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LOCAL AND REGIONAL INFLUENCES ON ARTHROPOD COMMUNITY STRUCTURE AND SPECIES COMPOSITION ON *METROSIDEROS POLYMORPHA* IN THE HAWAIIAN ISLANDS

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DEDICATION

This dissertation is dedicated to all the Hawaiian arthropods who gave their lives for the advancement of science and conservation.

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ABSTRACT

The overall aim of this research was to weigh the importance of local and regional influences in contemporary arthropod biodiversity and community structure. I manipulated vertebrate predation pressure and basal resources in arthropod food webs at a single model field site, and integrated these results into a historical evolutionary framework using a series of tightly constrained sites throughout the Hawaiian Islands.

The Hawaiian archipelago forms a linear time series of replicated communities, with ages of volcanic origin varying over four orders of magnitude. I sampled free-living arthropods in the canopies of the dominant Hawaiian tree ʻōhiʻa lehua (Myrtaceae: *Metrosideros polymorpha*) at five sites spanning this gradient on Hawaiʻi, Molokaʻi and Kauaʻi. Arthropod abundances and species richness were not related linearly to geological age, but were highest at more productive, intermediate-aged sites. Although historical and evolutionary processes generate diversity at broad scales, local communities were convergent in trophic structure and composition, and resource availability was predictive of arthropod numbers and richness.

I examined the interactive effects of carnivores (top-down) and resources (bottom-up) in a species-rich terrestrial food web. In a 33-mo manipulation, severe soil nutrient limitation on a 120-yr-old lava flow was alleviated by fertilization and combined with bird predator exclusion cages in a randomized block design. *Metrosideros* growth rate and foliar N increased with fertilization. Detritivores composed the largest fraction of arthropod density and biomass, and bottom-up factors controlled basal trophic levels. Conversely, top-down impacts were apparent but variable, concentrated on large-bodied higher order consumers, and did not cascade to indirectly affect primary producers. One previously rare non-indigenous spider species irrupted in the absence of birds, which demonstrated biotic resistance to this invasive species. Other spiders also increased with bird exclusion, but only in fertilized plots. Both treatments influenced species diversity and composition, primarily by altering the relative abundance of species. Foliar pubescence variation altered community composition independently of resource availability. Emergent properties of local food webs corroborated patterns from the gradient study, and reinforced the primacy of local resources as predictors of structure in these communities.

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INTRODUCTION

Introduction

The roots of community ecology lie in the description of patterns in the distribution and abundance of species. From the early days, ecologists wrangled over the processes responsible for the origin, maintenance and consequences of biological diversity in ecological communities. Frederic Clements believed plant communities acted as symbiotic super-organisms, each with a life cycle and evolutionary history comparable to individual organisms (Clements 1916). In contrast, Henry Gleason believed patterns in nature assembled through individualistic abiotic processes interacting uniquely with organisms and species in a particular time and place (McIntosh 1995). This basic tension among deterministic and stochastic viewpoints continues today as theories are developed to explain the form and causes of ecological phenomena, such as relative species abundance distributions (Hubbell 2001, Magurran and Henderson 2003). Where possible, ecologists uncover mechanisms for these emergent patterns with mathematical models and experimental tests in the field or laboratory. Experimental work means little if not substantiated by real patterns in nature, and patterns do not stand alone without attempts to demonstrate cause and effect experimentally.

In this study, I surveyed arthropod communities on *Metrosideros polymorpha* Gaudichaud-Beaupré (Myrtaceae) at five sites across the Hawaiian archipelago, looking for patterns in species abundance, biomass and diversity. The sites span four orders of magnitude in landmass age, but are highly constrained and well characterized with regards to abiotic factors and ecosystem processes. This allowed an uncommon opportunity to compare the relative importance of ecological and evolutionary processes in the maintenance of community structure. I sought to recreate these patterns with a large-scale factorial field experiment, where I manipulated predation pressure and underlying resource availability for 33 mo. Thus, I experimentally determined the explanatory power of local trophic interactions for Hawaiian arthropod community abundance, biomass and species diversity, and compared these communities to sites assembled over evolutionary time with differing regional species pools. Floristic and faunistic simplicity due to evolutionary isolation, combined with well constrained and characterized ecosystem attributes, make the Hawaiian Islands a uniquely appropriate natural laboratory for the study of community structure over multiple scales.

Trophic Dynamics

Food webs and trophic structure have been paradigmatic topics in ecology for decades (Lindeman 1942, Hairston et al. 1960, Paine 1980). Elton (1927) first proposed that organisms could be grouped into functional classifications based on foraging habits and nutritional needs. Lindeman (1942) applied the trophic level concept in relation to ecosystem dynamic analyses, exposing the fundamental interdependence of producers, consumers and the abiotic properties of ecosystems through nutrient cycling and energy flow. He suggested that conversion inefficiencies of trophic transfers attenuate energy availability and place constraints on the number of animals that can exist at the top of trophic chains. Further work has confirmed this proposition, and also added the importance of population dynamical cycles (Pimm and Lawton 1977) and the size of an ecosystem (Post et al. 2000) in limiting food chain length.

In 1960, Hairston, Smith and Slobodkin (HSS) introduced a provocative hypothesis of community-wide trophic regulation (Hairston et al. 1960). They observed that since the world is primarily green and cases of defoliation are rare, plants in general are not limited by herbivores. They hypothesized that predators limit herbivore abundance below outbreak levels, damping plant consumption and eliminating competition for resources among herbivores. Their hypothesis is "top-down" in the sense that higher order consumers in the food chain regulate all levels below. Elaborating on the "green world" hypothesis, the exploitation ecosystem hypothesis revives Lindeman (1942) and incorporates a "bottom-up" component, in that primary productivity determines the number of trophic levels and the interactive relationship between them (Fretwell 1977, Oksanen et al. 1981, Oksanen and Oksanen 2000). In very low productivity systems only primary producers may be supported, whereas in high productivity systems three or even four trophic levels are possible. Strong consumption at the highest trophic level leads to alternating levels of high and low biomass down the food chain. Formalizations of the HSS-type models are based on the assumption that trophic interactions are exploitative, a restricted form of predator-prey interaction (Rosenzweig 1971, 1973, Wollkind 1976, Oksanen et al. 1981). Exploitation models assume linear, non-overlapping food chains with homogeneous trophic levels.

Linear food chains and the trophic level concept have been criticized as overly simplistic and unrealistic (Ehrlich and Birch 1967, Yodzis 1984, Persson 1999). Nevertheless, empirical evidence suggests trophic levels or guilds are useful abstractions in food chain analyses, and some discrete trophic levels do exist: primary producers, obligate terrestrial herbivores, and true decomposers (Hairston and Hairston 1997). In general, communities viewed in terms of functional groupings may be more stable and predictable over time than when viewed in terms of species composition (Duggins 1981, Hay 1994). Species are not the only valid ecological currency; they may be redundant ecologically (Walker 1992) or unreliable for designating functional groups (Johnson et al. 1996). Hay (1994) argues that species are the "noise" of ecological communities, and only by lumping species into functional groupings can one stabilize the variance and find predictable, generalized pattern. Real food webs are complex (Polis 1991), but some reduction of phenomena and assumptions is necessary if general patterns are to be induced and compared among systems.

Bottom-up Processes

Numerous lines of evidence indicate bottom-up factors, broadly defined as resource quantity or quality, are influential to animal population dynamics and community structure. More resources or greater nutrient fluxes in a system have a greater potential for consumer exploitation (De Angelis 1992), and thus may result in more individuals or biomass. In a synthesis from many studies, herbivore biomass, consumption, and secondary productivity were significantly, positively correlated with net energy flux into food webs (McNaughton et al. 1989). However, secondary productivity did not increase at the same rate as herbivore biomass, suggesting energy attenuation with trophic transfers and carnivore sequestration of additional energy to their own biomass. Release of energetic constraints may completely alter the species composition of consumer levels, as seen in foraging seabird assemblages (Ballance et al. 1997), or may result in the addition of a trophic level (Moen and Collins 1996). As species diversity usually is a positive function of total abundance (Wright 1983), it is logical to predict that greater productivity would lead to greater species richness (Srivastava and Lawton 1998). Nevertheless, many high productivity systems have quite low diversity. A unimodal relationship between species richness and productivity, with greatest diversity at intermediate levels of productivity, is widespread across habitats and taxonomic assemblages (Rosenzweig and Abramsky 1993, Abrams 1995, but see Mittelbach et al. 2001). This suggests that other community-level controls, besides available basal resources, assume greater importance at high productivity.

Early criticism of HSS noted that primary producers are neither uniformly edible nor immediately available to consumers (Ehrlich and Birch 1967). Physical attributes, such as spines, trichomes, or tough and thickened leaf tissues, as well as a variety of constitutive or rapidly inducible chemical compounds, protect plants from herbivore consumption. Although HSS ignored evolutionary considerations, Ehrlich and Raven (1965) predicted an evolutionary arms race of plants and their consumers leading to lock-step diversification of both insects and plants. Their seminal contribution spurred a surge of interest in plant-herbivore interactions, and a body of theory predicting the response of plants and their consumers to resource supply. A set of hypotheses based on optimality predicted plants will develop adaptive defenses in proportion to the risk of herbivore consumption, but with tradeoffs to other plant functions such as growth and reproduction (Feeny 1976, Rhoades and Cates 1976).

Three other important hypotheses predict that defensive allocation is fundamentally dependent on resources available to producers. First, the growth rate hypothesis posits evolutionary trade-offs between growth rate and allocation to defense (Coley et al. 1985). This trade-off leads to divergence of life histories with plants growing rapidly to escape from herbivores under high resource conditions, and developing defenses under resource limitation. Second, the carbon-nutrient balance hypothesis predicts that defensive allocation will be related to resource supply, particularly N and light (Bryant et al. 1983). When N supply is limited and light is not, excess carbon-based photosynthate will be allocated to carbon-based secondary compounds (e.g., polyphenolics and terpenoids). With an excess of N or limitation of light, allocation to qualitative, or dose-dependent, N-rich compounds (e.g., alkaloids and cyanogenic glycosides) will increase. Finally, the growth-differentiation balance hypothesis applies similar nutrient limitation scenarios to general plant physiological processes (Loomis 1932, Herms and Mattson 1992). When important nutrients are not limited, plants allocate to production of new tissues and cell growth, whereas cell differentiation-related processes, such as secondary chemical production, leaf thickening, or trichome production are favored under limitation.

Evidence for these hypotheses from studies of plant-herbivore interactions is equivocal (Herms and Mattson 1992, Lerdau et al. 1994, Koricheva et al. 1998, Hamilton et al. 2001). A review of the population effects of fertilization on phytophagous insects showed numerous cases of positive, negative and non-significant responses (Kytö et al. 1996), and the physiological responses of plants to resource regimes have been just as varied (Koricheva et al. 1998). Although it is clear that bottom-up forces are crucial determinants of food web structure, a simple, generalized prediction of ecosystem and community-wide effects of variation in resources is not forthcoming within the current framework (Berenbaum 1995, Stamp 2003).

Top-Down Processes and Trophic Cascades

Theory and empirical evidence have solidified the importance of predators in shaping animal abundance and diversity in communities, but much of this work has been completed in isolation from consideration of bottom-up factors (Sih et al. 1985, Hunter and Price 1992). Effects of predators on their prey can run the gamut from total devastation or extinction (Huffaker 1958) to a "keystone" role in maintaining diversity where they feed on competitively dominant species (Paine 1966). In some systems, predators may exert no control or regulation at all, being limited instead by their prey, and indirectly by basal resources (De Angelis 1975, Hawkins 1992, Strong 1992, Sanchez-Pinero and Polis 2000).

There are now numerous examples of aquatic systems where primary producers are limited by trophic structure (Carpenter et al. 1987, Brett and Goldman 1996). In food chains with an odd number of trophic levels, predators limit herbivores and plants are limited by competition for resources. Alternatively, in food chains with an even number of levels, top predators release herbivores from intermediate predators, and thus indirectly limit the biomass of primary producers. Although most studies demonstrating these top-down "trophic cascades" are in aquatic systems, the degree to which this is a biological difference, an artifact of research emphasis, or ease of manipulation is a matter of some debate (Strong 1992, Hairston and Hairston 1997, Chase 2000, Shurin et al. 2002). Recent research has suggested that cascading top-down indirect effects are more common in terrestrial systems than previously believed (Pace et al. 1999, Schmitz et al. 2000, Halaj and Wise 2001, Walker and Jones 2001), although the proper diagnosis and terminology of trophic cascades is a matter of continuing debate (Holt 2000, Polis et al. 2000, Power 2000, Hunter 2001).

In terrestrial studies that excluded insectivorous birds from foliage, many have found positive effects on arthropods (e.g., Holmes et al. 1979, Fowler et al. 1991, Bock et al. 1992, Gunnarsson 1998, Sipura 1999, Murakami and Nakano 2000, Ritchie 2000, Strong et al. 2000). Some such studies also found increased insect damage on foliage (Atlegrim 1989, Marquis and Whelan 1994, Van Bael et al. 2003). Similar top-down effects have been revealed with the removal of predatory lizards (Spiller and Schoener 1990, Dial and Roughgarden 1995) and predatory arthropods (Carter and Rypstra 1995, Floyd 1996, Moran et al. 1996, Roininen et al. 1996, Schmitz 1997).

However, top-down effects in terrestrial systems appear highly variable in time and space (Floyd 1996), and not as likely to produce effects on autotrophic biomass as in aquatic systems (Strong 1992, Chase 2000). A number of factors may buffer the indirect influence of predators, including competitive and predatory relations within the natural enemy community (Polis and Holt 1992, Rosenheim et al. 1993, Floyd 1996, Spiller and Schoener 1996, Rosenheim 1998), shunts to detrital chains (Moore et al. 2004), allochthonous energy subsidies (Polis et al. 1997), or independent populations fluctuations in response to abiotic cues (Dunson and Travis 1991, Chase 1996).

Relative Strengths of Top-Down and Bottom-Up Forces

Recent studies have shown that the strength and effects of top-down forces can be mediated by, or entirely dependent on, the strength of bottom-up forces (Gutierrez et al. 1994, Forkner and Hunter 2000, Oedekoven and Joern 2000, Denno et al. 2002). The problem remains to uncover the *relative* strengths of top-down and bottom-up forces in terrestrial ecosystems, and then to predict in which ecosystems one should dominate the other. "The only way to overcome our ignorance is to pursue multi-trophic investigations (both experimental and theoretical) from the outset" (Hunter and Price 1992, p. 729).

Within the last decade, several investigators have examined the relative roles of top-down and bottom-up factors in terrestrial community structure in factorial experiments (Schmitz 1994, Haartvigsen et al. 1995, Stiling and Rossi 1997, Fraser 1998, Letourneau and Dyer 1998, Forkner and Hunter 2000, Oedekoven and Joern 2000, Moon and Stiling 2002b). These studies document *species-level* cascades in linear food chains, but there are few instances of community- or ecosystem-wide cascades (Polis 1999). The HSS "green world" and ecosystem exploitation hypotheses refer to community, ecosystem, or larger scale biomass patterns, but species-level cascades may not be significant to system dynamics (Polis 1999). Furthermore, the vast majority of terrestrial tests for top-down cascading interactions in natural terrestrial ecosystems come from grasslands (Halaj and Wise 2001, Shurin et al. 2002), presumably due to the relative ease of their manipulation.

Regional Scale Processes

In order to understand the general relevance of bottom-up and top-down forces across landscapes and biomes, findings at local scales must be integrated with larger temporal and spatial patterns across a range of ecosystem types. Ecologists now explicitly acknowledge that the temporal and spatial scale of observation influences variability and emergent patterns of a system (Levin 1992). The classical basis of community ecology relied heavily on theory of processes that limit the diversity and structure of local communities (Kingsland 1985), while neglecting the macroevolutionary and biogeographical processes such as speciation, colonization and chance historical events that add species over large temporal and spatial scales. Developing theory eventually included larger scale processes of colonization and extinction, but equilibrium conditions still were assumed (MacArthur and Wilson 1967, MacArthur 1972). Increasingly, it is apparent that the availability of regional diversity pools may be a major constraint on local species diversity and community structure (Cornell 1985, Ricklefs 1987, Ricklefs and Schluter 1993). If non-equilibrium regional inputs ultimately constrain community structure, local explanations such as bottom-up forces may be second-order phenomena (Lawton 1996), and interpretations of species diversity that fail to consider regional processes and "biogeographical accidents" (Elton 1958) may be fraught with risk (McPeek 1996).

A general method to explore the dependence of local diversity on the regional pool uses graphical techniques, plotting local α-richness against counts of species (γ-diversity) found in the greater biogeographical region (Terborgh and Faaborg 1980, Cornell and Lawton 1992). The predominant pattern of linear relationships between regional and local richness (reviewed in Hillebrand and Blenckner 2002), or "proportional sampling," implies that local interactions are insufficient to limit local diversity, which instead is a function of the regional pool of potential colonists. In a saturated community where interactions among species limit coexistence, by contrast, the number of local species should reach an asymptote with increasing regional richness. However, many of these studies suffered from pseudoreplication, spatial autocorrelation, and the associated risks from overfitting curves (Hartley 1998a, Srivastava 1999, Loreau 2000, Hillebrand and Blenckner 2002). Furthermore, alternative explanations, such as allopatric speciation over geological time, do not require saturating community interactions to create asymptotic relationships (Stephens and Wiens 2003), and saturated communities may not show an asymptote (Shurin et al. 2000). Alternative approaches are needed to resolve the relative influences of ecological versus evolutionary and historical explanations for community structure (McPeek and Brown 2000, Gering and Crist 2002, Stephens and Wiens 2003, Gillespie 2004).

***Metrosideros polymorpha* as a Model System for Community Ecology**

The Hawaiian Islands are an excellent location for ecological studies (Vitousek 1995). The volcanic archipelago is generated as the northwesterly moving Pacific plate passes over a stationary "hot-spot" of upwelling basaltic lava (Clague and Dalrymple 1989). Oceanic islands all go through similar physical processes as volcanoes are built, then erode and subside. Thus, the main high islands represent a replicated geological time series from northernmost Kaua‘i to the southernmost, volcanically active Hawai‘i. Major climatic gradients are largely independent, greatly facilitating the use of “natural” experiments to disentangle processes governing ecosystem development and community structure (e.g., Vitousek et al. 1994). One mesic chronosequence (Chadwick et al. 1999) consists of sites across the island chain at which elevation, annual average temperature and precipitation, topographic position, land use history, and the dominant tree species are all very similar. All soils on this substrate age gradient are derived from tephra parent material of the original volcanic shield surface (Lockwood et al. 1988, Wolfe and Morris 1996), but ecosystems span over four orders of magnitude difference in developmental age. Soil and foliar nutrients and rates of many ecosystem processes peak at sites of intermediate age: geologically new soils lack plant-available nitrogen, and older soils are deficient in plant-available phosphorus (Crews et al. 1995, Vitousek et al. 1995, Herbert and Fownes 1999). Because productivity and geological age follow different patterns, the relative contributions of ecological and evolutionary explanations for community structure can be disentangled.

The native tree *Metrosideros polymorpha* Gaudichaud-Beaupré (Myrtaceae) is the wet and mesic forest dominant tree on all major islands, and has adapted to broad ecological amplitude. It occurs in conditions ranging from early successional to old growth stands, from sea level to treeline, and from very dry forests (< 250 mm a.a.p.) to among the wettest forests on earth (> 11 m a.a.p., Dawson and Stemmerman 1999). Intraspecific genetic differences with associated distinct morphologies do exist among populations of *M. polymorpha* (Aradhya et al. 1993, Geeske et al. 1994, Cordell et al. 1998). However, these represent minor variations compared to species and family level differences confounding large scale community comparisons elsewhere (Kelly and Southwood 1999).

The *Metrosideros* fauna, composed primarily of birds and arthropods, is comparatively simple and well characterized relative to continental systems at similar latitudes (Gagné 1979, Stein 1983, Peck 1993, Fretz 2000). Reptiles, amphibians and mammals (except one species of bat) are absent naturally (Ziegler 2002). Although some bird or arthropod species may be restricted to a single island or habitat, species in similar habitats on different islands often are closely related members of the same lineages (Zimmerman 1948, Swezey 1954, Roderick and Gillespie 1998).

There is a rich history of entomological work on *M. polymorpha* in the Hawaiian Islands. Wayne Gagné pioneered pyrethrum fogging as a method for sampling arthropods in forest canopies as part of the Island Ecosystems unit of the International Biological Program. Gagné studied *M. polymorpha* and *Acacia koa* along the Mauna Loa elevational gradient and provided the first detailed lists of arthropods associated with these trees (Gagné 1976, Gagné 1979, Gagné 1981, Gagné and Howarth 1981). Stein (1983) later compiled these lists with anecdotal host information reported by Swezey (1954) and others (e.g., Zimmerman 1978). Since those descriptive studies, there have been several quantitative studies of *Metrosideros* arthropods to assess food resources for insectivorous birds at Hakalau Forest National Wildlife Refuge on Hawai'i island (Peck 1993, Fretz 2000). These studies focused on biomass and abundance of potential bird prey types without the taxonomic detail of earlier work. Additional studies have examined endemic psyllids (Homoptera: Triozidae), many of which are host-specific gall-formers on *Metrosideros,* and their herbivory (Nishida et al. 1980, Lee 1981). Most recently, Swift and Goff (2001) assessed in detail the mite fauna sampled from *Metrosideros*, and its various microhabitats, at two sites on Kaua'i.

Moreover, the *M. polymorpha* forest canopy may be one of best remaining habitats to study relatively undisturbed ecosystem and community pattern and process in Hawai'i. Beginning with Polynesian colonization (Kirch 1982), most native habitat below 1000 meters has been cleared for agriculture or other human uses, resulting in widespread extinction and a degraded lowland arthropod fauna (Roderick and Gillespie 1998). Montane mesic and wet forests still persist in wide swaths at elevations above 1000 meters, but invasions of exotic ungulates within the last two hundred years have led to devastation of many native understory plant and animal communities even in these areas (Vitousek et al. 1987). Thus, arthropod communities in *Metrosideros polymorpha* canopies are eminently well suited to robust and replicable comparisons across a variety of ecological regimes.

Overall Aims and Objectives

The overall objective of this research is to understand the relative importance of top-down and bottom-up factors in a natural terrestrial community, and to imbed these results in a historical evolutionary framework. I tested the predictions of the green world and ecosystem exploitation hypotheses at both a local and regional scale. I used a factorial field experiment to test the relative importance of resource limitation and avian predation on the arthropod community of the dominant tree in the Hawaiian Islands. These results were compared to patterns from arthropod surveys throughout the islands, at sites with vast differences in geological age and biogeographical history, to assess the general importance of local mechanisms in shaping biodiversity and community structure.

