comments. I acknowledge funding from NSF training grants DGE-9355055 and DUE-9979656 and the John D and Catherine T. MacArthur Foundation to the Center for Conservation Research and Training at the University of Hawai'i at Mānoa, the STAR program of the US Environmental Protection Agency, and NSF doctoral dissertation improvement grant DEB-0073055.

#### REFERENCES

- Abrams PA. 1995.** Monotonic or unimodal diversity – productivity gradients: what does competition theory predict? *Ecology* **76**: 2019–2027.
- Asquith A. 1995.** Evolution of *Sarona* (Heteroptera, Miridae): speciation on geographic and ecological islands. In: Wagner WL, Funk VA, eds. *Hawaiian biogeography: evolution on a hot spot archipelago*. Washington, DC: Smithsonian Institution Press, 90–120.
- Basset Y, Novotný V, Miller SE, Kitching RL. 2003.** *Arthropods of tropical forests: spatio-temporal dynamics and resource use in the canopy*. London: Cambridge University Press.
- Birks HJB. 1980.** British trees and insects: a test of the time hypothesis over the last 13,000 years. *American Naturalist* **115**: 600–605.
- Borges PAV, Brown VK. 1999.** Effect of island geological age on the arthropod species richness of Azorean pastures. *Biological Journal of the Linnean Society* **66**: 373–410.
- Brose U, Martinez ND, Williams RJ. 2003.** Estimating species richness: sensitivity to sample coverage and insensitivity to spatial patterns. *Ecology* **84**: 2364–2377.
- Buzas MA, Collins LS, Culver SJ. 2002.** Latitudinal difference in biodiversity caused by higher tropical rate of increase. *Proceedings of the National Academy of Sciences of the United States of America* **99**: 7841–7843.
- Carson HL. 1983.** Chromosomal sequences and interisland colonizations in Hawaiian *Drosophila*. *Genetics* **103**: 465–482.
- Carson HL. 1987.** Colonization and speciation. In: Gray, AJ, Crawley, MJ, Edwards, PJ, eds. *Colonization, succession and stability*. Oxford: Blackwell Scientific Publications, 187–206.
- Carson HL, Clague DA. 1995.** Geology and biogeography of the Hawaiian islands. In: Wagner WL, Funk VA, eds. *Hawaiian biogeography: evolution on a hot spot archipelago*. Washington, DC: Smithsonian Institution Press, 14–29.



- Carson HL, Lockwood JP, Craddock EM. 1990.** Extinction and recolonisation of local populations on a growing shield volcano. *Proceedings of the National Academy of Sciences of the United States of America* **87**: 7055–7057.
- Chown SL, Gaston KJ. 2000.** Areas, cradles and museums: the latitudinal gradient in species richness. *Trends in Ecology and Evolution* **15**: 311–315.
- Cody ML. 1975.** Towards a theory of continental species diversities. In: Cody ML, Diamond JM, eds. *Ecology and evolution of communities*. Cambridge, MA: Belknap Press of Harvard University, 214–257.
- Colwell RK. 1997.** *Biota: the biodiversity database manager*, Version 1.0. Sunderland, MA: Sinauer Associates.
- Colwell RK. 2004.** *Estimates: statistical estimation of species richness and shared species from samples*, Version 7.5. Available at <http://purl.oclc.org/estimates>.
- Colwell RK, Coddington JA. 1994.** Estimating terrestrial biodiversity through extrapolation. *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences* **345**: 101–118.
- Compton SG, Lawton JH, Rashbrook VK. 1989.** Regional diversity, local community structure and vacant niches: the herbivorous arthropods of bracken in South Africa. *Ecological Entomology* **14**: 365–373.
- Cornell HV, Lawton JH. 1992.** Species interactions, local and regional processes, and limits to the richness of ecological communities: a theoretical perspective. *Journal of Animal Ecology* **61**: 1–12.
- Cowie RH. 1995.** Variation in species diversity and shell shape in Hawaiian land snails: in situ speciation and ecological relationships. *Evolution* **49**: 1191–1202.