The first objective was to characterize the patterns of species diversity, abundance and biomass along a geological age gradient in the Hawaiian Islands (Chapter 2). Site productivity and geological age follow different trends, so it was possible to separate the influence of a dominant local ecological force from constraints of evolutionary and historical factors. I used a tightly constrained, well-characterized space-for-time chronosequence in the Hawaiian Islands (Chadwick et al. 1999) to examine the relative importance of local resource variables and geological age in canopy arthropod community structure. Hierarchical sampling protocols of local communities at five sites on three islands controlled for area effects and allowed analysis of diversity partitions at multiple scales. I predicted that if local resources are the primary determinants of structure, then arthropod abundance, biomass, α-richness and diversity should correlate with higher nutrient levels and productivity, previously shown to peak at intermediate-aged sites (Crews et al. 1995, Vitousek et al. 1995, Herbert and Fownes 1999). Alternatively, if accumulated speciation and biogeographical effects determine community structure, then local arthropod variables (particularly, α-richness) should increase with geological age across 4 million years of ecosystem development ("time-for-speciation" effect, *sensu* Stephens and Wiens 2003).

The second objective, covered in Chapters 3, 4 and 5, was to experimentally resolve the relative influence of top-down and bottom-up food web influences on arthropod trophic structure. Since Hairston et al. (1960), ecologists have debated the relative importance of resources and predators in controlling food web biomass and structure, but empirical data from species-rich terrestrial ecosystems are sparse. Using a well-replicated randomized block design over 33 mo on Hawai'i Island, I removed nutrient limitation by fertilization and avian predators with cages. Chapter 3 considers the results of the experiment on arthropod aggregate trophic level abundance and biomass. In line with recent work (Gutierrez et al. 1994, Stiling and Rossi 1997, Fraser 1998, Forkner and Hunter 2000, Denno et al. 2002), I predicted a preponderance of bottom-up effects, and a top-down influence only in fertilized plots.

Chapter 4 details a surprisingly strong effect of birds on one invading, and previously rare, spider species. Removal of birds led to a 25- to 80-fold irruption of the introduced *Achaearanea* cf. *riparia* (Theridiidae). In this era of increasing movement and naturalization of non-native species with human global commerce, understanding of the mechanism of species invasion success versus failure is of critical importance. This study provided rare field evidence for biotic resistance, or the ability of primarily native, generally species-rich, communities to suppress invading species (Elton 1958, Pimm 1991).

In Chapter 5, I explore the interactive effects of top-down and bottom-up treatments on arthropod biodiversity and species composition. Although there are numerous studies on the effects of productivity (Mittelbach et al. 2001) or predators (e.g., Schoener and Spiller 1996) on species diversity, precious few have analyzed interactive effects in experimental designs (e.g., Kneitel and Miller 2002, Worm et al. 2002, Dyer and Letourneau 2003). Diversity is expected to exhibit positive humped relationships, peaking at intermediate levels, with both productivity and predation intensity (Menge and Sutherland 1976, Rosenzweig and Abramsky 1993, Leibold 1996, Waide et al. 1999, but see Mittelbach et al. 2001). It is more difficult, however, to predict under what conditions either one will predominate, and how their relative influence will alter predictions (Leibold 1996, Proulx and Mazumder 1998, Kondoh 2001).

The third objective sought to disentangle two forms of bottom-up influence on arthropod communities: leaf morphology and resource supply. Taking advantage of the large-scale fertilizations undertaken for the second objective, I sampled arthropods from trees of three classes of foliar pubescence on both fertilized and unfertilized plots. Empirical results generally indicate the biomass and abundance of trophic levels increase with fertilization or productivity (Kytö et al. 1996, Begon et al. 1998). Foliar pubescence can also have strong effects on arthropod communities, ordinarily a negative relationship with increasing leaf hairiness or trichome density (Levin 1973, Schoener 1987, Andres and Connor 2003). This effect of pubescence has been suggested for arthropod communities on the morphologically diverse *Metrosideros polymorpha* (Lee 1981), thus it was important to isolate leaf traits from resource effects, *per se* (Chapter 6).

A subsidiary objective was methodological. Many of the analyses for the above objectives required precise estimates of arthropod dry biomass, but it was impossible to pursue careful biodiversity studies while also drying and weighing (and destroying) all the specimens for biomass measurements. Instead, I developed a series of taxonomically specific linear regressions that allowed accurate estimation of biomass from simple morphometrics (Chapter 7).

In the concluding chapter, I summarize and integrate the results found for each objective and discuss their ecological, evolutionary and conservation significance. I explore additional research questions generated by this research, and argue that Hawaiian arthropod communities are useful models for evolutionary ecological questions and crucial components of functioning native ecosystems.

CHAPTER 2

EFFECTS OF PRODUCTIVITY AND GEOLOGICAL AGE ON ARBOREAL ARTHROPOD COMMUNITY STRUCTURE IN THE HAWAIIAN ISLANDS

Abstract

At selected sites on a 4-Myr geological chronosequence in the Hawaiian Islands, major climatic and ecosystem state factors are held constant, but productivity and nutrient levels of the canopy monodominant *Metrosideros polymorpha* (Myrtaceae) peak at intermediate substrate age. These features allowed a test of the relative importance of local resource variables and geological age in canopy arthropod community structure. I used pyrethrum canopy fogging to sample free-living arthropods from *M. polymorpha* trees at five sites on Hawai‘i, Moloka‘i and Kaua‘i. The proportions of individuals and biomass in trophic groups, and in different taxonomic orders, differed widely across sites, but proportions of species in the trophic groups were strikingly constant. Total arthropod abundances and species richness, estimated by sample-based rarefaction, were highest at more productive, intermediate-aged sites. Local α-richness did not show a consistent upper limit, but instead increased with higher productivity. Individual-based rarefaction demonstrated no site differences, suggesting increased diversity is driven by higher abundance. Higher site productivity may allow rare species to persist in suboptimal habitats, as most species richness at local sites is explained by rare, native species at the largest scales. There was no evidence that local community diversity accumulated with increasing geological age to the oldest island; rather, intermediate-aged islands may be contemporary peaks of arthropod phylogenesis. Although historical and evolutionary

processes generate diversity at broad scales, local communities were convergent in aggregate structure and composition, and ecosystem resource availability was predictive of arthropod numbers and richness at local scales.

Introduction

> "The Hawaiian Islands present an ideal setting in which to weigh the relative influences of ecological phenomena (concerned with local conditions and species interactions) and historical phenomena (concerned with dispersal and speciation) on the composition of species assemblages" (p. 27, Price and Elliot-Fisk 2004).

The size of the regional species pool can constrain local species richness and community structure (Ricklefs 1987, Cornell and Lawton 1992, Ricklefs and Schluter 1993, Hillebrand and Blenckner 2002). Nowhere is this more apparent than with tropical arthropod communities, where non-asymptotic species accumulation curves and high proportions of unique species are widely reported (Novotný and Basset 2000, Stirling and Wilsey 2001, Basset et al. 2003, Ødegaard 2004). While many processes at local scales can reduce the diversity of communities, speciation and dispersal are the only means to increase global and local richness. Because of the long temporal scales involved (Pickett 1989), however, there have been few explicit studies of the relative influence of ecological and historical or evolutionary processes in shaping contemporary species diversity in local communities (e.g., McPeek and Brown 2000, Pärtel 2002, Stephens and Wiens 2003, Gillespie 2004).

The importance of area to species diversity patterns is axiomatic (Preston 1960, MacArthur and Wilson 1967, Connor and McCoy 1979, Rosenzweig 1995, Whittaker 1998), but Willis (1922) may have been the first to propose that diversity should be related directly to both area and geological age (see also Wallace 1878). Ignoring tempo and mode, the fossil record generally indicates long trends of species accumulation, interrupted only periodically by sudden extinction events (Signor 1990). May (2001) suggested that deterministic limits on local diversity might expand as niches contract with evolutionary species additions. On remote islands, most of the diversity is generated *in situ*, a result of local diversification from a small pool of colonist taxa (Zimmerman 1970, Carr 1987, Cowie 1995, Whittaker 1998). Thus, the time available for speciation on remote islands may exert as much or more control on species diversity than island area or the distance from the source pool (Wagner 1991, Paulay 1994, Heaney 2000). However, because oceanic islands subside and erode after initial shield building (Price and Elliot-Fisk 2004), geological age often is inversely correlated with island area (Cowie 1995).

Southwood (1961) suggested that the abundance of trees through quaternary history predicts insect species richness, thus initiating a long debate concerning the biogeographic and ecological correlates of insect biodiversity. Further analyses of these data convincingly showed that patterns of insect diversity on British trees were better explained by species-area relations (Strong 1974b, 1974a, Claridge and Wilson 1981, Southwood et al. 1982, Kennedy and Southwood 1984, Kelly and Southwood 1999). However, the quality of the original data for geological time (frequency of pollen records) has been questioned; re-analyses using radio-carbon estimates of continuous residence times of tree species revived the viability of the time hypothesis, although still granting the overall primacy of area relations (Birks 1980, Strong et al. 1984). To better test the influence of geological time, stronger data for ecosystem age over long geological time scales are needed in studies that control for the effects of area (Borges and Brown 1999).

Primary productivity is another key variable thought to influence species richness patterns (Huston 1994). However, decades of intensive research have yielded no consensus for the form of this relationship, particularly in animal communities (Rosenzweig and Abramsky 1993, Abrams 1995, Mittelbach et al. 2001, Mittelbach et al. 2003, Whittaker and Heegaard 2003). Studies of terrestrial animals have yielded more monotonic positive relationships than any other single pattern (Waide et al. 1999), but this generalization is cast into doubt by differing scales, taxonomic emphasis and resolution, and varying directness of productivity measures or surrogate indices (Mittelbach et al. 2001, Groner and Novoplansky 2003). Large-scale studies of terrestrial invertebrate diversity, using direct measures of mass production or biomass, are notably rare.

I used a space-for-time chronosequence across the Hawaiian Islands (Chadwick et al. 1999) to examine the relative importance of local resource variables and geological age in canopy arthropod community structure. The gradient spans four million years of geological substrate age, but sites were carefully selected to standardize climatic and ecosystem state variables. Spatially hierarchical sampling of local communities at five sites on three islands controlled for area effects and allowed analysis of diversity at multiple spatial scales. This design allowed a test of two alternative hypotheses, 1) if local resources constrain communities, then arthropod abundance, biomass, α-richness and diversity should correlate with nutrient levels and primary productivity, previously shown to peak at intermediate-aged sites on this chronosequence (Crews et al. 1995, Vitousek et al. 1995, Herbert and Fownes 1999); 2) alternatively, if accumulated speciation and biogeographical effects determine community structure, then local arthropod variables should increase with geological age ("age accumulation hypothesis").

Methods

Study system

The Hawaiian archipelago was generated as the Pacific plate passed northwesterly over a stationary "hot-spot" of upwelling basaltic lava (Clague and Dalrymple 1989). All the islands were subjected to the same sequence of physical processes as volcanoes were built, then eroded and subsided. Thus, the main high islands represent a replicated geological time series from northernmost Kaua'i to the southernmost, volcanically active Hawai'i. Major climatic gradients within islands are largely independent, greatly facilitating the use of "natural" experiments to disentangle processes governing ecosystem and evolutionary development and local community structure (e.g., Vitousek et al. 1994, Price and Elliot-Fisk 2004).

This study used five sites adjacent to a mesic chronosequence (Chadwick et al. 1999), where elevation, annual average temperature and precipitation, topographic position, land use history, and the dominant tree species are all standardized (Table 2.1, Figure 2.1). Soils at the age gradient sites are derived from tephra parent material of the original volcanic shield surface (Lockwood et al. 1988, Wolfe and Morris 1996), but ecosystems span over four orders of magnitude in developmental age. Net primary productivity, soil and foliar nutrient levels, and nutrient cycling rates peak at sites of intermediate age: geologically new soils lack sufficient fixed N, and older soils are leached and deficient in mobile P (Crews et al. 1995, Vitousek et al. 1995, Herbert and Fownes 1999). Thus, old and new sites at either end of the archipelago have very different biogeographic histories but similar productivity and ecosystem properties, as do intermediate-aged sites on Hawai'i and Moloka'i.

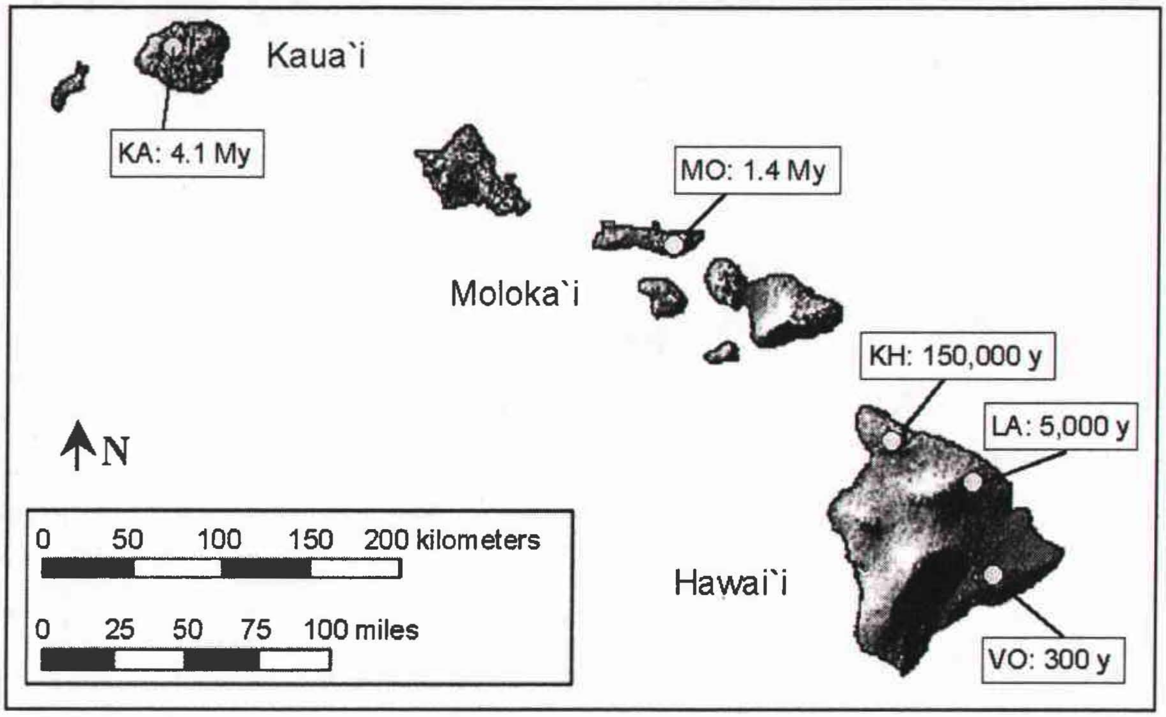

Figure 2.1. Location and surficial substrate age of the five arthropod sampling sites along a Hawaiian mesic chronosequence. From youngest to oldest, the sites are: Volcano (VO, Hawai'i Volcanoes National Park, Hawai'i Island); Laupāhoehoe Flow (LA, Laupāhoehoe Forest Reserve, Hawai'i Island); Kohala (KH, Kohala Forest Reserve, Hawai'i Island); Moloka'i (MO, Kamakou Preserve); and Kaua'i (KA, Nāpali-Kona Forest Reserve).

The myrtaceous tree *Metrosideros polymorpha* Gaudichaud-Beaupré is the wet and mesic forest dominant tree on all major islands. This tree dominates forests in a wide variety of conditions, from early successional to old growth stands, from sea level to treeline, and from very dry forests (< 250 mm average annual precipitation) to among the wettest forests on earth (> 11 m a.a.p.) (Dawson and Stemmerman 1999). Although there are 8 morphological varieties of *M. polymorpha* (Dawson and Stemmerman 1999, James et al. 2004), this variation is minor relative to species and family-level substitutions unavoidable in large-scale comparisons of local communities elsewhere (Kelly and Southwood 1999, but see Lawton and Gaston 1989). The *Metrosideros* fauna, composed primarily of birds and arthropods, is comparatively well characterized (Swezey 1954, Gagné 1979, Stein 1983, Gruner in press-a) and simple relative to continental tropical forests at similar latitudes.

Table 2.1. Site characteristics of the Hawaiian mesic chronosequence. All sites are on tephra substrate, at approximately similar elevation (~1200 m), mean annual temperature (16 °C), and mean annual precipitation (2500 mm) (Crews at al. 1995). Standard errors are presented in parentheses.

Site code	Parent material age $[\mathrm{x}10^3\ \mathrm{yr}]^a$	Elevation [m]	Community basal area $[\mathrm{m}^2\mathrm{ha}^{-1}]$ / % *Metrosideros*[a]	Net Primary Productivity $[\mathrm{kg}^1\mathrm{m}^{-2}\mathrm{yr}^{-1}]^b$	Foliar [N] [% dry mass][c]	Foliar [P] [% dry mass][c]
VO	0.30	1170	35.8 / 81	1.58 (0.13)	0.87 (0.04)	0.060 (0.006)
LA[d]	20	1170	33.6 / 83	1.60 (0.09)	1.42 (0.05)	0.101 (0.006)
KH	150	1120	35.7 / 83	1.78 (0.08)	1.14 (0.10)	0.113 (0.013)
MO	1400	1210	37.3 / 86	1.96 (0.10)	1.06 (0.06)	0.085 (0.004)
KA	4100	1130	38.0 / 88	1.43 (0.15)	0.86 (0.04)	0.061 (0.002)

[a] Data from Crews et al. (1995).

[b] Data from Vitousek et al. (1995).

[c] Data from Herbert and Fownes (1999).

[d] Data for "Laupāhoehoe ash" are given, although arthropods were sampled at "Laupāhoehoe flow", dated at 5,000 yrs B.P. Although community basal area and NPP data were unavailable for Laupāhoehoe ash, foliar nitrogen and phosphorus levels were nearly identical to Laupahoehoe flow (Vitousek et al. 1995).

Arthropod sampling

Pyrethrum canopy fogging is considered a reliable technique for broadly comparative ecological studies (Stork and Hammond 1997, Gering et al. 2003). In a hierarchical spatial design, I sampled arthropods from *Metrosideros polymorpha* at the five sites (Table 2.2) in June (Laupāhoehoe only), October and November of 1997 using "knockdown" fogging with pyrenone 100 (1% pyrethrins, 5% piperonyl butoxide, and 94% isoparafinnic petroleum). Sites were sampled during the same year and under similar local weather conditions, but sites could not be sampled simultaneously due to obvious logistical constraints (Table 2.2). I selected trees, generally of modal size, that were spatially separated to eliminate carryover effects of the fog. Trees flowering or growing on slopes were avoided to reduce potential confounding of uncontrolled variables.

Trees were fogged from sunrise to early evening in good weather conditions only (no precipitation or wind). On average, I obtained samples from 10 *M. polymorpha* trees at each of four sites (Table 2.2), with one individual of *Metrosideros waialealae* (Rock) Rock from Moloka‘i later excluded. Weather conditions limited sample size at the fifth site, Laupāhoehoe flow, so additional samples from June of 1997 (following the same methodology) were included in analyses following diagnostic comparison with November samples (Table 2.2).

Table 2.2. Sample size, sampling dates, and tree-level means (± SE) of ecological variables measured at the five sites of the Hawaiian mesic chronosequence. Site codes and locations are presented in Figure 2.1 and Table 2.1.

Site code	Trees (n)	Dates [1997]	Height [m]	Basal area [m^2]	Crown volume [m^3]	Canopy cover [%]	Foliar N [% d.m.]
VO	9	4-6 Oct	13.03 (0.49)	0.068 (0.010)	121.01 (19.42)	89.22 (1.16)	0.96 (0.026)
LA	8†	3-5 Jun, 6 Nov	11.75 (3.28)	0.521 (0.295)	450.21 (262.96)	n/a	n/a
KH	11	12,14 Oct	10.13 (0.45)	0.068 (0.011)	43.13 (7.09)	83.45 (2.15)	1.44 (0.042)
MO	10	23-24 Oct	8.46 (0.28)	0.130 (0.021)	57.23 (7.80)	90.6 (1.29)	1.13 (0.047)
KA	10	29-30 Oct	9.63 (0.49)	0.071 (0.017)	34.30 (5.46)	77.5 (4.45)	1.16 (0.034)

† Four trees sampled in both June and November 1997.

Individual trees were fogged until the entire crown was saturated for at least 10 sec. Arthropods dropped for one hour onto an array of 3 to 6 collection trays (1.5 m^2) arrayed to subsample all horizontal canopy zones (e.g., near bole) and cardinal directions. Trays suspended white sheets 0.75 m above the forest floor on collapsible PVC frames. Trees varied in size (Table 2.2), so the number of sampling trays varied in rough proportion to the canopy spread area. Arthropods were collected into 70% ethanol as they dropped, and later sorted, counted and identified to species or morphospecies. Length was measured with an ocular micrometer on alcohol-preserved specimens to the nearest millimeter class. Biomass was estimated using taxon-specific regression relationships of body morphometrics to dry mass (Gruner 2003).

Arthropods were assigned to feeding guilds and aggregated into one of five trophic groups: carnivores, detritivores, herbivores, and tourists, or undetermined. I assigned feeding guilds based on personal observation and morphological evidence, literature review, and communication with systematists. Carnivores included all parasitoids, spiders, and other predators; detritivores comprised saprophagic arthropods, dead-wood borers, and grazers of litter, fungi and microbes; herbivores consisted of sap feeders, gall-formers (mostly free living adults), and foliage chewers; 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.

Specimen data were managed using the *Biota* database program (Colwell 1997a). Specimens reside at the B.P. Bishop Museum, Honolulu.

Ecological variables

In addition to arthropods collected, I recorded a number of ecological variables from each tree. Foliar morphology was classified as either glabrous or pubescent. Tree height was estimated with a clinometer. I recorded diameter at breast height for each tree, but converted it to total stem basal area because some trees had multiple major stems. Crown volume was estimated by modeling a cylinder ($4/3\pi r^3$) using average measures of crown breadth in each cardinal direction and the difference between the minimum foliage height and total tree height. Canopy cover was estimated with a spherical densiometer, with measurements taken at four distances (0, 3, 6 and 12 m) from each tree bole in all 4 cardinal directions. An average of the 16 measurements was used for each tree.

In January and February of 1998, I clipped 1-3 terminal branches from each cardinal direction of all fogged trees at four sites (not at Laupāhoehoe) for nitrogen (N) analyses. Thus, for each tree, there were 4 subsamples, except in several cases where foliage did not extend beyond the bole in a particular cardinal direction. To standardize the compared unit, only the most recently expanded, mature cohorts of leaves were selected from sampled branches. Individual, discrete leaf flushes on *Metrosideros* are readily identifiable by searching for scars and leaf size attenuation between leaf clumps (Porter 1972). Indicators also include well-developed apical or lateral buds or additional but obviously recent leaf whorls or flower expansions beyond the target cohort. These mature cohorts most likely were the young leaves during the arthropod sampling four months prior. *Metrosideros* herbivores use young, expanding buds and leaves preferentially (Nishida et al. 1980, Gruner in preparation).

Foliar samples were dried to constant mass at 65 °C and analyzed for percent total N per leaf dry mass (Agricultural Diagnostic Service Center, Department of Agronomy and Soil Science, University of Hawai'i at Mānoa). I measured foliar N in plugs taken from non-vascular leaf tissues using a cork hole borer. N was analyzed on a per tree basis, but an equal area of plugs was included in the sample for each cardinal direction of a tree. Data from 10 uniform standards (0.918% ± 0.009 [SE]) showed the analysis was precise to within one hundredth of one percent foliar N.

Abundance and biomass

Arthropod abundance and biomass variables were averages over all trays for each tree expressed relative to tray area. To examine among-site differences in arthropod numbers, I used one-way analysis of variance with multiple comparisons (Tukey's HSD, joint $\alpha = 0.05$). Both abundance and biomass variables were natural log transformed prior to analysis to meet assumptions for normality. Site comparisons were made within taxonomic orders, within trophic groups, and for all arthropods combined. Orders with few species, or with spotty distributions across sites, were aggregated into more inclusive categories (Class Malacostraca: Isopoda and Amphipoda; all others: Blattodea, Collembola, Neuroptera, Thysanoptera, and all Class Myriapoda).

Pearson correlations of site means of arthropod trophic level abundance and biomass were tested against selected ecosystem productivity and cycling variables (Herbert and Fownes 1999) and the habitat variables measured for this study. From the Herbert & Fownes (1999) study, I chose four variables with low inter-correlations and which were hypothesized to be important for arthropod population dynamics or diversity: aboveground net primary productivity (ANPP), total NPP, the input rate of N in leaf litter (all units $g^{1}m^{-2}yr^{-1}$), and leaf area index (LAI, $m^{2}m^{-2}$). I used a liberal significance threshold ($\alpha = 0.10$) because these correlations each had low power with the small number of sites ($n = 5$ for most correlations, $n = 4$ for several). I therefore did not control the simultaneous significance of the 144 tests, as this would have further reduced their power. Instead, I inspected correlations for general patterns and assumed that 5-10% of tests yielded spurious results. I used the arcsine square root transformation to normalize percentage canopy cover and foliar nitrogen before averaging, and natural log transformations for tree height, basal area, and canopy volume. Common log transformations adjusted the substrate age variable. LAI was highly correlated with arcsine transformed canopy cover (r = 0.969, n = 4, $P = 0.031$), so the former was used because cover data for Laupāhoehoe were lacking.

Species richness and diversity

Several studies have suggested non-random constancy of predator-prey species ratios and guild proportionality across sites or through time (Evans and Murdoch 1968, Moran and Southwood 1982, Jeffries and Lawton 1985, Sugihara et al. 1989, but see Cole 1980, Wilson 1996b). Thus, I examined the proportionality of species richness within orders and trophic groups across chronosequence sites. 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 χ^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 richness among sites was not appropriate because sampling effort (the total number of trays) differed among sites, and species number per unit effort is expected to be nonlinear (Gotelli and Colwell 2001). As the observed species richness almost always underestimates true richness, I used non-parametric extrapolations to estimate total diversity at each site (Colwell and Coddington 1994). Individual tray samples for each site were shuffled and sampled randomly 100 times without replacement to produced smoothed species accumulation curves for seven incidence-based estimators

(Colwell 1997b). Inventory completion, or the ratio of observed richness to estimated richness, generally ranged between 70 and 80%. Thus, I used the second-order jackknife following the recommendations of Brose et al. (2003). The jackknife indices are considered to be among the least biased, but most precise and robust, of the non-parametric species richness estimators (Palmer 1991, Colwell and Coddington 1994, Walther and Martin 2001, Brose et al. 2003, but see Foggo et al. 2003, Scharff et al. 2003).

For direct comparisons of richness, estimates from each site were rarified to the smallest shared sample size of total trays at all sites (i.e., sample-based rarefaction, Gotelli and Colwell 2001). I also calculated Fisher's α, a scalar that controls for abundance and sampling effects (Rosenzweig 1995, Hubbell 2001, Kaspari et al. 2003), using the EstimateS software package (Colwell 1997b). Although other composite indices are used more widely and frequently (e.g., Shannon H'), α is preferred for its discriminant ability and robustness at even small sample sizes (Magurran 1988, Rosenzweig 1995). Fisher's α estimates from the smallest shared sample threshold (as above, for species richness) were used for site-level comparisons.

As with abundance and biomass variables, site means of richness and diversity were analyzed for correlations with productivity, nutrients, and physical variables.

To assess the contribution of speciation to species composition patterns, I computed the species-genus ratio for all native arthropods at each site (Simberloff 1970). Genera are a close proxy for unique lineages in Hawaiian arthropods, so these ratios represent the extent that species in individual lineages have proliferated and now coexist within a local community. To control for sampling effort and to generate estimates of variability, I computed rarefaction curves for 100 randomly selected native species within genera for each site. Monte Carlo simulations were run for 1000 iterations using EcoSim software (Gotelli and Entsminger 2002).

Diversity partitions

The hierarchical sampling design at multiple spatial scales allowed analysis of the α, β and γ components of local and regional diversity (Lande 1996, Loreau 2000, Crist et al. 2003). The additive model of diversity partitioning treats the sum of α and β diversities at any scale as the α diversity of the next larger scale (Lande 1996, Crist et al. 2003). Average within-sample diversity of individual collection trays represented point diversity: the spatial scale most likely to capture individual biotic interactions and the physical constraints of the habitat (Whittaker et al. 2001). The average diversity not explained by α diversity at a selected scale, or β diversity, was quantified at three scales: within trees, among trees, and among regions (γ diversity, *sensu* Cody 1975). Within- and among-tree β diversity represent community-level patterns, whereas γ diversity measures broad-scale, evolutionary, biogeographical and historical effects (Gering et al. 2003).

Diversity partitions were calculated using the program PARTITION, which uses an individual-based Monte Carlo randomization procedure and two-tailed test to distinguish patterns from null expectations (Crist et al. 2003, Veech and Crist 2003); in each analysis 1000 iterations were used. Partitions were calculated on the basis of individual sites using two levels of β diversity (within and among trees), and for the region as a whole adding a 3rd level of β diversity (among sites = γ diversity). To isolate potential evolutionary explanations, native and introduced species also were analyzed separately. In addition, I analyzed the relative contributions of rare and common species, defined as > 0.5% of total abundance and < 0.05% respectively (Gering et al. 2003), and individual trophic levels (detritivores, herbivores and carnivores).

Compositional comparisons

The compositional similarity of sites was examined with hierarchical clustering in PC-ORD (McCune and Mefford 1999). Pairwise distances of sites were computed 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. I used the group average linkage method and scaled the resulting dendrogram using Wishart's objective function (McCune and Grace 2002). Separate analyses examined the total community (excluding tourists) and native species only (excluding tourists, 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 (e.g., bees) and non-feedings species (e.g., moths) were excluded from this analysis, leaving 16,635 individuals in 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 presented in Appendix B.

Abundance and biomass differed among sites for all orders, though not all in the same way (Figure 2.2; numerator and denominator degrees of freedom for all F-ratios were 4, 43). Diptera, Heteroptera, Homoptera, Lepidoptera and Psocoptera abundance and

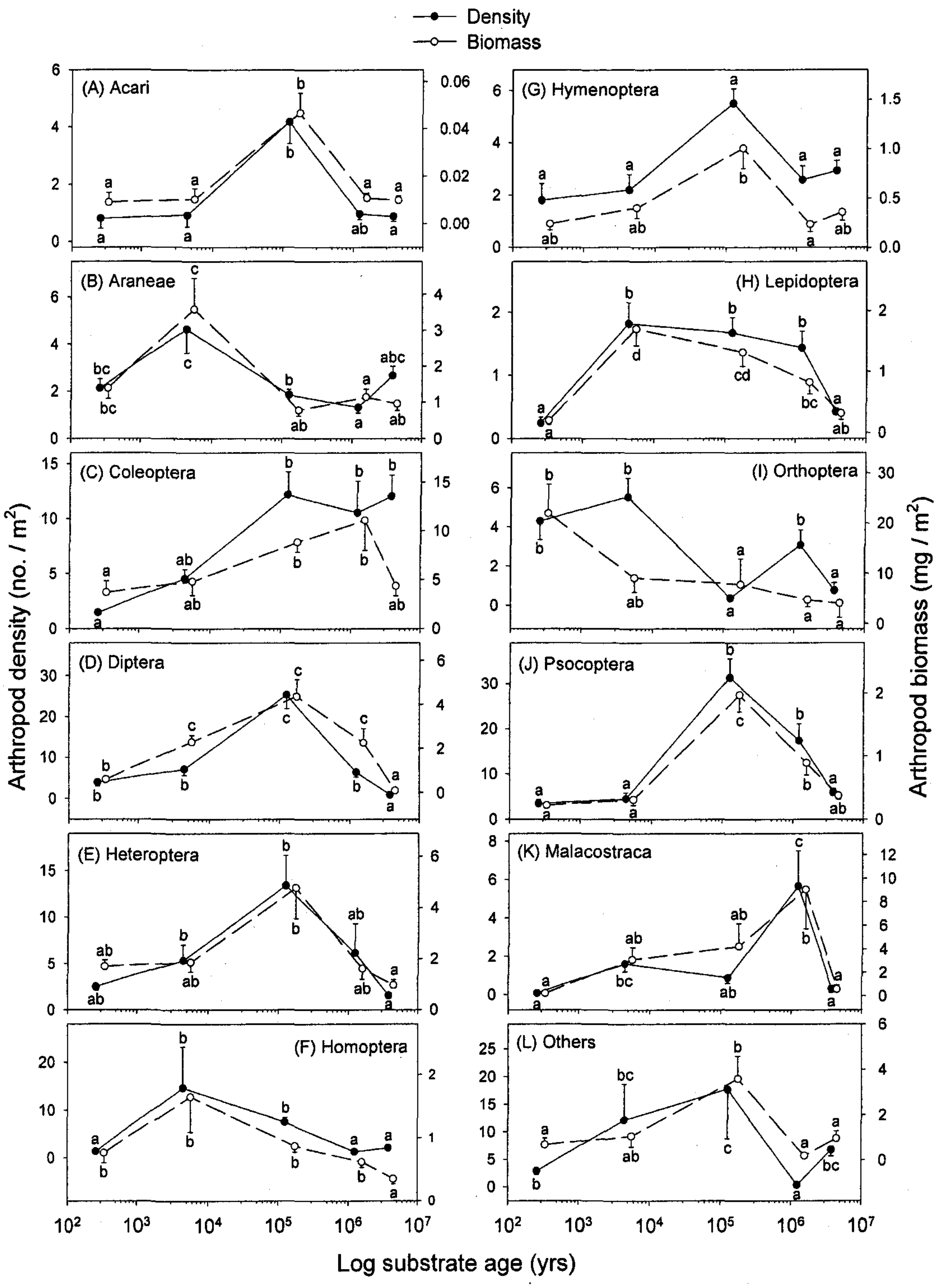

Figure 2.2. Ordinal arthropod abundance (filled circles) and biomass (open circles) at sites along the chronosequence. Orders are, A) Acari, B) Araneae, C) Coleoptera, D) Diptera, E) Heteroptera, F) Homoptera, G) Hymenoptera, H) Lepidoptera (caterpillars only), I) Orthoptera, J) Psocoptera, K) Malacostraca (Isopoda + Amphipoda), and L) all others (Blattodea, Collembola, Neuroptera, Thysanoptera, and all Myriapoda). Values are site means ± 1 SE. Unique letters indicate significant difference (Tukey's HSD).

biomass were high at two or more intermediate-aged sites, with lower numbers at the gradient endpoints. Several orders had high values only at one intermediate site: Araneae at Laupāhoehoe, Acari and Hymenoptera at Kohala, and Malacostraca at Molokaʻi (reflecting a large population of *Platorchestia* nr. *lanipo* [Amphipoda]). Coleoptera biomass also was highest on Molokaʻi and much lower at the older Kauaʻi site, but Coleoptera abundance was high on Kauaʻi, Kohala and Molokaʻi. Orthoptera a very different pattern, especially in biomass, with levels generally decreasing from Volcano, the youngest site (300 yrs).

Abundance and biomass of different trophic levels also differed widely across sites, but in no case were they linearly related to log substrate age (Figure 2.3, Table 2.3). Total arthropod abundance followed a unimodal pattern along the mesic chronosequence, peaking at Kohala (150,000 yrs), whereas total biomass was similar across sites, but was lower only at the oldest site on Kauaʻi. 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 biomass. Carnivore biomass was higher at the Molokaʻi site than elsewhere; carnivores were more abundant at intermediate sites, but this difference was not statistically significant ($F_{4,43} = 2.07$, $P = 0.105$).

Most correlations of arthropod variables with ecological and habitat variables across the five sites were not significant (Table 2.3). Arthropod densities were positively related only to nutrient status variables, with all trophic levels correlated with percent foliar N and with the input rate of N in leaf litter (except detritivores with N litter rate, r =

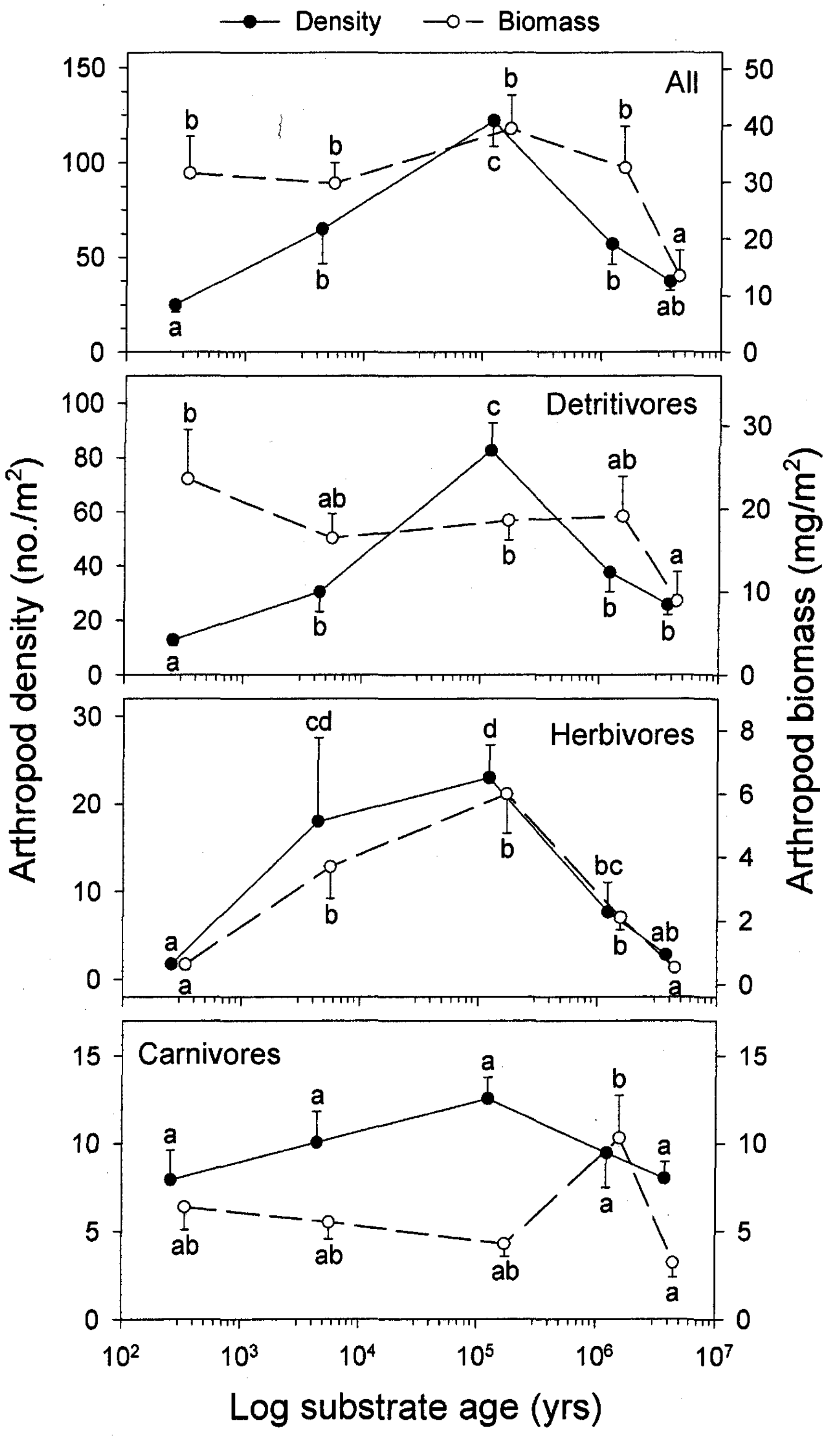

Figure 2.3. Total arthropod abundance (filled circles) and biomass (open circles) at sites along the chronosequence for all arthropods, detritivores, herbivores, and carnivores. Values are site means ± 1 SE. Unique letters indicate significant difference (Tukey's HSD).

0.741, $P = 0.152$). Biomass was even less strongly related to environmental variables, with the exception of herbivore biomass, which was related to N cycling, and carnivore biomass, which showed a nearly one-to-one relation with aboveground net primary productivity.

Table 2.3. Pearson correlation statistics (r) among site-level means of ecological and arthropod community variables. Abundance and biomass values were standardized by capture tray area (m^2); species richness values are non-parametric second-order jackknife estimators rarified to the smallest shared sample size of total trays at all sites; species diversity estimates are the Fisher's α index rarified to the smallest shared sample size of total trays at all sites.

	Parental material age	ANPP^{a}	NPP^{a}	Leaf litter N rate^{a}	LAI^{a}	Height^{b}	Basal area^{b}	Crown volume ^{b}	Leaf N^{c}
	n = 5	n = 5	n = 5	n = 5	n = 5	n = 5	n = 5	n = 5	n = 4
Abundance^{b}									
Total	0.209	-0.087	0.470	0.863*	-0.221	-0.305	-0.028	-0.260	0.946*
Detritivores	0.332	-0.088	0.486	0.741	-0.311	-0.360	-0.164	-0.454	0.963**
Herbivores	-0.016	-0.111	0.353	0.966**	-0.074	-0.181	0.204	0.103	0.924*
Carnivores	0.107	-0.010	0.515	0.920**	-0.096	-0.256	0.064	-0.139	0.904*
Biomass^{b}									
Total	-0.401	0.485	0.713	0.753	0.594	0.143	0.211	0.230	0.338
Detritivores	-0.704	0.593	0.486	0.271	0.875*	0.504	0.143	0.437	-0.266
Herbivores	0.013	-0.055	0.444	0.955**	-0.061	-0.184	0.113	-0.012	0.898
Carnivores	-0.016	0.995**	0.776	0.050	0.737	-0.302	0.675	0.189	-0.369
Richness									
Total	0.291	0.292	0.763	0.860*	0.004	-0.511	0.271	-0.223	0.816
Detritivores	-0.141	0.625	0.804	0.846*	0.551	-0.276	0.704	0.354	0.381
Herbivores	0.653	0.319	0.742	0.618	-0.207	-0.829*	0.326	-0.452	0.760
Carnivores	0.328	-0.052	0.517	0.774	-0.28	-0.384	-0.102	-0.418	0.956**
Diversity									
Total	0.323	0.647	0.951**	0.688	0.246	-0.620	0.493	-0.179	0.534
Detritivores	0.197	0.632	0.857*	0.769	0.334	-0.587	0.733	0.111	0.470
Herbivores	0.544	0.644	0.859*	0.170	0.083	-0.633	0.120	-0.595	0.396
Carnivores	0.389	0.315	0.764	0.830*	-0.037	-0.629	0.367	-0.230	0.802

[a] Data from Herbert and Fownes (1999); NPP = net primary productivity; ANPP = aboveground NPP; LAI = leaf area index.

[b] Tree-level data natural log transformed prior to averaging within sites.

* $0.10 > P > 0.05$; ** $P < 0.05$.

Arthropod species diversity

Proportions of species in different orders did not differ significantly among sites (Figure 2.4; $\chi^2 = 34.566$, d.f. = 36, $P = 0.537$). Diptera, Hymenoptera, and Coleoptera had the most species overall and at most of the sites, and relative taxonomic proportions generally were similar. However, there were fewer species of flies at the Kaua‘i site, and of beetles at Volcano. Arthropod trophic structure showed marked constancy in proportions of species distributed across broadly defined feeding groups (Figure 2.5),

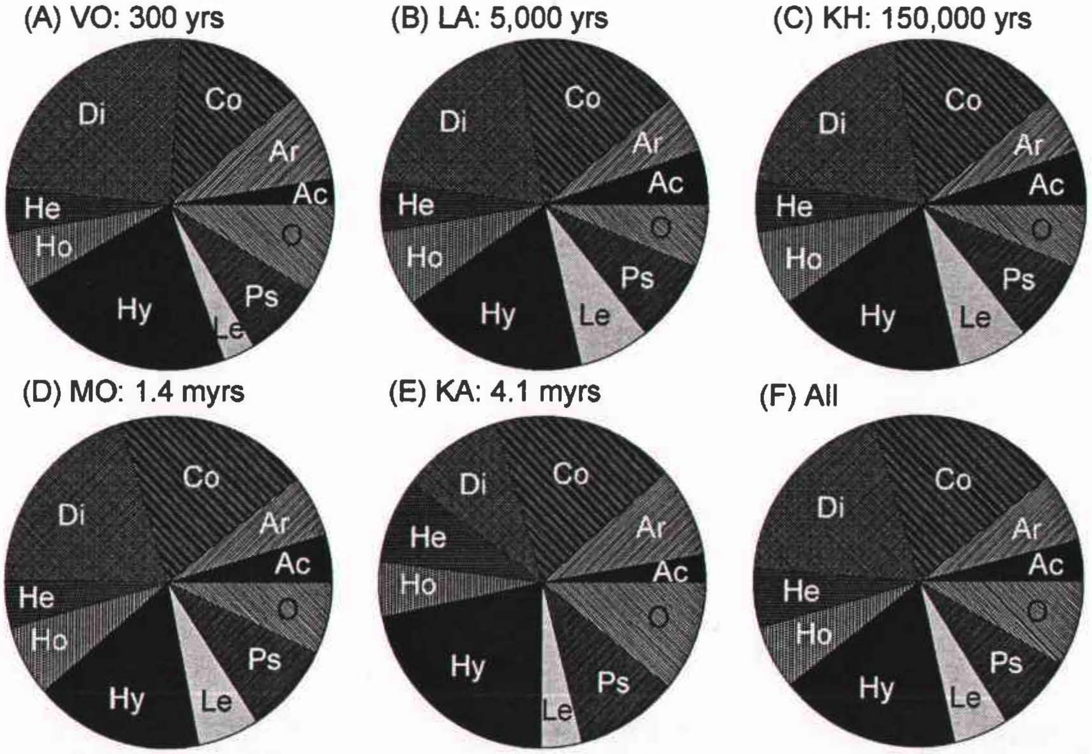

Figure 2.4. Distributions of ordinal species richness at chronosequence sites: (A) Volcano, (B) Laupāhoehoe, (C) Kohala, (D) Moloka‘i, (E) Kaua‘i, and (F) all sites combined. Orders are as follows: Ac = Acari, Ar = Araneae, Co = Coleoptera, Di = Diptera, He = Heteroptera, Ho = Homoptera, Hy = Hymenoptera, Le = Lepidoptera, Ps = Psocoptera, O = all others, including Blattodea, Collembola, Malacostraca, Myriapoda, Neuroptera, Orthoptera, Thysanoptera.