- Crews TE, Kitayama K, Fownes JH, Riley RH, Herbert DA, Mueller-Dombois D, Vitousek PM. 1995.** Changes in soil phosphorus fractions and ecosystem dynamics across a long chronosequence in Hawaii. *Ecology* **76**: 1407–1424.
- Crist TO, Veech JA, Gering JC, Summerville KS. 2003.** Partitioning species diversity across landscapes and regions: a hierarchical analysis of  $\alpha$ ,  $\beta$ , and  $\gamma$  diversity. *American Naturalist* **162**: 734–743.
- Dawson JW, Stemmerman L. 1999.** *Metrosideros* Banks ex Gaertn. In: Wagner WL, Herbst DR, Sohmer SH, eds. *Manual of the flowering plants of Hawai'i*, 2nd edn. Honolulu: Bernice P. Bishop Museum Press. 964–970.
- De Angelis DL. 1980.** Energy flow, nutrient cycling, and ecosystem resilience. *Ecology* **61**: 764–771.
- Edwards AWF. 1986.** Are Mendel's results really too close? *Biological Reviews* **61**: 295–312.
- Erwin TL. 1981.** Taxon pulses, vicariance, and dispersal: an evolutionary synthesis illustrated by carabid beetles. In: Nelson G, Rosen DE, eds. *Vicariance biogeography: a critique*. New York, NY: Columbia University Press, 159–196.
- Evans FC, Murdoch WW. 1968.** Taxonomic composition, trophic structure and seasonal occurrence in a grassland insect community. *Journal of Animal Ecology* **37**: 259–273.
- Fischer AG. 1960.** Latitudinal variations in organic diversity. *Evolution* **14**: 64–81.
- Fisher RA. 1936.** Has Mendel's work been rediscovered? *Annals of Science* **1**: 115–137.
- Gagné WC. 1979.** Canopy-associated arthropods in *Acacia koa* and *Metrosideros* tree communities along an altitudinal transect on Hawaii island. *Pacific Insects* **21**: 56–82.
- Gagné WC. 1997.** *Insular evolution, speciation, and revision of the Hawaiian genus Nesiomiris (Hemiptera: Miridae)*. Bishop Museum Bulletin in Entomology, Vol. 7. Honolulu: Bishop Museum Press.
- Gavenda RT. 1992.** Hawaiian quaternary paleoenvironments: a review of geological, pedological, and botanical evidence. *Pacific Science* **46**: 295–307.
- Gering JC, Crist TO, Veech JA. 2003.** Additive partitioning of species diversity across multiple spatial scales: implications for regional conservation of biodiversity. *Conservation Biology* **17**: 488–499.
- Gillespie RG. 1992.** Impaled prey. *Nature* **355**: 212–213.
- Gillespie RG. 2004.** Community assembly through adaptive radiation in Hawaiian spiders. *Science* **303**: 356–359.
- Gotelli NJ, Colwell RK. 2001.** Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters* **4**: 379–391.
- Gotelli NJ, Entsminger GL. 2002.** *Ecosim: null models software for ecology*, Version 7. Burlington, VT: Acquired Intelligence Inc. & Kesey-Bear.
- Groner E, Novoplansky A. 2003.** Reconsidering diversity-productivity relationships: directness of productivity estimates matters. *Ecology Letters* **6**: 695–699.
- Gruner DS. 2003.** Regressions of length and width to predict arthropod biomass in the Hawaiian Islands. *Pacific Science* **57**: 325–336.
- Gruner DS. 2004a.** Arthropods from 'ōhi'a lehua (Myrtaceae: *Metrosideros polymorpha*), with new records for the Hawaiian Islands. Bishop Museum Occasional Papers **78**: 33–52.
- Gruner DS. 2004b.** Attenuation of top-down and bottom-up forces in a complex terrestrial community. *Ecology* **85**: 3010–3022.
- Gruner DS. 2005.** Biotic resistance to an invasive spider conferred by generalist insectivorous birds on the island of Hawai'i. *Biological Invasions* **7**: 541–546.
- Gruner DS, Polhemus DA. 2003.** Arthropod communities across a long chronosequence in the Hawaiian Islands. In: Basset Y, Novotný V, Miller SE, Kitching RL, eds. *Arthropods of tropical forests: spatio-temporal dynamics and resource use in the canopy*. London: Cambridge University Press, 135–145.
- Gruner DS, Taylor AD. 2006.** Richness and species composition of arboreal arthropods affected by nutrients and predators: a press experiment. *Oecologia* **147**: 714–724.
- Gruner DS, Taylor AD, Forkner RE. 2005.** The effects of foliar pubescence and nutrient enrichment on arthropod communities of *Metrosideros polymorpha* (Myrtaceae). *Ecological Entomology* **30**: 428–443.
- Herbert DA, Fownes JH. 1999.** Forest productivity and efficiency of resource use across a chronosequence of tropical montane soils. *Ecosystems* **2**: 242–254.
- Hillebrand H, Blenckner T. 2002.** Regional and local impact on species diversity – from pattern to processes. *Oecologia* **132**: 479–491.

- Hoch H. 2006.** Systematics and evolution of *Iolania* (Hemiptera: Fulgoroidea: Cixiidae) from Hawai'i. *Systematic Entomology* **31**: 302–320.
- Hormiga G, Arnedo M, Gillespie RG. 2003.** Speciation on a conveyor belt: sequential colonization of the Hawaiian Islands by *Orsonwelles* spiders (Araneae, Linyphiidae). *Systematic Biology* **52**: 70–88.
- Hotchkiss S, Vitousek PM, Chadwick OA, Price J. 2000.** Climate cycles, geomorphological change, and the interpretation of soil and ecosystem development. *Ecosystems* **3**: 522–534.
- Howarth FG. 1987.** Evolutionary ecology of aeolian and subterranean habitats in Hawaii. *Trends in Ecology and Evolution* **2**: 220–223.
- Howarth FG. 1990.** Hawaiian terrestrial arthropods: an overview. *Bishop Museum Occasional Papers* **30**: 4–26.
- Hubbell SP. 2001.** *The unified neutral theory of biodiversity and biogeography*. Princeton, NJ: Princeton University Press.
- Huston MA. 1994.** *Biological diversity: the coexistence of species on changing landscapes*. Cambridge: Cambridge University Press.
- Jeffries MJ. 2002.** Evidence for individualistic species assembly creating convergent predator: prey ratios among pond invertebrate communities. *Journal of Animal Ecology* **71**: 173–184.
- Jeffries MJ, Lawton JH. 1985.** Predator-prey ratios in communities of freshwater invertebrates: the role of enemy free space. *Freshwater Biology* **15**: 105–112.
- Jordan S, Simon C, Polhemus DA. 2003.** Molecular systematics and adaptive radiation of Hawaii's endemic damselfly genus *Megalagrion* (Odonata: Coenagrionidae). *Systematic Biology* **52**: 89–109.
- Juvik SP, Juvik JO. 1998.** *Atlas of Hawai'i*, 3rd edn. edn Honolulu: University of Hawai'i Press.
- Kitayama K, Mueller-Dombois D. 1995.** Vegetation changes along gradients of long-term soil development in the Hawaiian montane rainforest zone. *Vegetatio* **120**: 1–20.
- Krüger O, McGavin GC. 2001.** Predator-prey ratio and guild constancy in a tropical insect community. *Journal of Zoology* **253**: 265–273.
- Lande R. 1996.** Statistics and partitioning of species diversity, and similarity among communities. *Oikos* **76**: 5–13.
- Leather SR. 1986.** Insect species richness of the British Rosaceae: the importance of host range, plant architecture, age of establishment, taxonomic isolation and species-area relationships. *Journal of Animal Ecology* **55**: 841–860.
- Liebherr JK, Hajek AE. 1990.** A cladistic test of the taxon cycle and taxon pulse hypotheses. *Cladistics* **6**: 39–59.
- Liebherr JK, Zimmerman EC. 2000.** *Hawaiian Carabidae (Coleoptera), part 1: introduction and tribe Platynini. Insects of Hawaii*, Vol. 16. Honolulu, HI: University of Hawaii Press.
- Lockwood JP, Lipman PW, Peterson LD, Warshauer FR. 1988.** *Generalized ages of surface flows of Mauna Loa Volcano, Hawaii*, Map I-1908. Washington, DC: US Department of the Interior.