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 guild-level diversity measures did not correlate linearly with most ecosystem and habitat variables (Table 2.3). Species richness for all arthropods and detritivores was weakly correlated with N cycling rates, and with foliar N for carnivores. Herbivore species richness was negatively related to canopy height. Relative diversities (Fisher's α) of both detritivores and herbivores, and for all arthropods combined, were positively associated with NPP. Carnivore relative diversity was weakly correlated with litter N input rates.

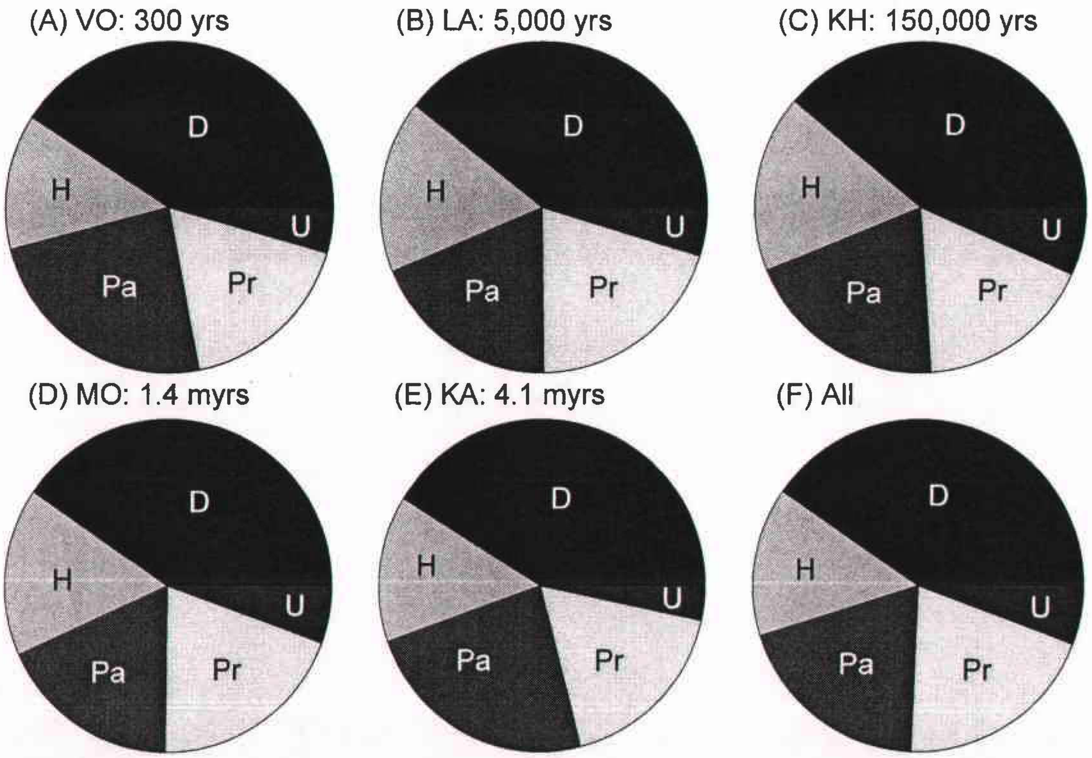
(A) VO: 300 yrs
(B) LA: 5,000 yrs
(C) KH: 150,000 yrs
(D) MO: 1.4 myrs
(E) KA: 4.1 myrs
(F) All

Figure 2.5. Distributions of species richness within trophic groups at chronosequence sites: (A) Volcano, (B) Laupāhoehoe, (C) Kohala, (D) Moloka'i, (E) Kaua'i, and (F) all sites combined. Trophic groups are labeled as follows: D = detritivores, H = herbivores, Pa = parasitoids, Pr = predators, and U = unassigned.

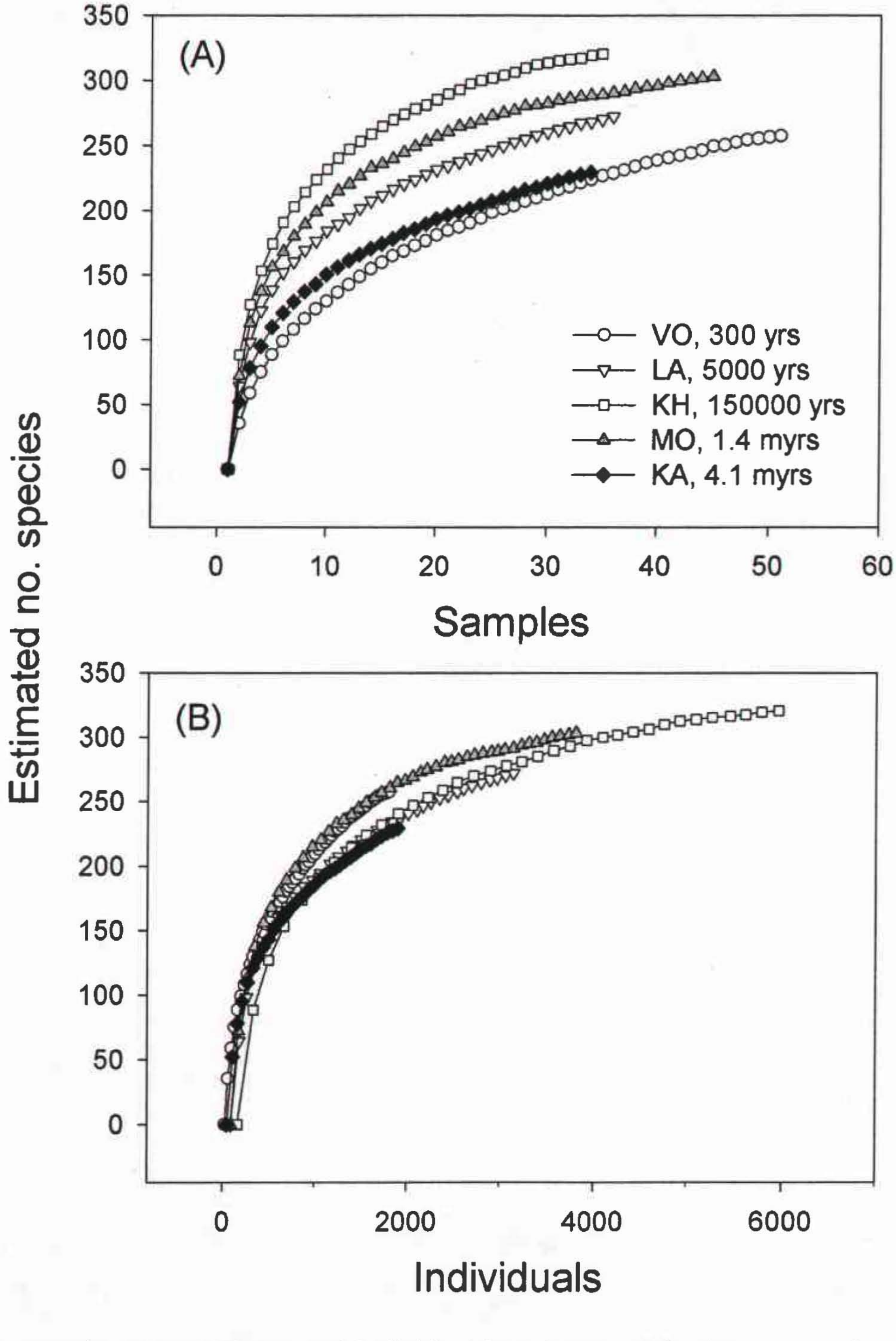

Figure 2.6. Sample-based (A) and individual-based (B) rarefaction curves for the five chronosequence sites estimated with the second-order jackknife index. Unshaded symbols represent sites on Hawai'i Island, grey triangles show Moloka'i, and black diamonds are Kaua'i samples (see Figure 2.1, Table 2.1 for site descriptions).

Sample-based rarefactions of the second-order jackknife estimator showed higher site-level richness for Kohala, Moloka‘i, and Laupāhoehoe (Figure 2.6A). The sites on chronosequence endpoints, Volcano and Kaua‘i, had a lower richness than more productive sites. Individual-based rarefaction, however, showed similar richness trajectories as a function of abundance across all sites (Figure 2.6B).

The total observed richness of native genera mirrored results for abundance and species richness, with a unimodal pattern peaking at Kohala (Table 2.4). However, the ratio of species to genera was greatest on Moloka‘i. Moloka‘i remained the highest after rarefaction to the common level of 100 native species; all other sites were comparable at slightly lower values.

Diversity partitions

Species diversity partitioned similarly across sites, with the largest fraction found in the among-tree components (Figure 2.7A; β_2 range: 57.3—66.1%). This β_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 β_1: 15.4%, $P = 0.936$; α_1 range: 13.3—20.3%; β_1 range: 15.4—23.1%). Within trees at Volcano, Laupāhoehoe and Moloka‘i sites, variation across trays explained more diversity on average than typical α-diversity on single trays, whereas these levels were comparable on Kaua‘i, and α_1 was higher at Kohala. Partitions of native species diversity were similar to the totals, with most of the richness occurring among trees (Figure 2.7B; β_2 range: 58.5—62.8%). Laupāhoehoe and Kohala supported a higher α-diversity of introduced species than the other sites, and the fewest introduced species overall were collected on Kaua‘i (Figure 2.7C).

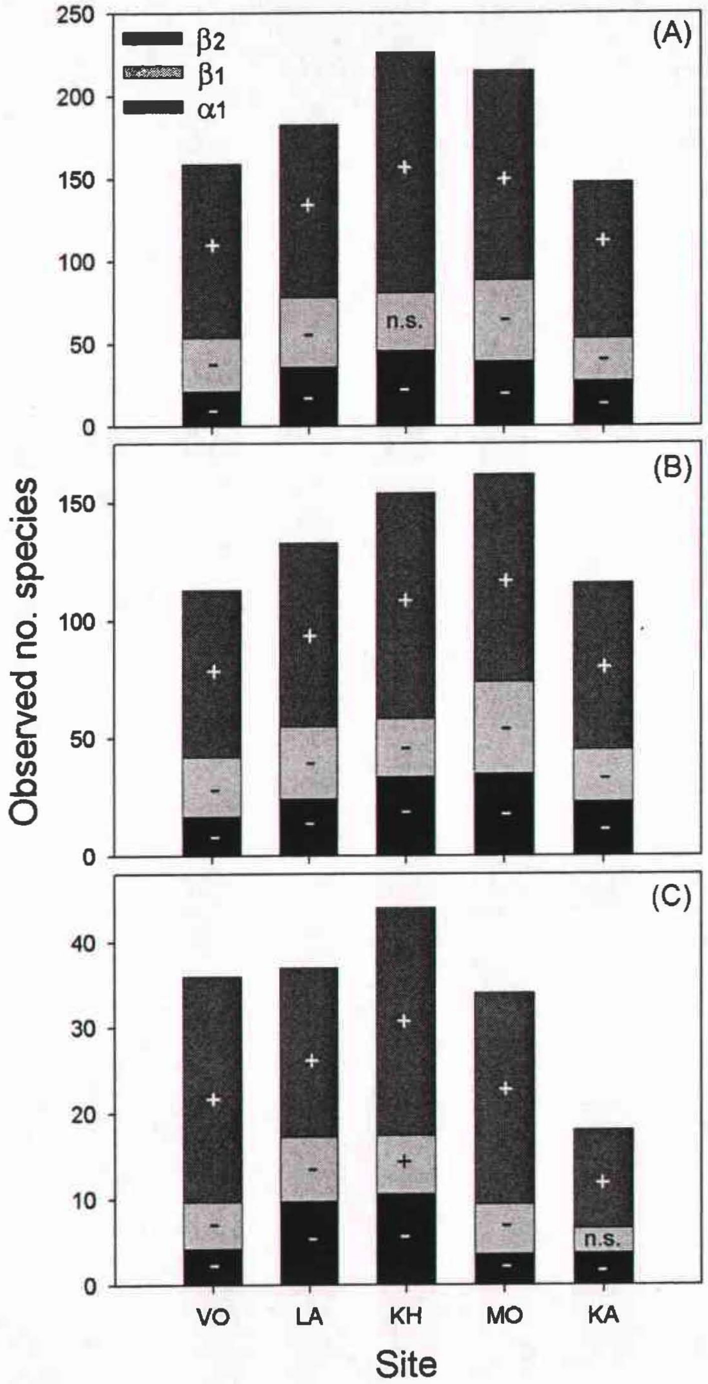

Figure 2.7. Total observed richness of (A) all non-tourist arthropods, (B) native species, and (C) introduced species in additive partitions of α and β components at two spatial scales (samples and trees) within the five chronosequence sites (see Figure 2.1, Table 2.1 for site descriptions). Symbols within plots indicate diversity components larger (+), smaller (-), or not different (n.s.) than null expectations.

Table 2.4. Species to genus ratios for native species (S) and genera (G) from chronosequence sites. The total measured native genera and ratios are given, followed by estimates obtained by rarefaction to the common baseline of 100 native species (± SD).

	Observed		Rarefaction	
Site	No. G	S/G	No. G	S/G ± SD
Volcano (VO)	66	1.71	59.7	1.66 ± 0.016
Laupāhoehoe (LA)	74	1.80	60.5	1.64 ± 0.024
Kohala (KH)	82	1.89	60.7	1.65 ± 0.028
Moloka'i (MO)	78	2.08	57.2	1.75 ± 0.028
Kaua'i (KA)	65	1.79	59.0	1.68 ± 0.019

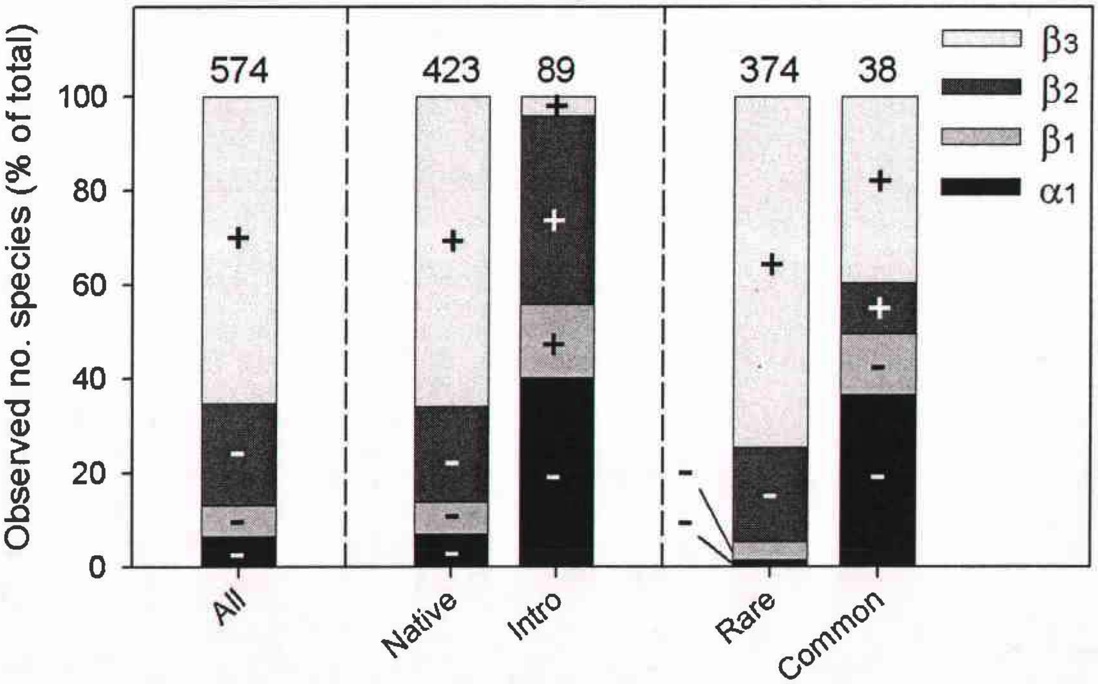

Figure 2.8. Percentage of total observed arthropod species in additive partitions of α and β components at three spatial scales: samples, trees, and sites. Partitions also are shown for native and introduced community subsets, and for all rare (< 0.05% of absolute abundance) and common species (> 0.5%). Numbers above bars indicate the total species count for each comparison. Symbols within plots indicate diversity components larger (+), smaller (-), or not different (n.s.) than null expectations.

Regional scale analysis showed that the greatest fraction of richness was found among sites, the top hierarchical level of diversity in this study ($\beta_3 = \gamma$; Figure 2.8). For the total community excluding only tourists, all diversity components within sites showed significantly fewer species than expected by chance but γ-diversity was significantly larger. 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 α-diversity. Regional diversity was the smallest fraction of richness for introduced taxa ($\beta_3 = 4.3\%$), presumably because some of these species were widely distributed. The γ-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 β-diversity of introduced species were significantly greater than expected by chance; for common species, richness within trees (β_1) was significantly less than random.

Hierarchical cluster analysis

Cluster analysis for the total community showed the three Hawai‘i Island sites were most similar, and Moloka‘i was the most unique (Figure 2.9A). When all non-indigenous and undetermined species were excluded, the most similar sites were the two youngest sites, Laupāhoehoe and Volcano (Figure 2.9B). However, sites on different islands, Moloka‘i and Kohala, clustered together at the next level, and Kaua‘i was distinct.

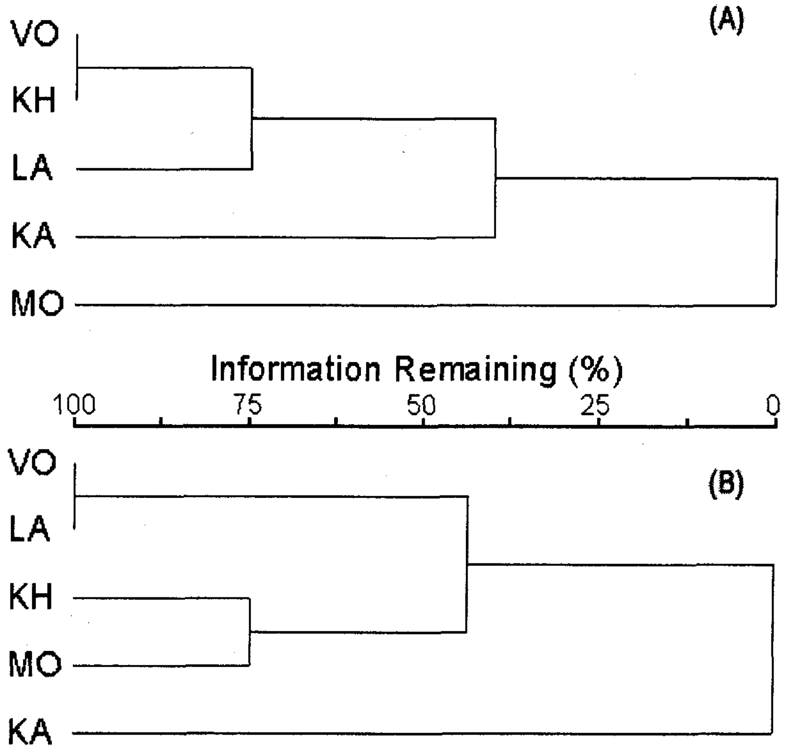

Figure 2.9. Hierarchical cluster analysis of similarity among sites, for A) all non-tourist species, and B) native species only. Sites are coded as in Table 2.1: Volcano (VO), Laupahoehoe (LA), Kohala (KH), Moloka‘i (MO), Kaua‘i (KA). Distances were computed using the relative Sørensen index and sorted by the group average linking method (McCune and Grace 2002).

Discussion

Local resources and community structure

Kohala had the highest overall abundance, biomass and total species richness of canopy arthropods, and numbers were generally lower at the endpoints of the gradient (Figures 2.2, 2.3, 2.6A, 2.7, Gruner and Polhemus 2003). Fisher’s α of all arthropods, and of herbivores and detritivores, was positively, linearly related to net primary productivity (Table 2.3). This supports a small but growing number of studies from terrestrial invertebrate communities that show monotonic increases in diversity with productivity (Mittelbach et al. 2001). Dynamic equilibrium models (e.g., De Angelis 1980) predict faster growth rates, and thus greater organismal abundance and diversity, with higher resource fluxes. However, the nature of the relationship revealed in this study was highly dependent on the variables selected (Table 2.3), which highlights the quandaries of synthesizing studies using different diversity metrics and surrogate measures for productivity (Abrams 1995, Waide et al. 1999, Mittelbach et al. 2001, Groner and Novoplansky 2003). Elevated abundances at more productive sites (Figure 2.3) drove the increased richness on a sample-standardized basis (Figure 2.6A). Site differences disappeared after individual-based rarefaction (Figure 2.6B), which corroborate similar effects on *M. polymorpha* arthropod communities following fertilization in a low productivity volcanic savannah (Chapters 5 and 6). These studies show that richness is tied ultimately to local abundance, and support the hypothesis that productivity increases diversity by allowing locally rare species to invade or coexist in larger local populations ("consumer rarity hypothesis" *sensu* Siemann 1998, "more individuals hypothesis" *sensu* Srivastava and Lawton 1998).