- Loreau M. 2000.** Are communities saturated? On the relationship between  $\alpha$ ,  $\beta$  and  $\gamma$  diversity. *Ecology Letters* **3**: 73–76.
- Losos J, Schluter D. 2000.** Analysis of an evolutionary species-area relationship. *Nature* **408**: 847–850.
- Magurran AE. 1988.** *Ecological diversity and its measurement*. Princeton, NJ: Princeton University Press.
- May RM. 2001.** *Stability and complexity in model ecosystems*, 2nd edn. Princeton, NJ: Princeton University Press.
- McCune B, Grace JB. 2002.** *Analysis of ecological communities*. Glenden Beach, OR: MJM Software Design.
- McCune B, Mefford MJ. 1999.** *PC-ORD: multivariate analysis of community structure*, Version 4.0. Glenden Beach, OR: MJM Software.
- McPeck MA, Brown JM. 2000.** Building a regional species pool: diversification of the *Enallagma* damselflies in eastern North American waters. *Ecology* **81**: 904–920.
- Mendelson TC, Shaw KL. 2005.** Rapid speciation in an arthropod. *Nature* **433**: 375–376.
- Mittelbach GG, Steiner CF, Scheiner SM, Gross KL, Reynolds HL, Waide RB, Willig MR, Dodson SI, Gough L. 2001.** What is the observed relationship between species richness and productivity? *Ecology* **82**: 2381–2396.
- Montgomery SL. 1975.** Comparative breeding site ecology and the adaptive radiation of picture-winged *Drosophila* (Diptera: Drosophilidae) in Hawaii. *Proceedings of the Hawaiian Entomological Society* **22**: 65–103.
- Moran VC, Southwood TRE. 1982.** The guild composition of arthropod communities in trees. *Journal of Animal Ecology* **51**: 289–306.
- Mouquet N, Loreau M. 2002.** Coexistence in metacommunities: the regional similarity hypothesis. *American Naturalist* **159**: 420–426.
- Nishida GM, ed. 2002.** *Hawaiian terrestrial arthropod checklist*. Honolulu: Bishop Museum Press.
- Novotný V, Basset Y. 2000.** Rare species in communities of tropical insect herbivores: pondering the mystery of singletons. *Oikos* **89**: 564–572.
- Otte D. 1994.** *The crickets of Hawaii*. Philadelphia, PA: The Orthopterists' Society.
- Paine RT. 1966.** Food web complexity and species diversity. *American Naturalist* **100**: 65–75.
- Pärtel M. 2002.** Local plant diversity patterns and evolutionary history at the regional scale. *Ecology* **83**: 2361–2366.
- Paulay G. 1994.** Biodiversity on oceanic islands: its origin and extinction. *American Zoologist* **34**: 134–144.
- Peck SB, Wigfull P, Nishida G. 1999.** Physical correlates of insular species diversity: the insects of the Hawaiian Islands. *Annals of the Entomological Society of America* **92**: 529–536.
- Pickett STA. 1989.** Space-for-time substitution as an alternative to long-term studies. In: Likens GE, ed. *Long-term studies in ecology: approaches and alternatives*. Berlin: Springer-Verlag, 110–135.
- Polhemus DA. 2004.** Further studies on the genus *Orthotylus* (Heteroptera: Miridae) in the Hawaiian Islands, with descriptions of thirty-four new species. *Journal of the New York Entomological Society* **112**: 227–333.

- Porder S, Asner GP, Vitousek PM. 2005.** Ground-based and remotely sensed nutrient availability across a tropical landscape. *Proceedings of the National Academy of Sciences of the United States of America* **102**: 10909–10912.
- Preston FW. 1962.** The canonical distribution of commonness and rarity. *Ecology* **43**: 410–432.
- Price JP. 2004.** Floristic biogeography of the Hawaiian Islands: influences of area, environment and paleogeography. *Journal of Biogeography* **31**: 1–14.
- Price JP, Clague DA. 2002.** How old is the Hawaiian biota? Geology and phylogeny suggest recent divergence. *Proceedings of the Royal Society of London Series B, Biological Sciences* **269**: 2429–2435.
- Price JP, Elliot-Fisk D. 2004.** Topographic history of the Maui Nui complex, Hawai'i, and its implications for biogeography. *Pacific Science* **58**: 27–45.
- Ricklefs RE, Schluter D, eds. 1993.** Species diversity in ecological communities. *Historical and geographical perspectives*. Chicago, IL: University of Chicago Press.
- Roderick GK, Gillespie RG. 1998.** Speciation and phylogeography of Hawaiian terrestrial arthropods. *Molecular Ecology* **7**: 519–531.
- Rosenzweig ML. 1995.** *Species diversity in space and time*. Cambridge: Cambridge University Press.
- Rosenzweig ML, Abramsky Z. 1993.** How are diversity and productivity related? In: Ricklefs RE, Schluter D, eds. *Species diversity in ecological communities: historical and geographical perspectives*. Chicago, IL: University of Chicago Press, 52–65.
- Russo CAM, Takezaki N, Nei M. 1995.** Molecular phylogeny and divergence times of drosophilid species. *Molecular Biology and Evolution* **12**: 391–404.
- Sanderson MJ, Donoghue MJ. 1994.** Shifts in diversification rate with the origin of angiosperms. *Science* **264**: 1590–1593.
- Schoener TW, Spiller DA. 1996.** Devastation of prey diversity by experimentally introduced predators in the field. *Nature* **381**: 691–694.
- Scott JM, Conant S, van Riper C III, eds. 2001.** *Evolution, ecology, conservation, and management of Hawaiian birds: a vanishing avifauna*. Lawrence, KS: Cooper Ornithological Society.
- Scott JM, Mountainspring S, Ramsey FL, Kepler CB. 1986.** *Forest bird communities of the Hawaiian Islands: their dynamics, ecology, and conservation*. *Studies in Avian Biology*, 9. Los Angeles, CA: Cooper Ornithological Society.
- Shaw KL. 1996.** Sequential radiations and patterns of speciation in the Hawaiian cricket genus *Laupala* inferred from DNA sequences. *Evolution* **50**: 237–255.
- Siemann E. 1998.** Experimental tests of effects of plant productivity and diversity on grassland arthropod diversity. *Ecology* **79**: 2057–2070.
- Signor PW. 1990.** The geologic history of diversity. *Annual Review of Ecology and Systematics* **21**: 509–539.
- Simberloff DS. 1970.** Taxonomic diversity of island biotas. *Evolution* **24**: 23–47.
- Srivastava DS, Lawton JH. 1998.** Why more productive sites have more species: an experimental test of theory using tree-hole communities. *American Naturalist* **152**: 510–529.
- Stein JD. 1983.** Insects infesting *Acacia koa* (Leguminosae) and *Metrosideros polymorpha* (Myrtaceae) in Hawaii: an annotated list. *Proceedings of the Hawaiian Entomological Society* **24**: 305–316.
- Stephens PR, Wiens JA. 2003.** Explaining species richness from continents to communities: the time-for-speciation effect in emydid turtles. *American Naturalist* **161**: 112–128.
- Sturner RW, Elser JJ. 2003.** *Ecological stoichiometry: the biology of elements from molecules to the biosphere*. Princeton, NJ: Princeton University Press.
- Stirling G, Wilsey B. 2001.** Empirical relationships between species richness, evenness, and proportional diversity. *American Naturalist* **158**: 286–299.
- Stork NE, Hammond PM. 1997.** Sampling arthropods from tree-crowns by fogging with knockdown insecticides: lessons from studies of oak tree beetle assemblages in Richmond Park (UK). In: Stork NE, Adis J, Didham RK, eds. *Canopy arthropods*. London: Chapman & Hall, 3–26.
- Strong DR. 1974.** Rapid asymptotic species accumulation in phytophagous insect communities: the pests of cacao. *Science* **185**: 1064–1066.
- Swezey OH. 1954.** *Forest entomology in Hawaii*. Honolulu: Special Publication 76 of the Bishop Museum.
- Van Bael SA, Brawn JD, Robinson SK. 2003.** Birds defend trees from herbivores in a Neotropical forest canopy. *Proceedings of the National Academy of Sciences of the United States of America* **100**: 8304–8307.