Cluster analyses of native arthropod composition ranked Kohala as more similar to Moloka‘i than to other sites on the same island (Figure 2.9B). This same pattern has been reported for plant communities, with intermediate-aged sites on the chronosequence the most similar in composition (Crews et al. 1995) despite a monotonic increase in plant species diversity with geological age (Kitayama and Mueller-Dombois 1995). Although species identities and total richness were determined ultimately by differing regional floristic richness (Wagner 1991, Price 2004), conforming to an age-accumulation model, quantitative changes in vegetation composition were affected by local soil fertility and forest structure (Crews et al. 1995, Kitayama and Mueller-Dombois 1995). Regional pools of invertebrate diversity in the Hawaiian Islands are less well understood, and studies using catalogues and species lists for diversity analyses have been equivocal on the role of geological age (Cowie 1995, Peck et al. 1999). However, incomplete taxonomy, the lack of comprehensive sampling across lineages and localities, and unknowable historical and prehistorical anthropogenic impacts limit the utility of current databases (Nishida 2002) to precisely delimit the total species pools on each island.

Local and regional processes

Diversity partitions in this study universally showed less α-richness but greater γ-richness than predicted from null randomizations (Figures 2.7, 2.8). Although this finding for α-richness is consistent with limits on local diversity imposed by interspecific competition (Gillespie 2004), intraspecific aggregation behaviors also can explain the pattern (Veech et al. 2003). Intraspecific aggregation is well-documented in arthropod communities (e.g., Novotný and Basset 2000), and can arise from local processes of mating behavior, habitat selection, patchiness of resources, and the legacies of oviposition combined with limited juvenile dispersal (Veech et al. 2003).

At broad scales, the high observed species turnover and γ-diversity 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 in press-a) such that composition differs but functionality is similar. Even with large differences in overall abundance and biomass proportions, however, trophic structure of species was strikingly constant among sites (Figure 2.5).

Numerous community studies have asserted constancy of guild structure or predator to prey ratios (Evans and Murdoch 1968, Moran and Southwood 1982, Jeffries and Lawton 1985, Stork 1987, Krüger and McGavin 2001), but most have not distinguished these claims from null hypotheses or random expectations (Wilson 1996b, but see Jeffries 2002). In the present case, the ratios of trophic groups were even more regular than expected by chance, despite the 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 and 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 (Figure 2.8), local α and β components of diversity and the total site-level richness correlated most strongly to productivity and energetic variables (Figure 2.7, Table 2.3), rather than to the underlying age of the landmass. Richness at the α-level correlated with site richness and constituted similar proportions (but differing absolute levels) of the total site diversity at all sites (Figure 2.7; $r = 0.922$, $n = 5$, $P = 0.026$). Thus, there is no evidence of a single upper limit of species coexistence at local scales, or "saturation" (Cornell and Lawton 1992, Loreau 2000). Ricklefs (1989) noted that long-term historical effects and speciation can override local equilibria, simultaneously adding to γ- and α-diversity. However, the species to genus ratio within native genera on *Metrosideros* was elevated only on Moloka'i, but not at productive sites on Hawai'i Island where richness and diversity were also high (Table 2.4). Speciation does not continue to expand coexistence of arthropod species at the α-level over four million years, and it is not the sole force generating higher richness at intermediate-aged sites. Instead, increased resource quantity or quality may allow rare species from the regional pool to persist in larger local populations, or to coexist across a metacommunity landscape linked by dispersal (Mouquet and Loreau 2002).

Geological age, speciation and species accumulation

The predominant diversification pattern within lineages of the Hawaiian biota follows a stepwise progression from Kaua'i to younger islands (Carson 1983, Wagner and Funk 1995, Shaw 1996, Liebherr and Zimmerman 2000, Hormiga et al. 2003, Jordan et al. 2003, Gillespie 2004). Few molecular clock estimates exist for Hawaiian arthropod lineages (Price and Clague 2002). However, many of the analyzed lineages were present on the current oldest island, Kaua'i (4.6-5.1 myrs) at least as long, and often much longer, than on the other islands, and thus have had more opportunity to accumulate species there (Asquith 1995, Russo et al. 1995, Hormiga et al. 2003, Jordan et al. 2003, C.P. Ewing personal communication). In some groups for which adequate information is available, species ranges are smallest and the area-corrected total richness is highest on the older islands, O'ahu and Kaua'i (Thornton 1984, Otte 1989, Gillespie et al. 1997, Roderick and Gillespie 1998).

Why then does the age accumulation model fail to describe the patterns in local diversity seen in the present study? First, lineage age may be linked only loosely to speciation, and speciation does not necessarily translate to high α-diversity. Individual lineages may vary in their underlying diversification rates (Sanderson and Donoghue 1994, Buzas et al. 2002) and in their capacity to diversify by adaptive or non-adaptive mechanisms (Paulay 1994). The modal diversity of all arthropod lineages in Hawai'i is only one species per lineage, many of which are widespread species (Zimmerman 1948, Roderick and Gillespie 1998, J.P. Price unpublished data). Secondly, physical characteristics may change speciation rates or catalyze speciation events (Losos and Schluter 2000), and the balance between speciation and extinction on islands may differ systematically in concordance with ecosystem development over time. Volcanic activity has always been most vigorous on the youngest, growing islands of the Hawaiian chain (Carson and 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 et al. 2004). A similar scenario of diversification without adaptation has been proposed for *Enallagma* damselflies on the margins of retreating glaciers in North America (McPeek and Brown 2000).

On older islands, by contrast, erosion and subsidence reduce island area and elevational range even as topographic diversity increases (Price and Elliot-Fisk 2004). . The taxon cycle and taxon pulse hypotheses assume irreversible habitat specialization and range restriction over time within diversifying lineages (Wilson 1959, 1961, Erwin 1981, Liebherr and Hajek 1990), which may increase vulnerability to extinction in this changing environment. Indeed, the highly eroded island of Kaua'i may be a 'graveyard' for invertebrate diversity (Asquith 1995). Examples of relictual, presumably ancient endemic lineages survive on Kaua'i but are found nowhere else. For instance, two monotypic spiders, *Doryonychus raptor* Simon (Tetragnathidae) and *Adelocosa anops* Gertsch (Lycosidae), exhibit bizarre behavioral, ecological and morphological shifts that are unlike any other extant species (Howarth 1987, Gillespie 1992), prompting the suggestion that the bulk of diversity, in the form of intermediates and sibling species, must once have existed but have gone extinct (Asquith 1995, Roderick and Gillespie 1998).

Community-wide species to genus ratios, adjusted for effort and sample size, show Moloka'i with the highest diversification level per lineage (roughly approximated by genera; Table 2.4). Moloka'i, Maui, Lana'i and Kaho'olawe were coalesced for much of their history into one land mass ("Maui Nui") that once was larger than the current largest island of Hawai'i (Price and Elliot-Fisk 2004). Thus, the regional pool of species available to Moloka'i and other islands in this complex is potentially larger than predictable by their current size, although island endemism rates may be lower (Price 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 et al. 1990). Volcanism and sea level changes suggest mechanisms for young and intermediate aged islands to generate diversity, acting as the 'cradles' (Chown and Gaston 2000) or 'crucibles' (Carson et al. 1990) of evolutionary change.

History of *Metrosideros* arthropod communities

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). Milankovitch climatic oscillations on scales of 10—100 kyr may cause opposing selection pressures that forestall long-term evolutionary change (Bennett 2004, Coope 2004). 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 Hawaiʻi (Dawson and Stemmerman 1999). Although its distribution may have shifted, this morphologically and physiologically plastic and variable tree (Cordell et al. 2001) probably persisted in comparable abundances under differing climatic regimes.

Metrosideros arthropod communities on Kauaʻi may not be more diverse because the tree was not present when Kauaʻi arose from the sea. Molecular clocks date the colonization of *Metrosideros* in the Hawaiian Islands within the Pleistocene, or approximately 1-1.5 million years (Wright et al. 2000). Pollen records from the Salt Lake tuff on Oʻahu place *Metrosideros* in the islands for a minimum of 300,000 years (Gavenda 1992). These dates place *Metrosideros* in the archipelago near the time Maui Nui was formed, but beyond the shield-building phase of Oʻahu and Kauaʻi (Carson and Clague 1995). The *Metrosideros* lineage may be older than these estimates; the apparent lack of molecular differentiation observed between Hawaiian and other Pacific species (Wright et al. 2000) might be explained by intermittent gene flow or introgression because of the high vagility of the seeds (Corn 1979, Choler et al. 2004).

If *Metrosideros* is a recent arrival, however, then contemporary arthropod communities are subsets of regional species pools that have colonized hosts within a short evolutionary time frame. Host shifts of phytophagous species without speciation from sympatric, distantly related plants may occur in several hundred years or less (Strong 1974c, Strong et al. 1977, Strong et al. 1984). A widely cited example of endemic

Omiodes (Lepidoptera: Crambidae) moths on the introduced banana plant, if true, would imply a modest radiation occurring *in situ* within 1000 years (Zimmerman 1970). Presumably, predaceous and detritivorous species would face fewer adaptive obstacles to utilization of *Metrosideros* habitat than would phytophagous insects (Strong et al. 1984). Carnivores and detritivores did not differ from herbivores in their relative diversity patterns across these sites (Figure 2.5), suggesting the patterns are not tightly bound to a coevolutionary history with *Metrosideros*, but more broadly representative of local arthropod communities and ecological conditions.

Alternative hypotheses

The observed positive correlations of arthropod abundance and diversity with resource variables suggest causal effects of productivity. There are, however, several alternative explanations of these correlations that must be considered. First, these canopy fogging samples report abundances per unit tray area, when in reality 3-dimensional volumes above trays were sampled. Thus, crowns that are larger or denser may hold higher arthropod numbers. However, only 2 of 64 correlations of arthropod variables with leaf area index (Herbert and Fownes 1999), tree basal area, canopy cover, and crown volume were significant at the $P = 0.10$ level (Table 2.3). This suggests that sampling difficulties associated with site differences in tree architecture were minor.

Another possible explanation predicts highest richness of species within the center of bounded domains resulting from random overlap of species' geographical ranges (Willig and Lyons 1998, Colwell and Lees 2000, Zapata et al. 2003, Colwell et al. 2004). This "mid-domain effect" (Colwell and Lees 2000) is probably of little relevance to this system. Because most native arthropod species are endemic to single islands (Howarth

1990, Nishida 2002) or even single volcanoes within islands (e.g., Otte 1994), the oceanic boundary around each island is an effective barrier to colonization except under extraordinary circumstances. Within Hawai'i Island, the Laupāhoehoe site might be considered the middle of a domain with Volcano and Kohala on the boundaries, but Laupāhoehoe did not show a peak in local diversity.

A final alternative interpretation is that the differences in arthropod diversity are caused by differences in predation by birds, which were—probably coincidentally—negatively correlated with productivity. Insectivorous birds can depress the abundance and biomass of forest arthropods (e.g., Marquis and Whelan 1994, Van Bael et al. 2003), and more generally, top predators can influence the diversity of prey (e.g., Paine 1966, Schoener and Spiller 1996). Prehistorical and historical 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 et al. 2001). The Moloka'i and Kohala sites, which showed the highest arthropod abundance and total richness in this study, have sustained the most local bird extinctions in historical times and currently have the lowest population abundances of all the compared sites (Scott et al. 1986, Gruner personal observation). It follows that the depressed abundance of insectivorous birds might be responsible for higher arthropod numbers and diversity. A three-year field experiment comparing the importance of birds and resource on *Metrosideros* arthropods found that birds affect arthropod communities, but their quantitative effects are restricted to arthropod carnivores, especially spiders (Gruner in press-b, in press-c). Fertilization increased arthropod numbers and diversity, especially detritivores and herbivores, in a manner analogous to this study; thus, the resource hypothesis is more consistent with the available data.

Conclusions

Contemporary arthropod diversity 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, mediated through their effects on abundance. Geological age, ecosystem productivity, and evolutionary change may be so tightly linked as to be inseparable in broad community studies. In a study of *Tetragnatha* spider richness across the Hawaiian archipelago also showing a unimodal peak with geological age, Gillespie (2004) argued that evolutionary processes assembled nonrandom communities that mimicked equilibria on ecological scales. 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. 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.

CHAPTER 3

ATTENUATION OF TOP-DOWN AND BOTTOM-UP FORCES IN A COMPLEX TERRESTRIAL COMMUNITY

Abstract

Carnivore (top-down) and resource (bottom-up) influences in food webs are strong and pervasive, but few studies have investigated their interactive effects in species-rich terrestrial ecosystems. This study focused on arthropods associated with the dominant tree species, *Metrosideros polymorpha* (Myrtaceae), in Hawaiian forests. Severe soil nutrient limitation on a 120-year-old lava flow was removed by fertilization and combined with bird predator exclusion cages in a randomized block design. Arthropod densities were measured from clipped foliage at the outset and conclusion of a 33-mo experiment, and their biomass was estimated using regression equations. *Metrosideros* foliar N, tree growth, and biomass increased directly in response to fertilization, but did not change with bird exclusion. Fertilization increased detritivore densities but not biomass, and both density and biomass of herbivores, while bird exclusion increased both density and biomass of carnivores. Fertilization also increased spider density and biomass, but bird exclusion increased spider numbers (15 species) only in high resource plots. Overall, trophic level biomass responses were less pronounced than density because smaller-bodied individuals responded more to enrichment. Bottom-up factors controlled basal trophic levels and detritivores comprised the largest fraction of arthropod density and biomass. Conversely, top-down impacts were apparent but variable, limited to higher order consumers, and did not cascade to the

level of primary producers. These experimental results were consistent with the view that complex forest ecosystems are structured on a bottom-up template.

Introduction

Theoretical models of trophic interactions predict that the intensity of consumer control in food webs depends on potential productivity (Oksanen et al. 1981, Abrams 1993, Moore et al. 2003). Numerous aquatic studies have examined if and how predation ("top-down") and resource ("bottom-up") constraints interact to determine densities and biomass of mid-trophic level species (Osenberg and Mittelbach 1996). In terrestrial systems, vertebrate predators can have large impacts on species-rich arthropod communities with indirect effects propagated to primary producers (e.g., Marquis and Whelan 1994, Van Bael et al. 2003), but top-down factors are often contingent on strong bottom-up influences (e.g., Sipura 1999, Ritchie 2000). This suggests that bottom-up forces determine the maximum productivity and range of possibilities in an ecosystem, while top-down forces govern details of realized growth and structure (Gutierrez et al. 1994).

Several recent reviews and meta-analyses assert that top-down trophic cascades are more widespread in terrestrial ecosystems than previously thought (Pace et al. 1999, Schmitz et al. 2000, Halaj and Wise 2001, Walker and Jones 2001). These reviews draw on literature demonstrating strong top-down indirect effects in both temperate (e.g., Marquis and Whelan 1994) and tropical systems (e.g, Dyer and Letourneau 1999), but come primarily from agroecosystems and grasslands, often restricted to a single species of plant, herbivore and predator. However, many terrestrial food webs are reticulate, with heterogeneous weak interactions dampening cascading indirect effects among nonadjacent levels (Polis and Strong 1996, McCann et al. 1998, Neutel et al. 2002). Interactions among species pairs, perhaps clear and consistent in isolation, can display unpredictable behavior, changing intensity or even direction of interactions when combined with additional species (Wootton 1994). Thus, it is not clear if linear food chain models and strong cascading indirect effects are germane to species-rich communities.

Few terrestrial studies have attempted to partition the relative impacts of top-down and bottom-up forces among speciose trophic levels or feeding guilds (but see Forkner and Hunter 2000). The original green world (Hairston et al. 1960) and ecosystem exploitation hypotheses (Oksanen et al. 1981) refer to community, ecosystem, or larger scale biomass patterns. Moreover, when trophic cascades are defined precisely to include only predator-mediated indirect effects on *biomass* of producer standing crop (Hunter 2001), they appear less common and weaker in terrestrial than aquatic systems (Shurin et al. 2002). Community-level cascading indirect effects may represent emergent properties unpredictable through studies of pairwise interactions (Persson 1999, Polis 1999, but see Schmitz and Sokol-Hessner 2002). Due to logistical difficulties of manipulating communities at appropriate temporal and spatial scales, experimental studies from terrestrial ecosystems examining plant biomass responses to predators are scarce, more so for tropical systems.

Here I describe a 33-mo manipulation of the resources and avian predators of an arboreal arthropod food web in the Hawaiian Islands. Two principal questions were addressed in this study: 1) what are the relative influences of top-down and bottom-up forces on trophic-level biomass and abundance of the *Metrosideros polymorpha* ecosystem, and 2) do the impacts of avian predators cascade to affect primary producer biomass via intermediate level consumers? In accord with theoretical predictions (Oksanen et al. 1981, Moore et al. 2003) and empirical findings (e.g., Gutierrez et al. 1994, Uriarte and Schmitz 1998, Forkner and Hunter 2000, Moran and Scheidler 2002), I predicted that resource limitation would be pervasive, but expected greater bird response or recruitment, and subsequent top-down impacts, would occur only under enriched nutrient conditions. Because of the complexity of this food web, cascading influences of birds on biomass or growth of *M. polymorpha* were not expected. Furthermore, the experimental results ought to differ according to trophic group or feeding guild. I predicted increased biomass and abundance of all trophic groups with fertilization, but with stronger impacts on primary consumers (herbivores and detritivores) than on carnivores. Bird exclusion was expected to influence carnivores and herbivores, but not detritivores, consistent with bird diet studies (Perkins 1903, Baldwin 1953, Ralph et al. unpublished data). Finally, I estimated the relative strength of top-down and bottom-up forces and compared these effect sizes to those of other systems (Shurin et al. 2002).

Methods

Site descriptions and study species

The experiments were located on a basaltic lava flow of the pāhoehoe morphology dated to 1881 in the Upper Waiākea Forest Reserve, on the windward slope of Mauna Loa, Island of Hawai‘i (Figure 3.1; 19.6642°N, 19.2817°W; ~1200 m; 4000 mm average annual precipitation, Giambelluca et al. 1986). Soils at this site are thin, patchy, and extremely nutrient limited, especially by nitrogen (N), responding to fertilizer addition with up to a 10-fold increase in photosynthesis and net primary productivity

(Raich et al. 1996). ‘Ōhi‘a lehua (*Metrosideros polymorpha* Gaudichaud-Beaupré: [Myrtaceae]) dominates native forests from sea level to 2400 m (Dawson and Stemmerman 1999), and is the first woody colonist and most abundant species on recent lava flows. Although trees are of short stature (2-3 m) in open canopies, *Metrosideros* is a key contributor to ecosystem biomass and productivity (Raich et al. 1997, Herbert and Fownes 1999). A variety of shrubs, herbs, ferns and fern allies are also present at the site, the most abundant of which are *Dicranopteris linearis* (Burm.) Underw. (Gleicheniaceae), *Machaerina angustifolia* (Gaud.) T. Koyama (Cyperaeae), *Coprosma ernodeoides* A. Gray (Rubiaceae), *Vaccinium* spp. (Ericaceae), and *Palhinhaea cernua* (L.) Franco & Crav. Vasc. (Lycopodiaceae).

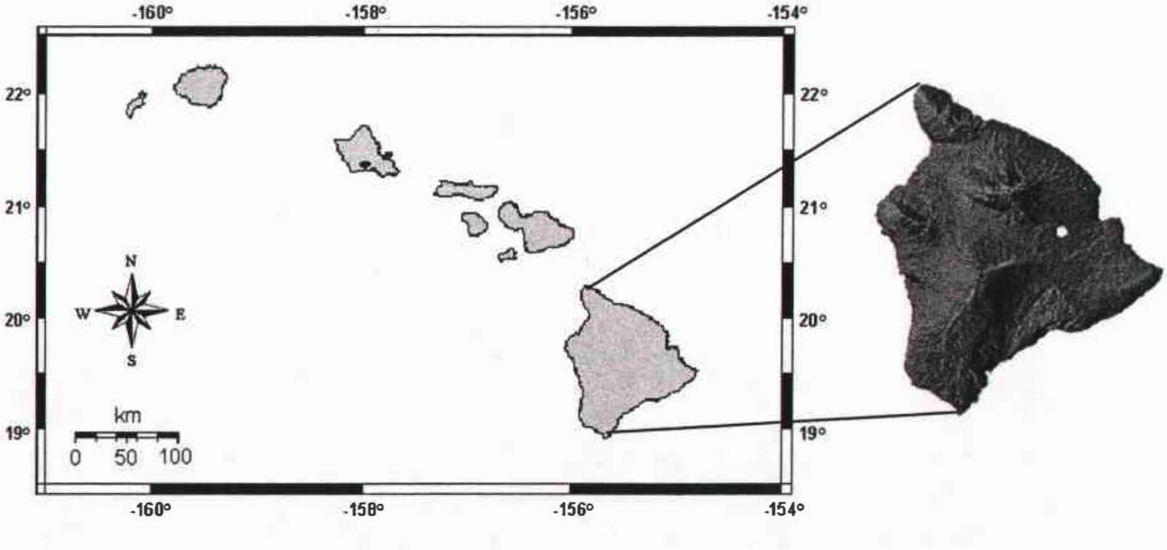

Figure 3.1. Location of the experimental plots within the main Hawaiian Islands. The island of Hawai‘i is enlarged and the study area highlighted.

Three passerine bird species were relatively common on the recent lava flows at this elevation: the native ‘apapane (*Himatione sanguinea*) and ‘oma‘o (*Myadestes obscurus*), and the introduced Japanese white-eye (*Zosterops japonicus*). *Zosterops* *japonicus* is predominantly insectivorous, *H. sanguinea* nectarivorous, and *M. obscurus* frugivorous, but foraging observations and stomach, crop, gizzard, and fecal samples indicate year round opportunistic insectivory by all species, and a reliance on arthropods while provisioning nests in the spring (Perkins 1903, Baldwin 1953, van Riper and Scott 1979, Ralph et al. unpublished data). Less common birds included the insectivorous ‘elepaio (*Chasiempis sandwichensis*), which is otherwise common at this elevation on Hawai‘i Island, but restricted territorially to complex vegetation structure (VanderWerf 1994). The insectivorous ‘amakihi (*Hemignathus virens virens*) and nectarivorous ‘i‘iwi (*Vestiaria coccinea*) were observed occasionally at the site.

Experimental design

The experiment was a randomized block design, with fertilization and avian predator exclusion as crossed, fixed factors. Thirty-two 400 m^2 plots were laid out in pairs along a compass bearing (245^o) determined by aerial photographs to closely parallel the edge of mature forest on older substrate of greater soil fertility, which provided an allocthonous pool of foraging birds. Buffer strips of 10 m wide, at minimum, separated all plots. Before assigning treatments to plots, I randomly selected for observational focus a tree or clump of trees (1-6 individuals) from all possible clumps within the central 8x8m of each plot. Clumps were defined by one or more trees at least 2 m tall, but not taller than 3.5 m. Trees taller than 4 m were unusual, but were excluded from consideration for logistical reasons. All other trees were included within a clump if it could be confined within a cage (see below). There were a total of 88 focal trees distributed among 32 plots in 8 blocks along a modest elevational gradient.