- Vandergast AG, Gillespie RG, Roderick GK. 2004.** Influence of volcanic activity on the population genetic structure of Hawaiian *Tetragnatha* spiders: fragmentation, rapid population growth and the potential for accelerated evolution. *Molecular Ecology* **13**: 1729–1743.
- Veech JA, Crist TO. 2003.** *PARTITION, software for partitioning species diversity*, Version 1.0. [http://www.unco.edu/nhs/biology/facultystaff/Veech/software\\_page.htm](http://www.unco.edu/nhs/biology/facultystaff/Veech/software_page.htm)
- Veech JA, Crist TO, Summerville KS. 2003.** Intraspecific aggregation decreases local species diversity of arthropods. *Ecology* **84**: 3376–3383.
- Vitousek PM. 2004.** *Nutrient cycling and limitation: Hawai'i as a model system*. Princeton, NJ: Princeton University Press.
- Vitousek PM, Chadwick OA, Crews TE, Fownes JH, Hendricks DM, Herbert D. 1997.** Soil and ecosystem development across the Hawaiian Islands. *GSA Today* **7**: 1–8.
- Vitousek PM, Turner DR, Kitayama K. 1995.** Foliar nutrients during long-term soil development in Hawaiian montane rain forest. *Ecology* **76**: 712–720.
- Wagner WL. 1991.** Evolution of waif floras: a comparison of the Hawaiian and Marquesan archipelagoes. In: Dudley EC, ed. *The unity of evolutionary biology*. Portland, OR: Dioscorides Press, 267–284.
- Wagner WL, Funk VA, eds. 1995.** *Hawaiian biogeography: evolution on a hot spot archipelago*. Washington, DC: Smithsonian Institution Press.
- Waide RB, Willig MR, Steiner CF, Mittelbach G, Gough L, Dodson SI, Juday GP, Parmenter R. 1999.** The relation-

- ship between productivity and species richness. *Annual Review of Ecology and Systematics* **30**: 257–300.
- Wallace AR. 1878.** *Tropical nature and other essays*. New York, NY: Macmillan.
- Wardle DA, Walker LR, Bardgett RD. 2004.** Ecosystem properties and forest decline in contrasting long-term chronosequences. *Science* **305**: 509–513.
- Warren PH, Gaston KJ. 1992.** Predator-prey ratios: a special case of a general pattern? *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences* **338**: 113–130.
- Whittaker RJ. 1998.** *Island biogeography: ecology, evolution and conservation*. Oxford: Oxford University Press.
- Whittaker RJ, Heegaard E. 2003.** What is the observed relationship between species richness and productivity? *Ecology* **84**: 3384–3390.
- Whittaker RJ, Willis KJ, Field R. 2001.** Scale and species richness: towards a general, hierarchical theory of species diversity. *Journal of Biogeography* **28**: 453–470.
- Willis JC. 1922.** *Age and area: a study in the geographical distribution and origin of species*. Cambridge: Cambridge University Press.
- Wilson EO. 1961.** The nature of the taxon cycle in the Melanesian ant fauna. *American Naturalist* **95**: 169–193.
- Wilson JB. 1996.** The myth of constant predator: prey ratios. *Oecologia* **106**: 272–276.
- Wright SD, Yong CG, Dawson JW, Whittaker DJ, Gardner RC. 2000.** Riding the ice age El Niño? Pacific biogeography and evolution of *Metrosideros* subg. *Metrosideros* (Myrtaceae) inferred from nuclear ribosomal DNA. *Proceedings of the National Academy of Sciences of the United States of America* **97**: 4118–4123.
- Yanoviak SP, Nadkarni NM, Gering JC. 2003.** Arthropods in epiphytes: a diversity component that is not effectively sampled by canopy fogging. *Biodiversity and Conservation* **12**: 731–741.
- Zimmerman EC. 1948.** *Introduction. Insects of Hawaii*, Vol. 1. Honolulu: University of Hawaii Press.
- Zimmerman EC. 1970.** Adaptive radiation in Hawaii with special reference to insects. *Biotropica* **2**: 32–38.