Within each of the blocks, I randomly assigned one of four treatments to each plot: 1) control, 2) fertilization only, 3) bird exclusion cage only, and 4) fertilization and cage. Fertilization treatments consisted of semi-annual hand broadcast of granular essential nutrients following the "NPT" protocol of Raich et al. (1996). Beginning in September 1998, N (½ ammonium nitrate, ½ urea), P, K, Ca, and a micronutrient mix each were spread at a level of 100 kg/ha, and Mg was applied at a level of 50 kg/ha. Later applications were half the initial level. The final fertilization occurred in October of 2000.

Bird exclosure cages were constructed (4 m tall x 4-6 m each side) with sheer UV-resistant polypropylene mesh (2x2 cm, Ross Daniels, Incorporated) draped over lightweight aluminum conduit piping (4 m high) slotted on steel rebar pounded into the basalt substrate. Galvanized wire was strung between poles and as guy wire to rebar anchors. Openings in the mesh were stitched together and secured to the ground to minimize gaps. Insects pass freely through this mesh, but birds are excluded completely. In previous studies, bird exclosure cages with similar-sized mesh had no impacts on microclimate parameters such as rainfall, temperature in full sun, and temperature in shade (Bock et al. 1992).

Plant variables

Leaves were collected from each focal tree for the measurement of foliar N and leaf mass per area on four occasions: at the start and conclusion of the experiment, and after 10 and 22 mo (the 1/3 and 2/3 points in the experiment, respectively). I haphazardly collected 3-6 whorls of mature sun leaves representing the existing range of height, cardinal position, and relative size, and randomly selected 8-19 leaves from within the whorls. Leaves with herbivore damage were avoided, as were branches tagged for an ongoing herbivory study. I clipped petioles and measured area of fresh leaves (± 0.01 cm^2). Leaves were dried to constant mass at 65 °C (at least 48 h), weighed (± 0.001 g), hand crushed and homogenized, and analyzed by automated Kjeldahl digestion and colorimetric methods for percent total N per leaf dry weight (Agricultural Diagnostic Service Center, Department of Agronomy and Soil Science, University of Hawai‘i).

Prior to the application of treatments, and continuing at 6-mo intervals until study conclusion, I measured basal area and height of the 88 focal trees on the plots. Since it was not possible to measure diameter at breast height for these small trees, basal area was estimated as the sum of the area of all stems larger than 2 cm in diameter above the root crown. All diameter measurements were taken from the same point marked with a small nail. Tree height was measured from the ground (± 0.05 m), calibrated to the position of the nail because of the uneven surface (Raich et al. 1996). Total tree foliage biomass was estimated from basal area and height with regressions generated from one *M. polymorpha* dataset (Gerrish 1990), and corroborated with independent data (Raich et al. 1997).

Arthropod sampling and analysis

I sampled arthropods by branch clipping, which enables absolute population estimates of both sessile and mobile taxa (Basset et al. 1997), before the application of the experimental treatments (Aug. 25-28, 1998) and at the study conclusion (Apr. 16-May 3, 2001). The final collection period coincides with the nesting and fledging period of the most common passerines at the site (Baldwin 1953, Ralph and Fancy 1994), a time when avian demand for arthropods should be high, but preceding expected declines in some arthropods over the summer (Gruner unpublished data). I clipped the terminal (~50 cm) twigs and foliage, the primary microhabitat exploited by many insectivorous birds in the Hawaiian Islands and the locus of highest arthropod concentrations (Fretz 2000), into doubled white plastic garbage bags. I selected 5-10 branches haphazardly from the full range of heights and compass bearings available for each plant. Reproductive structures (seeds, flowers) were avoided. Extreme care was exercised in avoiding disturbance of branches and arthropods before branches were quickly bagged and clipped.

I collected foliage in the morning hours, in one randomly selected block per day, and transported it to the laboratory at Kilauea Field Station, Hawai'i Volcanoes National Park, for immediate processing. Foliage was shaken and beaten on to a white cloth, and arthropods were collected with an aspirator and stored in 70% ethanol. I continued shaking branches until no additional arthropods were observed. Finally, I sifted the detrital remainder for arthropods and oven-dried the vegetation. Foliage was separated from wood, re-dried to constant mass, and both components weighed to mg precision.

All arthropods were counted, measured to millimeter length classes, and identified to species or morphospecies, and assigned to one of four trophic groups: predators, detritivores, herbivores and tourists. I determined feeding assignments based on personal observation, literature review, and communication with systematists. Predators include all spiders, cursorial hunters and parasitoids; detritivores comprise saprophagic arthropods and grazers of litter, fungi and microbes; herbivores consist of sap feeders, gall-formers (mostly free living adults), wood-borers, and foliage chewers; and tourists include species known to be incidental or non-feeding on *Metrosideros*, or with unknown or highly omnivorous feeding habits. Taxonomic groups also were classified as potential prey based on bird foraging observations and stomach, crop, gizzard, and fecal samples of passerine birds known from the site (Perkins 1903, Baldwin 1953, Ralph et al.

unpublished data). Prey items generally included Araneae, Diptera, Homoptera, Lepidoptera and Psocoptera larger than 1.5 mm in body length, while most Acari, Coleoptera, Collembola, Heteroptera, Hymenoptera, Isopoda and all arthropods less then 1.5 mm long were treated as non-prey items. I estimated biomass using regression relationships of body morphometrics to dry mass (Gruner 2003). Arthropod abundance and biomass are reported per 100 g dry foliage mass ("load, " *sensu* Root 1973). Analyses of abundance or biomass per unit leaf area gave similar results and are not reported.

Specimens data were managed with the biodiversity collections database software, *Biota* (Colwell 1997a). Specimens are deposited at the B.P. Bishop Museum, Honolulu.

Statistical analyses

Data were analyzed with mixed general linear models (GLM), with fertilization and bird exclusion treated as fixed factors. I treated the block term as random and included all two-way interactions in accordance with model 1 of Newman at al. (1997). Block interactions are included because the effect of fertilization may vary spatially with heterogeneity in the lava substrate texture (Raich et al. 1996), while distance from adjoining older substrates, augmentative source pools of nesting and foraging birds, may result in heterogeneous responses to the cage effect. In this model, each fixed main effect was tested using the mean square of its interaction with the block factor, rather than the mean squared error, as the denominator of the F-ratio (Newman et al. 1997). In most cases, results were qualitatively identical to models without interactive effects with blocks. I used Systat 10.0 unless noted otherwise (Systat 2000).

I used a regression approach to estimate *M. polymorpha* foliage biomass from height and basal area measurements. Using data from Gerrish (1990), I generated a power equation as the most useful predictive model for dry leaf biomass in grams ($R^2 = 0.957$, n = 12, $P < 0.001$). Predictions from this model were tightly congruent to actual foliar biomass measured in an independent dataset (final foliar dry mass: r = 0.989, n = 88, $P < 0.001$; Raich et al. 1997). Although initial tree height, basal area, and foliar biomass did not differ significantly among treatments, there was a trend towards larger trees randomly assigned to caged treatments. Thus, I calculated the relative growth (RG) of plant morphometric variables, which factors the initial plant size into the analysis of final size ($\ln X_{t1} - \ln X_{t0}$). Plot average of RG values were analyzed using the mixed model GLM described above.

Because foliar N results from the same trees over time were not independent, I tested this response with a repeated measures analysis. I tested all main effects and two-way interactions as in the previous GLM model, but added their within-subjects interactions with time. To meet assumptions of normality, I used the arcsine transformation (Zar 1999) for percentage foliar N.

Because I detected no significant initial differences in arthropod densities or biomass among treatments, only final collections data were used in GLMs. To avoid lending equal weight to trees of different sizes, arthropod totals and clipped foliage mass for all trees were summed to create load estimates for each plot. Natural log transformation on plot totals was necessary and sufficient to meet assumptions of normality and homoscedasticity for all arthropod variables. Separate GLMs were run for individual trophic levels: predators, herbivores, and detritivores, for bird prey vs. non-prey classifications, and numerically important taxonomic groups. Tourists represented less than 1 % of total abundance and biomass, and were not explored further. Post hoc multiple comparisons, using the joint significance level of $\alpha = 0.05$, were run for each GLM using Tukey's HSD. There were no qualitative differences in GLM results from those estimated with maximum likelihood procedures for mixed model designs (Saavedra and Douglass 2002) using SAS PROC MIXED (SAS 2001). I report only the least squares results.

I tested the multivariate response of all trophic levels using the MANOVA procedure of PROC GLM (SAS 2001). To test if each group differed from the others in their response to treatments, I contrasted trophic pairs using profile analysis on the fertilization and caging factors and their interaction. I used Wilks' lambda for all hypothesis tests, but it did not differ appreciably from other F-ratio estimations (e.g., Pillai's trace).

To compare the magnitude of top-down and bottom-up effects, I estimated the log response ratio (L) and 95% confidence intervals for the effects of treatments on *M. polymorpha* foliar biomass relative growth rate [effect size $L = \ln(N_{EXPERIM}/N_{CONTROL})$]; Hedges et al. 1999, Shurin et al. 2002). There is some debate whether these estimates should include a temporal component ($\Delta r = L/t$; Osenberg et al. 1997). This experimental duration is among the longest published factorial manipulations of top-down and bottom-up processes (Shurin et al. 2002, Bell et al. 2003), and it is likely that new equilibrium conditions are reached. I evaluated this assumption by plotting biomass RG log ratios over all 6-mo measurement intervals. I also computed log response ratios for final density and biomass of arthropod detritivores, herbivores, and predators, and for prey and non-prey arthropods. As there were no significant interactions between fertilization and bird exclusion in the GLM analysis for any of these arthropod variables, I used all replicates (n = 16) for the two main effects to calculate the ratios ($L_{TD} = \ln[N_{(CAGE+BOTH)} / N_{(FERT+CONTROL)}]$; $L_{BU} = \ln[N_{(FERT+BOTH)} / N_{(CAGE+CONTROL)}]$). I used an index of relative effect strength (relative effect size = $\ln[|L_{BU}|/|L_{TD}|]$; Denno et al. 2003) to quantify these comparisons.

Results

Plant variables

The fertilization treatments positively influenced the growth and foliage quality of *Metrosideros polymorpha*. The growth response of the vegetation was dramatic, with many new flushes on *M. polymorpha* trees and increased biomass of the surrounding plant community, but no apparent changes in response to the cages (Figure 3.2).

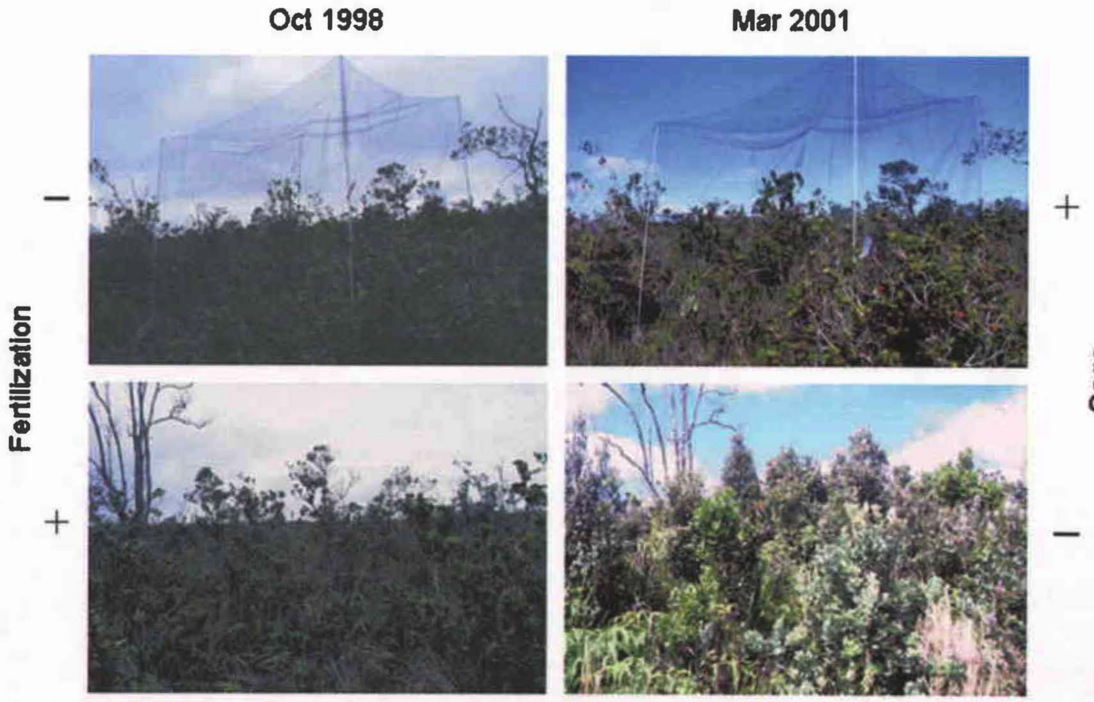

Figure 3.2. Long-term effects of fertilization and caging on vegetation structure on the 1881 flow. The only woody plant visible in all photos is *Metrosideros polymorpha*.

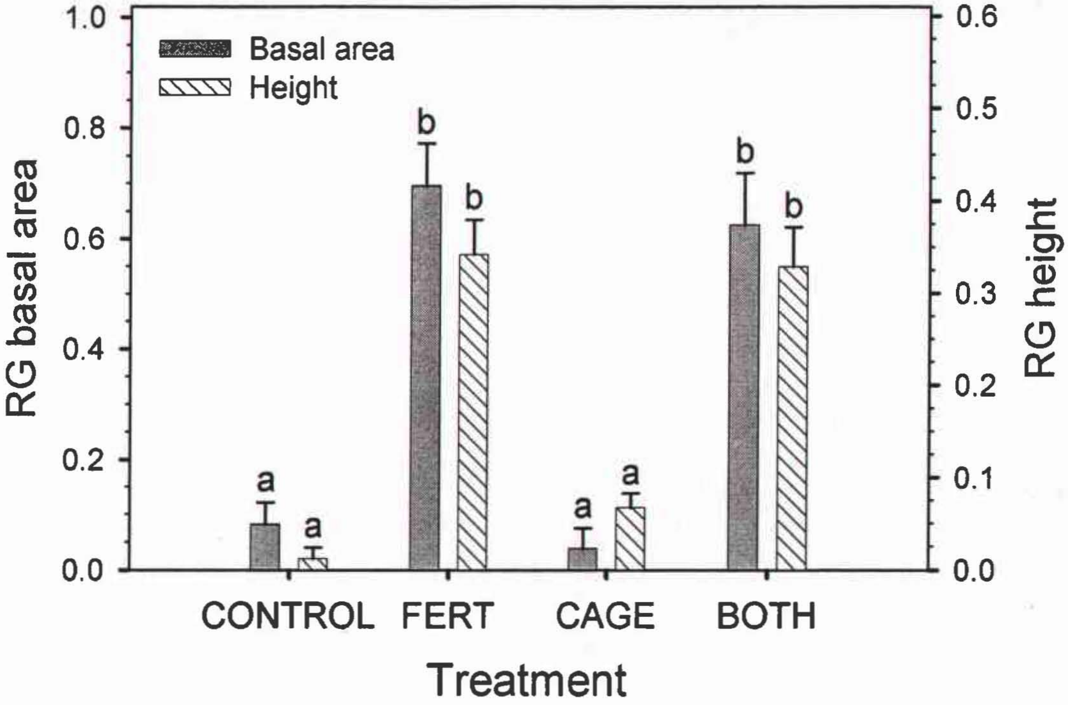

Figure 3.3. Relative growth (RG = ln[Y_{final} / lnY_{init}]) of tree height and basal area from initiation of plots (Aug. 1998) to final measurements (March 2001). Bars represent the mean of plot means + 1 SE. Letters denote significantly different comparisons tested by Tukey's H.S.D (joint $\alpha = 0.05$).

As with the analysis of basal area and height alone (Figure 3.3; basal area RG: $F_{1,7} = 73.96$, $P < 0.001$; height RG: $F_{1,7} = 60.84$, $P < 0.001$), only fertilization changed final *M. polymorpha* foliar biomass ($F_{1,7} = 38.65$, $P < 0.001$). Trees grew larger and more rapidly when fertilized, with growth rates peaking after 1 yr, while unfertilized trees did not add biomass over 2.5 yrs (overall means, leaf biomass change ± 1 SE, n = 16; unfert. = 89.5 g ± 114.4; fert. = 1408.2 g ± 201.5). Log response ratios of biomass relative growth in fertilized treatments peaked and stabilized after 1 yr, and caging did not alter this pattern (Figure 3.4). Log ratios were not adjusted for temporal scale because estimates appear to level at equilibrium over the final two sampling periods. The cage-only treatments initially responded negatively, rebounded to a positive log ratio after 1 yr, then stabilized at no net effect. Final effect strengths (± 95% CI) on *Metrosideros* biomass relative growth were estimated as follows: fert. = 1.95 ± 1.1; cage = -0.11 ± 2.3; both = 1.92 ± 1.1.

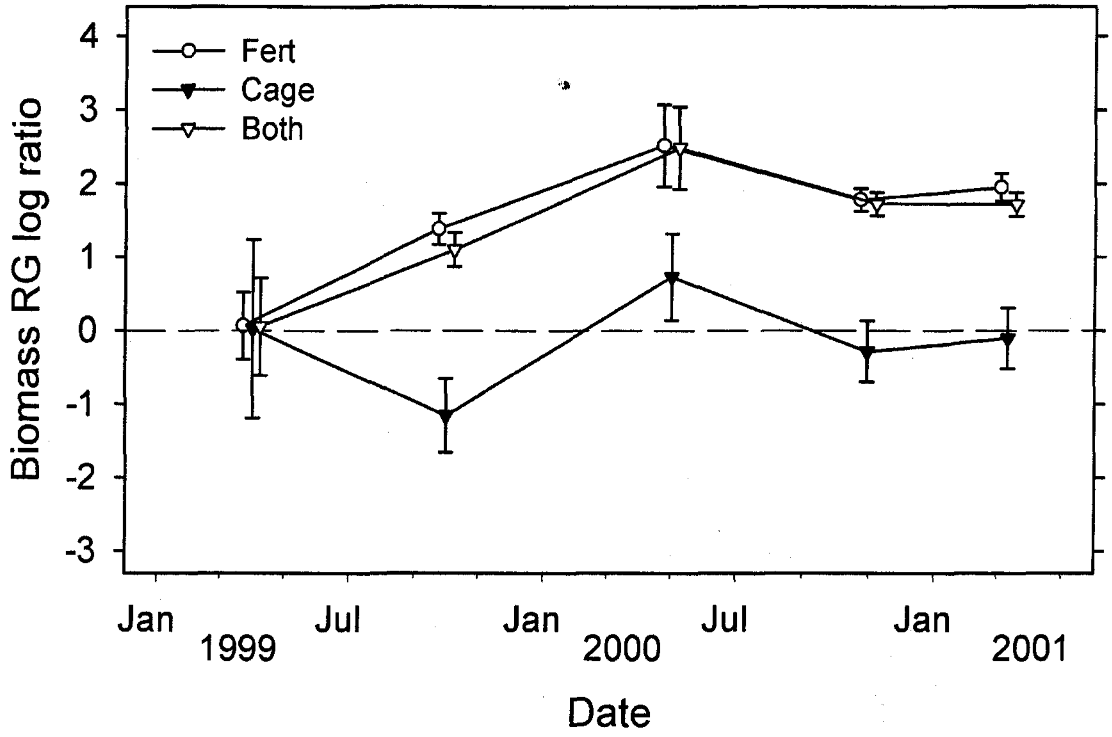

Figure 3.4. Effect sizes ($\log_e$ ratio, $\ln[BRG_E / BRG_C]$) of fertilization only, bird exclusion, and the fertilization X exclusion treatments on *M. polymorpha* foliar biomass relative growth. Estimates are calculated from the difference in the means of the treatments (BRG_E) and the control (BRG_C). Errors represent ± 1 SE, calculated with the variance equations of Hedges et al. (1999). The dashed line represents no difference of experimental means from control means.

Fertilization increased foliar N (fert.: $F_{1,7} = 44.25$, $P < 0.001$), but no other between-subjects factors were significant (Table 3.1, Figure 3.5). Within-subjects, time was strongly significant (time: $F_{3,21} = 154.91$, $P < 0.0001$), as was its interaction with fertilization and with the block term (time X fert.: $F_{3,21} = 54.179$, $P < 0.0001$; time X block: $F_{3,21} = 2.284$, $P < 0.033$). Foliar N was elevated 25-30% after one year and remained at that level for the duration of the experiment (final pooled mean ± SE, unfert.: 0.58 ± 0.02%; fert.: 0.80 ± 0.02%).

Arthropod densities and biomass

Prior to the application of experimental treatments in August 1998, there were no differences in overall arthropod abundance (total arthropods = 2894; overall mean / 100 g foliage ± SE = 49.0 ± 3.6) and biomass (overall mg / 100 g foliage ± SE = 19.06 ± 3.1), or in trophic level abundance (detritivores = 40.4 ± 3.6; herbivores = 1.4 ± 0.2; predators = 3.2 ± 0.4) and biomass (det. = 16.11 ± 3.1; herb. = 0.9 ± 0.2; pred. = 1.7 ± 0.3) among blocks or treatments.

Table 3.1. Repeated-measures ANOVA on foliar N (arcsine-square root transformed) from four annual sampling events. The initial sampling was taken before treatments were imposed. All factors involving the *Block* term are random; others are fixed. Boldface *P*-values are significant at $\alpha = 0.05$.

Source	df	MS	F	*P*
Between Subjects				
Fertilization (F)	1	7.149	44.246	**< 0.001**
Cage (C)	1	0.411	4.419	0.074
F X C	1	0.054	0.337	0.580
Block (B)	7	0.264	1.643	0.264
F X B	7	0.158	0.985	0.507
C X B	7	0.093	0.577	0.757
Error	7	0.160		
Within Subjects				
Time (T)	3	2.549	154.906	**< 0.0001**
T X F	3	0.892	54.179	**< 0.0001**
T X C	3	0.004	0.265	0.850
T X B	21	0.038	2.284	**0.033**
T X F X C	3	0.007	0.404	0.751
T X F X B	21	0.026	1.567	0.155
T X C X B	21	0.028	1.700	0.116
Error	21	0.016		

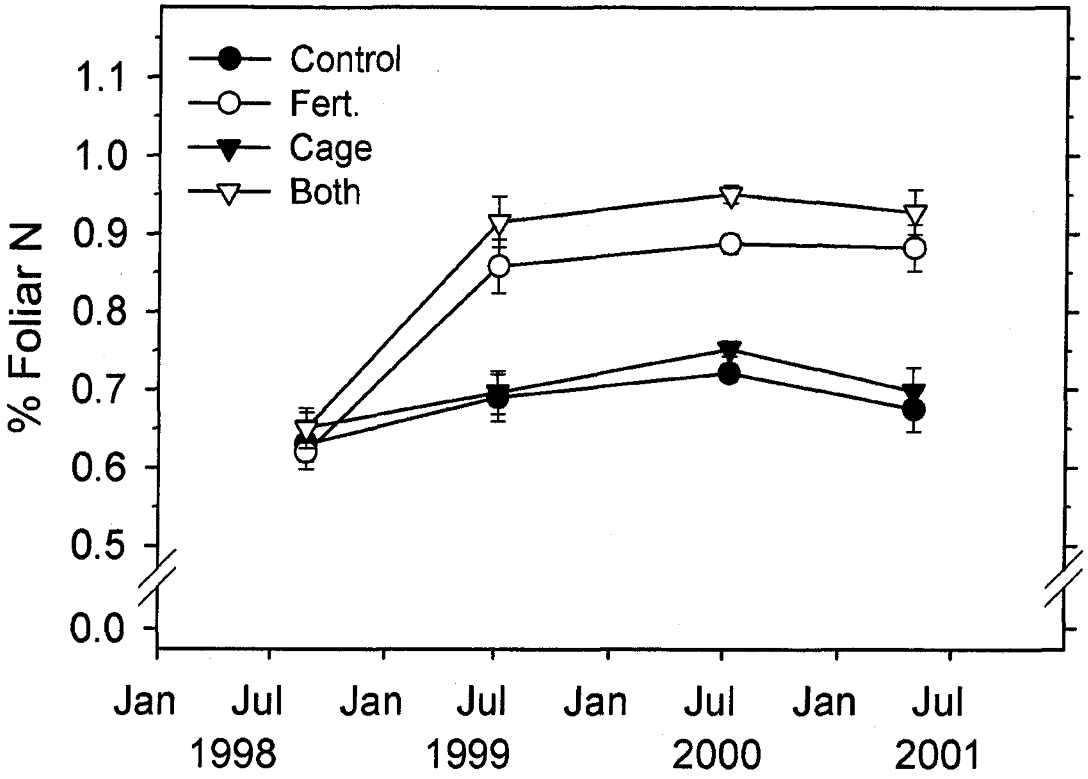

Figure 3.5. Foliar N for *M. polymorpha* in response to the factorial treatments over 33 months. Unshaded symbols represent fertilized treatments, and upside down triangles represent bird exclusion treatments. Symbols represent the mean of plot means ± 1 SE.

A total of 16354 arthropods were collected at the conclusion of the study in April and May of 2001. Foliage collections were larger than initial samples because there were no limitations with the destructive clipping method. After 33 mo, densities in control plots were comparable to initial densities (mean = 42.2 ± 6.9), while total arthropod densities were significantly higher in fertilized plots (Table 3.2, Figure 3.6A). The cage main effect and cage X fertilization interactions showed positive trends ($0.10 > P > 0.05$), and all factorial combinations were significantly greater than densities found in control plots. In a reduced model dropping nonsignificant block interactions, the cage factor is

Table 3.2. Results of general linear models for arthropod trophic density and biomass (natural log transformed) from the final sampling in April and May 2001. Boldface *P*-values are significant at $\alpha = 0.05$. Total model fit is presented as the R^2.

Source		All		Predators		Herbivores		Detritivores	
	df[a]	F	*P*	F	*P*	F	*P*	F	*P*
Density Load									
Fertilization (F)	1,7	12.869	**0.009**	1.674	0.237	29.399	**0.001**	13.892	**0.007**
Cage (C)	1,7	4.219	0.079	11.321	**0.012**	2.333	0.171	0.710	0.427
F X C	1,7	4.552	0.070	2.700	0.144	2.499	0.158	0.875	0.381
Block (B)	7,7	7.507	**0.008**	2.339	0.142	1.183	0.415	6.329	**0.013**
F X B	7,7	2.547	0.120	1.174	0.419	0.979	0.511	1.241	0.392
C X B	7,7	2.713	0.106	1.937	0.202	0.516	0.799	1.164	0.423
R^2		0.952		0.902		0.880		0.920	
Biomass Load									
Fertilization (F)	1,7	0.420	0.538	0.071	0.734	12.356	**0.010**	0.092	0.770
Cage (C)	1,7	3.431	0.106	8.781	**0.021**	2.804	0.138	0.433	0.532
F X C	1,7	1.142	0.321	1.246	0.301	1.815	0.220	1.370	0.280
Block (B)	7,7	1.864	0.215	1.325	0.360	0.666	0.698	0.839	0.589
F X B	7,7	1.913	0.206	2.605	0.115	0.454	0.935	0.607	0.737
C X B	7,7	2.374	0.138	3.654	0.054	0.684	0.686	0.946	0.528
R^2		0.884		0.925		0.729		0.726	

[a] Numerator, denominator degrees of freedom

significant ($F_{1,21}$ = 5.499, *P* = 0.029). The block factor was also significant in both models, indicating spatial heterogeneity in arthropod abundance. However, treatment differences apparent for total arthropod density disappeared when considering biomass load. Although total arthropod biomass appears elevated in the combined fertilized and caged treatment (Figure 3.6B), this increase was accompanied by elevated variability, and no factors were statistically significant. Moreover, there were no significant correlations among trophic level biomass loads. MANOVA and profile analyses revealed generally similar but weaker trends. For density, the fertilization effect is significant, with a marginal, positive trend of the cage treatment, whereas no factors are significant for arthropod biomass (Table 3.3).

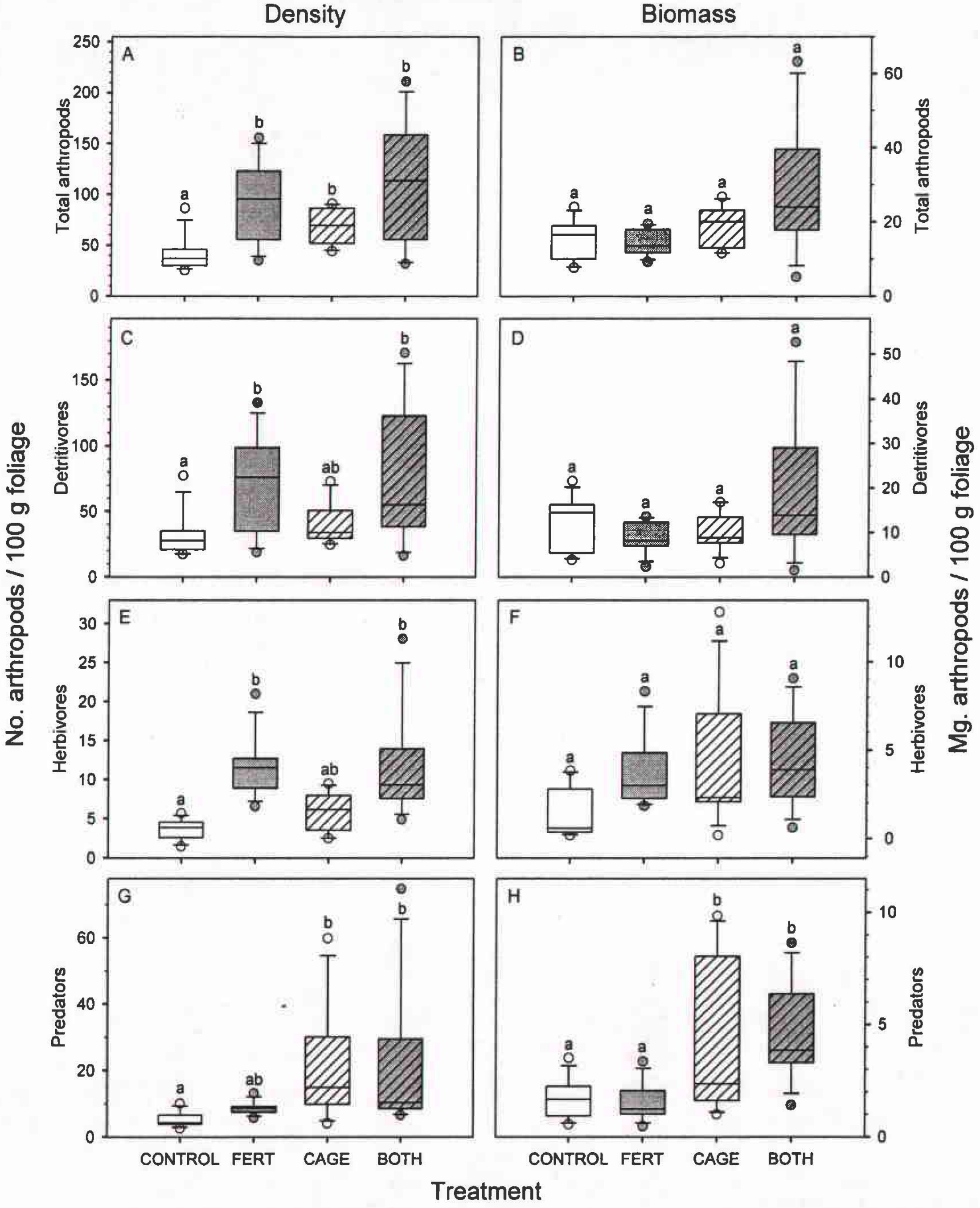

Figure 3.6. Box and whisker plots of trophic level density and biomass of arthropods in response to treatments: A-B) all arthropods, C-D) detritivores, E-F) herbivores, G-H) predators. Boxes represent second and third quartiles around the median, bars are 90% of the data, and circles indicate outlying points. Shaded symbols are fertilized treatments, and hatched boxes represent bird exclusion treatments. Note the differing scales of arthropod variables, measured as a function of dry foliage biomass, for each trophic level. Lowercase letters denote significantly different comparisons tested by Tukey's HSD (joint $\alpha = 0.05$).

Table 3.3. Multivariate ANOVA results for density and biomass of all trophic levels (natural log transformed) from final sampling. Trophic level responses are compared with profile analysis, where H = herbivores, D = detritivores, and P = predators. All F-tests use Wilk's Λ statistic. Boldface *P*-values are significant at $\alpha = 0.05$.

				Profile Analysis						
Source	MANOVA				H-D		D-P		H-P	
	df[a]	F	*P*	df[a]	F	*P*	F	*P*	F	*P*
Density Load										
Fertilization (F)	3,5	7.676	**0.026**	1,7	7.49	**0.029**	2.25	0.177	6.18	**0.042**
Cage (C)	3,5	3.339	0.114	1,7	0.10	0.757	8.26	**0.024**	5.51	**0.051**
F X C	3,5	1.834	0.258	1,7	0.38	0.557	0.50	0.504	0.02	0.906
Block (B)	21,14	1.80	0.124	1,7	1.22	0.402	4.36	**0.035**	1.31	0.365
F X B	21,14	0.798	0.690	1,7	0.30	0.934	0.75	0.646	0.99	0.505
C X B	21,14	0.865	0.629	1,7	0.70	0.674	1.09	0.456	1.17	0.421
Biomass Load										
Fertilization (F)	3,5	6.734	**0.033**	1,7	9.64	**0.017**	0.01	0.932	2.94	0.130
Cage (C)	3,5	3.515	0.105	1,7	0.77	0.410	3.99	0.086	0.38	0.558
F X C	3,5	0.468	0.717	1,7	1.96	0.204	0.46	0.517	1.83	0.218
Block (B)	21,14	1.51	0.210	1,7	0.46	0.835	3.03	0.083	0.24	0.962
F X B	21,14	1.274	0.320	1,7	0.14	0.991	1.76	0.238	0.57	0.765
C X B	21,14	1.953	0.094	1,7	0.53	0.787	2.86	0.095	0.87	0.573

[a] Numerator, denominator degrees of freedom

There were clear differences in the responses of different trophic groups to the experimental treatments (Figure 3.6). Fertilization increased detritivore densities but neither caging nor its interaction with fertilization was significantly different (Table 3.2, Figure 3.6C). Both fertilized treatments were distinct from controls, but not significantly different than cage-only treatments. Detritivore densities varied among blocks, generally decreasing with elevation, or some factor correlated with elevation (linear regression, $R^2 = 0.793$, df = 7, $P = 0.003$). However, all effects were small for detritivore biomass (all F-ratios < 1.0). Numerically, small-bodied Collembola were the dominant group of detritivores responding to fertilization and block factors (fert: $F_{1,7} = 10.110$, $P = 0.016$; block: $F_{7,7} = 3.154$, $P = 0.076$). Collembola biomass also responded positively to fertilization treatments (fert.: $F_{1,7} = 6.334$, $P = 0.040$; block: $F_{7,7} = 3.266$, $P = 0.071$), but the large and mobile isopod *Porcellio scaber* Latreille (Porcellionidae) swamped the biomass signal of Collembola (all F-tests n.s.).

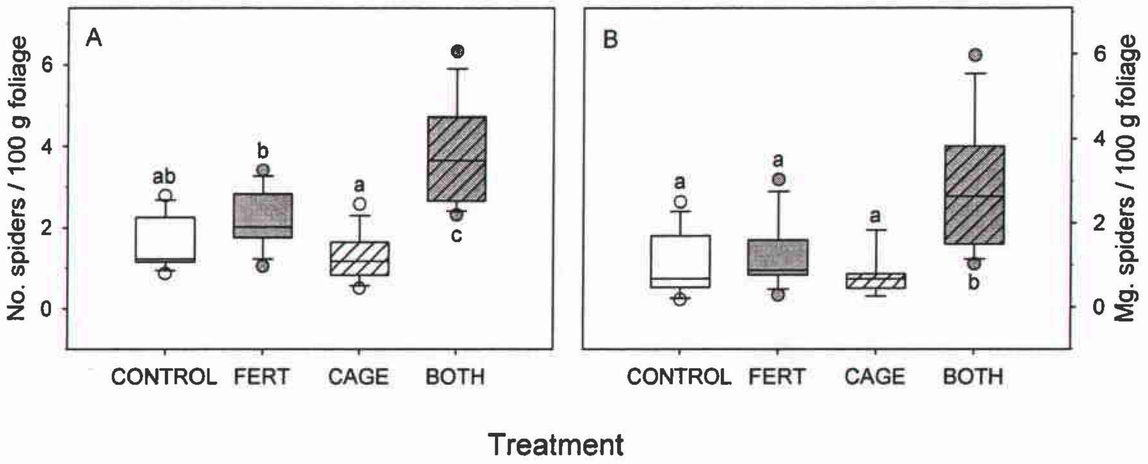

Figure 3.7. Box and whisker plots for spider response to treatments, excluding *Achaearanea* cf. *riparia*: A) density, B) biomass. Boxes represent second and third quartiles around the median, bars are 90% of the data, and circles indicate outlying points. Shaded symbols are fertilized treatments, and hatched boxes represent bird exclusion treatments. Lowercase letters denote significant differences in density or biomass tested by Tukey HSD (joint $\alpha = 0.05$).

Herbivore density and biomass increased with fertilization, but no other factors were statistically significant in the GLM analysis (Table 3.2, Figure 3.6E-F). As with detritivores, both fertilized treatments were distinct from controls, but not significantly different than caged treatments. Herbivore biomass appeared elevated in all three treatments relative to the control, but these differences were not significant. Herbivore and detritivore densities correlated strongly and positively ($r = 0.777$, $df = 30$, $P < 0.0005$), but biomass did not ($r = 0.129$, $P < 0.483$).

Bird exclusion alone elevated predator abundance and biomass (Table 3.2, Figure 3.6G-H). The response of predators to bird exclusion is attributable to spiders, numerically the most dominant group of invertebrate predators in the system (cage: $F_{1,7}$ = 18.538, P = 0.004). A single spider species, the introduced *Achaearanea* cf. *riparia* (Theridiidae), irrupted in abundance 25- to 80-fold in caged plots compared to uncaged plots (Gruner submitted manuscript). The bird exclusion effect on biomass varied across blocks (cage X block interaction) because of the variable presence of *A. riparia* outbreaks in the absence of predation. Because of its disproportionate influence, I removed this single species and re-analyzed all remaining spiders (15 species) in a GLM. Bird exclusion alone did not change spider densities or biomass (density: $F_{1,7}$ = 1.37, P = 0.280; $F_{1,7}$ = 2.62, P = 0.150), while both fertilization and its interactive effect with caging emerged as significant for both density (fert.: $F_{1,7}$ = 19.75, P = 0.003; fert. X cage: $F_{1,7}$ = 9.88, P = 0.016) and biomass (fert.: $F_{1,7}$ = 8.22, P = 0.024; fert. X cage: $F_{1,7}$ = 6.50, P = 0.038). Spiders (other than *A. riparia*) were most abundant on plots both fertilized and caged, intermediate on plots fertilized only, and lowest on unfertilized plots, caged or not (Figure 3.7). Predaceous arthropod densities and biomass did not correlate with the other trophic levels.

I examined the heterogeneity of the top-down effect of birds across trophic groups by dividing arthropods into categories of potential prey and non-prey items. The cage effect was highly significant for both prey density and biomass (density: $F_{1,7}$ = 18.703, P = 0.003; biomass: $F_{1,7}$ = 26.705, P = 0.001), but not for non-prey items (density: $F_{1,7}$ = 4.336, P = 0.076; biomass: $F_{1,7}$ = 1.379, P = 0.448). As with total arthropods, fertilization and block factors remained significant for non-prey density (fert.: $F_{1,7}$ = 13.307, P = 0.008; block: $F_{1,7}$ = 7.270, P = 0.009), but no factor was significant in the biomass model.

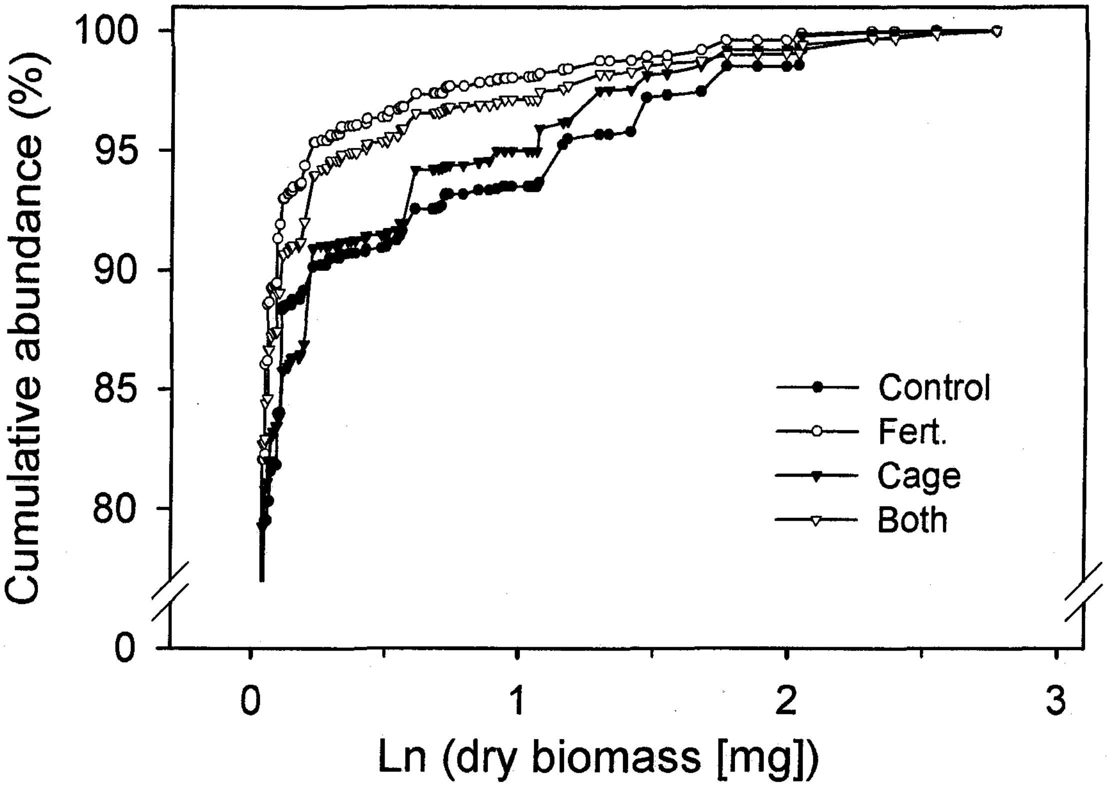

Figure 3.8. Cumulative biomass distribution of arthropods collected from each treatment in final collections of April and May 2001. Each line represents the cumulative frequency of individuals as a function of increasing dry biomass, natural log transformed. Arthropods were aggregated across all replicates within treatments and tested for distributional differences using the Kolmogorov-Smirnov 2-sample *D* statistic.

Arthropod biomass frequency distributions

The striking differences in results for arthropod density and biomass prompted an investigation into the distributions of biomass among treatments. I examined cumulative biomass frequency distributions using the sum total of all individuals in all replicates within treatment levels, and for trophic level components separately. I used the Kolmogorov-Smirnov two-sample statistic *D* to test for differences in the accumulation patterns of arthropod body size, and applied the Bonferroni adjustment to account for six post hoc tests within each component ($\alpha = 0.0083$). Smaller juveniles generally dominated herbivore and predator recruitment in response to treatments, and detritivores shifted composition to a greater proportion of small-bodied species in fertilized treatments (e.g., Collembola). The only two nonsignificant pairwise comparisons from total arthropod abundance-biomass distributions were within levels of the fertilization treatment (unfertilized: control vs. caged, Kolmogorov-Smirnov 2-sample $D = 0.208$, uncorrected $P = 0.021$; fertilized: control vs. caged, $D = 0.196$, $P = 0.021$; Figure 3.8)

Relative strengths of top-down versus bottom-up forces

I plotted the relative log ratios for top-down versus bottom-up main effects on trophic levels, prey items, non-prey, and all arthropods combined (Figure 3.9). Since the fertilization X cage interaction was not significant for any of these factors, those data were pooled into main effects. Bottom-up effects were stronger than top-down effects for primary consumers, non-prey arthropods, and for the community overall. Top-down effects dominated for invertebrate predators and taxa common in bird diets. Across all categories, bottom-up effects usually were stronger than top-down effects for arthropod density, while the opposite was true for biomass. The pattern of the overall community is qualitatively similar to results for detritivores and non-prey items, which each comprise the majority of individuals and biomass within their respective categories. Smaller bodied individuals responded disproportionately to fertilization (Figure 3.8), but the top-down effect is stronger for total community biomass, influenced by responses of large bodied insects and spiders to bird removal. All arthropod log response ratios are presented in Table 3.4.

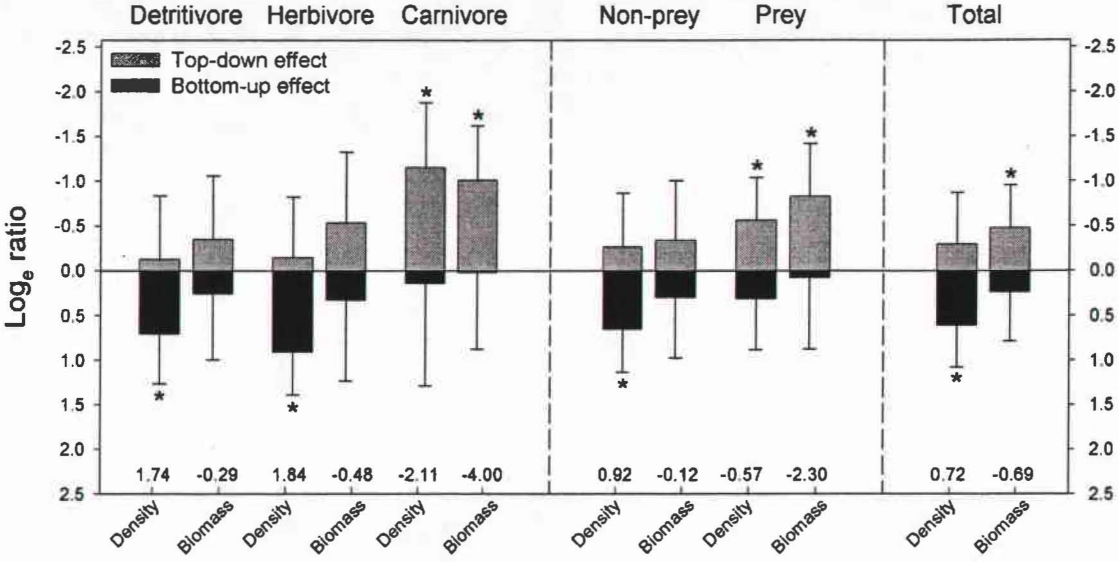

Figure 3.9. The relative effect size (log$_e$ ratio) of top-down (insectivorous bird predation) and bottom-up (nutrient resources) forces on *Metrosideros* arthropods. Log$_e$ ratios of top-down effects are the top gray bars, and black bars below the zero line represent bottom-up effects. Errors represent 95% confidence intervals; an asterisk above or below bars indicates C.I. not overlapping zero. Signs of log ratios from bird exclusion are changed from positive to negative to indicate the impact of bird presence. Numbers above the abscissa represent the magnitude of bottom-up relative to the top-down main effects (relative effect size = $\ln[|\text{effect size}_{BU}|/|\text{effect size}_{TD}|]$; Denno et al. 2003) on both density and biomass for trophic levels, prey and non-prey items, and all arthropods in sum. A positive value indicates a preponderance of bottom-up forces, a negative number specifies greater top-down effects, and a value of zero shows equal influence.

Discussion

Although birds reduced the numbers and biomass of spiders, this effect did not propagate to *M. polymorpha* standing crop or growth, either under low or high resource conditions (Figure 3.2). Bottom-up forces impacted basal trophic levels strongly but top-down effects were more influential to higher order consumers. These factors acted independently, with the sole exception that birds limited the spider assemblage only in fertilized treatments (Figure 3.7). In this forested ecosystem, low productivity and abiotic stress, strong detrital flows, heterogeneity within and among trophic levels, inefficient generalist predators, and compensatory interactions decoupled bottom-up and top-down forces to eliminate cascading indirect effects. Below, I discuss the influence of each of these factors on emergent patterns of arthropod trophic structure.

Nutrient limitation and detrital shunts

Among terrestrial systems, top-down cascades are more frequent and stronger in productive, unstressed ecosystems, on small plants with high nutrient levels (Shurin et al. 2002). In general, forest ecosystems have slower turnover of nutrients and biomass than grasslands (Scheu and Setälä 2002), where most terrestrial trophic cascades have been reported (Halaj and Wise 2001). Primary productivity on a nearby, slightly older substrate (145 yrs), was estimated at approximately 300 $g^{1}m^{-2}y^{-1}$ (Raich et al. 1997), substantially lower than the typical range for tropical forests (Clark et al. 2001) and the average for terrestrial systems worldwide (Field et al. 1998). Moreover, new basaltic substrates are physiologically stressful (*sensu* Menge and Sutherland 1987), with shallow and patchy soils which undergo rapid fluxes in moisture content (Raich et al. 1996). Waterlogging at poorly drained sites, as is common with the pāhoehoe lava morphology, can be a proximate cause of stand-level *Metrosideros* dieback (Akashi and Mueller-Dombois 1995).

Fertilization treatments alleviated nutrient limitation and enhanced *M. polymorpha* growth and foliage quality for primary consumers. Foliar N concentrations were consistently higher with fertilization. Nitrogen is the most common nutrient limiting primary production in terrestrial ecosystems and may be the "critical resource underpinning productivity gradients for insect herbivores" (Ritchie 2000). At sites on substrate of comparable composition and age, complete spectrum fertilization, as in this

Table 3.4. Natural log response ratios, or effect sizes, and 95% confidence intervals for arthropod trophic levels, spiders including and excluding *A. riparia*, and taxonomic and size-based categories of bird prey and non-prey, which are further divided into primary consumers (detritivores and herbivores) and secondary consumers (carnivores). Log response ratios and CIs are calculated using equations in Hedges et al. (1999), and are presented for (A) all factorial comparisons with the control, and (B) by pooling data from fertilized and caged treatments into main effects. In (B), data are pooled only when there was no significant fertilization X cage interaction, and the inverse of the cage effect is taken to assess the effects in the presence of birds. Boldface entries represent log ratios with CIs non-overlapping with zero.

A	Density			Biomass		
	Fertilization	Cage	Both	Fertilization	Cage	Both
All arthropods	**0.78 (0.32)**	**0.49 (0.34)**	**0.98 (0.51)**	-0.06 (0.45)	0.20 (0.37)	**0.63 (0.53)**
Detritivores	**0.78 (0.47)**	0.22 (0.49)	**0.86 (0.65)**	-0.32 (0.56)	-0.21 (0.51)	0.49 (0.70)
Herbivores	**1.17 (0.84)**	0.49 (0.98)	**1.18 (0.52)**	**0.98 (0.37)**	1.14 (0.40)	**1.13 (0.86)**
Predators	0.51 (0.57)	**1.42 (0.71)**	**1.45 (0.83)**	-0.10 (0.37)	**0.93 (0.70)**	**1.00 (0.53)**
All spiders	0.06 (0.69)	**2.13 (0.78)**	**1.07 (1.06)**	0.08 (0.41)	**1.29 (0.80)**	**1.21 (0.62)**
A. riparia	-1.14 (1.31)	**3.27 (1.18)**	**3.04 (1.48)**	**-2.26 (1.38)**	**3.54 (1.11)**	**2.28 (1.42)**
Other spiders	0.31 (0.74)	-0.22 (0.78)	**0.87 (0.39)**	0.16 (0.39)	-0.28 (0.47)	**1.01 (0.68)**
Tourists	-0.10 (0.76)	0.00 (1.33)	0.35 (1.21)	0.95 (1.20)	0.37 (1.29)	0.12 (0.89)
Non-prey	**0.81 (0.46)**	0.44 (0.48)	**0.98 (0.55)**	-0.25 (0.49)	-0.2 (0.42)	0.52 (0.65)
1° consumers	**0.85 (0.47)**	0.24 (0.49)	**0.90 (0.65)**	-0.25 (0.56)	-0.21 (0.52)	0.50 (0.69)
2° consumers	0.21 (0.70)	**1.73 (0.81)**	**1.84 (1.03)**	-0.39 (0.57)	-0.01 (0.81)	**0.78 (0.77)**
Prey	**0.54 (0.51)**	**0.76 (0.67)**	**0.96 (0.39)**	0.60 (0.36)	**1.24 (0.44)**	**1.11 (0.54)**
1° consumers	0.63 (0.83)	0.31 (0.95)	**0.85 (0.54)**	**0.89 (0.50)**	**1.22 (0.46)**	**1.10 (0.87)**
2° consumers	0.29 (0.67)	**1.56 (0.76)**	**1.29 (0.64)**	0.03 (0.58)	**1.29 (0.77)**	**1.13 (0.61)**

B	Density		Biomass	
	Resources	Birds	Resources	Birds
All arthropods	**0.61 (0.46)**	-0.30 (0.57)	0.24 (0.55)	-0.48 (0.47)
Detritivores	**0.71 (0.56)**	-0.12 (0.71)	0.26 (0.73)	-0.35 (0.71)
Herbivores	**0.90 (0.49)**	-0.14 (0.68)	0.33 (0.91)	-0.53 (0.79)
Predators	0.14 (1.15)	**-1.15 (0.73)**	0.02 (0.85)	**-1.01 (0.60)**
All spiders	-0.05 (1.67)	**-2.07 (0.87)**	-0.05 (0.97)	**-1.21 (0.69)**
A. riparia	-0.25 (2.17)	**-3.58 (1.37)**	-1.28 (1.99)	**-3.69 (1.60)**
Other spiders	*	*	*	*
Tourists	0.15 (1.04)	-0.24 (1.04)	0.42 (1.14)	0.34 (1.11)
Non-prey	**0.65 (0.48)**	-0.26 (0.61)	0.30 (0.67)	-0.34 (0.67)
1° consumers	**0.75 (0.56)**	-0.11 (0.72)	0.30 (0.71)	-0.32 (0.70)
2° consumers	0.12 (1.52)	**-1.68 (0.91)**	0.37 (0.85)	-0.64 (0.79)
Prey	0.32 (0.57)	**-0.56 (0.48)**	0.08 (0.79)	**-0.83 (0.59)**
1° consumers	**0.57 (0.48)**	-0.25 (0.57)	0.22 (0.92)	-0.62 (0.80)
2° consumers	-0.15 (1.04)	0.16 (2.10)	-0.12 (0.97)	**-1.19 (0.69)**

study, elevated primary productivity ten-fold, increased *M. polymorpha* foliar concentrations of N, P, K and Mg, and reduced the mass percentage of lignin (Raich et al. 1996, Vitousek 1998). Lignin deters or slows insect feeding on plants (Coley and Aide 1991), is digested very slowly, and only by fungi and microbes (Melillo et al. 1982). *Metrosideros* litter decomposability correlates inversely with initial lignin levels and positively to foliar N (Austin and Vitousek 2000, Hobbie and Vitousek 2000).

These trends favored increases of both herbivorous and detritivorous arthropods in response to fertilization (Figures 3.6, 3.9, Tables 3.2-3.4). In this *Metrosideros* community, herbivores were comprised largely of sap-suckers in several homopteran and heteropteran families. Although there are conflicting hypotheses for plant allocation of increased mineral resources (Stamp 2003), and numerous contradictory findings (Hamilton et al. 2001), fertilization more often benefited populations of phloem- or xylem-feeding insects on trees than leaf chewers (Kytö et al. 1996, see also Lightfoot and Whitford 1987, Boyer et al. 2003). Nevertheless, detritivorous arthropods were dominant in abundance and biomass (Figure 3.6), suggesting that most available energy shunts directly to decomposers (Polis and Strong 1996). Top-down cascading effects are observed infrequently in detrital systems (Halaj and Wise 2001, Scheu and Setälä 2002, Moore et al. 2003).

Abundance and body size

Although detritivores, particularly *Salina celebensis* (Schaeffer) (Collembola: Entomobryidae), increased on fertilized trees at this site, fertilization had no effect on their total biomass (Figure 3.6D). Regression procedures to estimate biomass, rather than direct measurement, may result in reduced precision and fewer biomass effects. However, in a fertilized prairie system where arthropods were weighed directly, arthropod biomass also showed fewer treatment effects than numerical variables (Kirchner 1977). As predicted by Hutchinson (1959), individuals of numerically dominant species in the present system weighed less than rare species in all treatments. Smaller-bodied Collembola and juvenile phloem- and xylem-feeding Homoptera responded strongly to fertilization, and were relatively more abundant in fertilized treatments (Figure 3.8). The biomass effects of increased Collembola abundances were swamped by variable responses of mobile, large detritivores (e.g., *Porcellio scaber*). Boyer et al. (2003) observed a similar effect with large grasshoppers in a fertilized grassland.

When arthropods were grouped as potential prey on the basis of size and taxonomic characteristics reported from diet studies, the top-down factor dominated effect sizes in the prey subset, while the converse was true for arthropods deemed less vulnerable to birds (Figure 3.9). However, birds had a proportionally greater effect on prey biomass, which translated to dominance of top-down forces on total arthropod biomass. For biomass, the top-down effect was generally stronger than the bottom-up effect (Figure 3.9), despite fewer significant biomass responses in GLM analyses (Table 3.2). The reverse pattern was apparent for density and for non-prey arthropod biomass. This suggests birds had a disproportionate impact on large arthropods, whereas bottom-up influences dominated for smaller arthropods, and for density overall.

Top-down heterogeneity and predator efficiency

Detritivore and herbivore density and biomass were unaffected by the exclusion of avian predators, despite increased arthropod abundance in fertilized plots (Figure 3.6). Many herbivorous taxa (e.g., Homoptera, Lepidoptera larvae) were found commonly in the diets of passerine birds in the region, while detritivores, with the exception of Psocoptera, were not (Perkins 1903, Baldwin 1953, Ralph et al. unpublished data). Nevertheless, cage effects were not significant for herbivores (Figure 3.6E, Table 3.2), and log response ratios demonstrated a negative impact of birds on herbivores (cage only, inverse log ratio ± SD = -0.486 ± 0.205) lower than values reported from other terrestrial systems (Shurin et al. 2002) with either vertebrate (mean log ratio ± SD = -1.04 ± 1.56) or invertebrate carnivores (-0.72 ± 0.92). The weak top-down effects on herbivores in this system may be explained by the preponderance of endophagous species (e.g. gall-formers, bud-miners) that are virtually immune to avian predation in their immature stages. In addition, it is possible that compensatory predation by increasing populations of enemies released by bird exclusion mitigated any positive effects on herbivore populations (Pacala and Roughgarden 1984, but see Spiller and Schoener 1994).

The estimated changes in arthropod loads due to fertilization may be conservative from an avian standpoint. Load variables, relative to foliar biomass, were measured at the scale most appropriate for comparing population and community dynamics of arthropod prey. However, fertilized plots showed tree growth rates an order of magnitude higher and standing biomass more than double that of unfertilized plots (Figures 3.3, 3.4). Due to the larger individual tree size, increased foliage density, and increased density and biomass of prey (Figure 3.9), fertilization increased absolute arthropod numbers per unit ground area, which may be the most appropriate scale for evaluating resource availability for insectivorous birds (Fretz 2002). Rough estimates of abundance and biomass at larger spatial scales were extrapolated using the product of final arthropod loads and estimated tree foliar biomass. Although plant demographic data were not measured on the basis of ground area, total arthropod abundance increased 2.7-fold and biomass was 1.9 times higher on a per tree basis in fertilized plots (abundance: $F_{1,7} = 39.46$, $P = 0.0004$; biomass: $F_{1,7} = 11.96$, $P = 0.011$). This effect was also strongly significant for detritivores and herbivores, but was only a marginal effect for carnivore density ($P = 0.037$) and a positive trend for carnivore biomass and for spiders ($0.05 < P < 0.10$).

As expected, no cascading top-down effects of insectivorous bird predation on plant biomass or growth were observed. Consistent with some trophic dynamic theory (Oksanen et al. 1981, Moore et al. 2003), abundance of top predators (insectivorous birds) was lower at this unproductive site than in mature forest, possibly regulated by limited resource supply. Fretz (2000) documented a strong positive interannual correlation among reproductive success of two native insectivorous passerines and *M. polymorpha* arthropod abundance over 3 yr. This, in addition to evidence for interspecific competition among Japanese white-eyes and several native passerines, including ‘elepaio, ‘amakihi and ‘i‘iwi, suggests that arthropod food resources were limiting for birds in some habitats and times (Mountainspring and Scott 1985). I predicted that birds would recruit to increased vegetation complexity and arthropod abundance on fertilized plots, thus increasing top-down effects in these treatments. Anecdotally, more birds and bird species were observed in fertilized plots, but structural differences in vegetation among fertilization treatments biased all attempts to census and compare bird densities. Community effects of this prediction generally were not supported, as cage and fertilization treatments interacted only within the spider assemblage, exclusive of *A. riparia* (Figure 3.7).

Bio-energetic models, coupled with diet selection and arthropod abundance studies, in steppe ecosystems (Rotenberry 1980) predict that avian generalists are functionally insignificant, "inefficient" insectivores (*sensu* Power 1992) that will not exhibit top-down control. If birds focus their efforts on restricted taxa within arthropod communities, however, their impact may be greater than predicted by these models. For instance, leaf-chewing Lepidoptera larvae were by far the most common herbivores in an oak sapling system, and exclusion of birds led to increased herbivory to the oaks (Marquis and Whelan 1994). In a similar system without cascading indirect effects, the herbivore community was more varied (Lichtenberg and Lichtenberg 2002). In Hawaiian systems, Baldwin (1953) augmented diet analyses of forest birds with field estimates of prey availability on dominant plant species. Although some taxa appeared to be avoided or ignored (e.g., heteropterans, isopods), he found that most prey types were taken in proportion to their field availability, a pattern consistent with donor control (De Angelis 1980, Chase 1996). In the present study, however, birds did have an impact on carnivores, particularly spiders (Figures 3.6, 3.7). When likely prey items from other trophic levels are considered, however, a significant negative effect of birds is maintained (Figure 3.9). These data reveal within- and between-trophic level heterogeneity (Hunter and Price 1992), muting indirect effects that might otherwise propagate in linear fashion among adjacent trophic levels down the food web (McCann et al. 1998, Neutel et al. 2002). Examples where birds exhibit strong top-down control and indirect effects on producers may involve less heterogeneity or birds with more selectivity on key taxa.

Compensatory indirect interactions

Overall, nutrient augmentation did not cascade up to the aggregate level of invertebrate natural enemies, but enemy densities increased an order of magnitude in the absence of birds (Figure 3.6G). This effect was less pronounced but still apparent for carnivore biomass (Figure 3.6H). Upon closer examination of the composition of the carnivore trophic level, the effect was attributable to spiders. Araneae were among the three most abundant prey items for all five bird species for which there were sufficient fecal samples (Ralph et al. unpublished data), and are the most important prey items for Hawaiian passerines in general (Perkins 1903, Baldwin 1953). Other exclusion studies of birds have shown marked effects on spiders (Askenmo et al. 1977, Gunnarsson 1996, Evelegh et al. 2001, Van Bael et al. 2003). Unlike many herbivorous taxa, which can sequester toxic secondary compounds from their food resources, spiders are usually undefended chemically and are favored prey to vertebrates (Oxford and Gillespie 1998).

The effect of bird exclusion was particularly pronounced on one introduced species (Theridiidae: *Achaearanea* cf. *riparia*) that irrupted in the absence of birds (Gruner in press-c). The strong numerical response of *Achaearanea* cf. *riparia* to bird exclusion was driven by large aggregations of juvenile spiders (Gruner in press-c), which may have resulted from the escape of small numbers of females from bird predation. While *A. riparia* has not been studied in this habitat, tangle-web theridiids generalize on mobile arthropods (e.g., Collembola) but probably do not regulate their prey populations (Wise 1993). Neither densities nor biomass of this spider correlated with numbers of other major groups.

The irruption of *A. riparia* masked a significant fertilization X cage interactive effect on the remaining spider assemblage (Figure 3.7A). Spider numbers cascaded up in fertilized plots with birds present, but the effect nearly doubled in their absence. Bird predation and resource limitation acted in compensatory fashion, showing some support for the hypothesis that top predator control is mediated by productivity (Gutierrez et al. 1994). In resource-limited environments, spider-spider interactions may be more intense, with intraguild predation or competition for prey or space negating their release from bird predation (Rypstra 1983, Spiller 1984). Fertilization caused a dramatic vegetation response, concomitantly increasing shade, humidity and abundance of living and dead plant material, both in litter and suspended in the canopy. Increased vegetation complexity may reduce abiotic stressors (Wise 1993), increase hunting or prey capture efficiency (Riechert and Bishop 1990, Halaj et al. 2000), or may protect spiders from other foraging predators, such as birds and other spiders (Gunnarsson 1990, Finke and Denno 2002). Alternatively, spiders may benefit from increases in herbivorous and detritivorous insects in fertilized plots (Chen and Wise 1999, Denno et al. 2002, Miyashita et al. 2003) and reduced competition for those resources (Spiller 1984).

Conclusions

Trophic levels are artificial conceptualizations (Persson 1999) that subsume ecological processes, such as omnivory and intraguild predation, found to be prevalent in terrestrial food webs (Coll and Guershon 2002). However, in this complex community comprising over one hundred species, trophic level analyses revealed biologically explicable differences in response to bottom-up and top-down forces. Bottom-up forces predominated for both trophic levels directly consuming primary productivity (living and dead), while top-down effects influenced predaceous arthropods most strongly (McQueen et al. 1986, 1989). These factors appeared to compensate and dissipate, rather than propagate (Pace et al. 1999), within the assemblage of generalist, inefficient spider predators.

CHAPTER 4

BIOTIC RESISTANCE TO INVASIVE SPIDERS CONFERRED BY GENERALIST INSECTIVOROUS BIRDS ON HAWAI‘I ISLAND

Abstract

A central problem for ecology is to understand why some biological invasions succeed while others fail. Species interactions frequently are cited anecdotally for establishment failure, but biotic resistance is not well supported by quantitative experimental studies in animal communities. In a 33-month experiment on Hawai‘i Island, exclusion of native and alien forest birds resulted in a 25- to 80-fold increase in the density of a single non-indigenous spider species (Theridiidae: *Achaearanea* cf. *riparia*). Spiders in cages were also larger, suggesting large reproductive individuals are highly susceptible to bird predation. Most examples of biotic resistance involve competition for limiting resources among sessile marine animals or terrestrial plants. The present results show that generalist predators can limit the success of introductions, even on oceanic islands, generally assumed less resistant to invasion.

Introduction

A central question in ecology is why some biological invasions succeed while others fail. Numerous mechanisms may alter the fate of non-indigenous species in a foreign range, including the number and quality of introduced propagules (Green 1997), levels of human disturbance (Hobbs and Huenneke 1992), compatibility of physiological tolerances with abiotic site characteristics (Blackburn and Duncan 2001), or biotic resistance of the recipient community (Maron and Vilà 2001).

Following Chapman's (1931) formulation of the concept of ecological resistance, Elton (1958) proposed that a strongly interacting community of native species may resist invasion, predicting species-rich communities should be more stable and resistant. Although several examples of resistance exist from marine systems (e.g., Reusch 1998) and sessile organisms in plant communities (e.g., Hector et al. 2001), there have been few experimental evaluations in terrestrial animal communities (but see Lake and O'Dowd 1991). Aside from biological control examples in agroecosystems (Luck et al. 1999), most studies have ignored functional diversity and the role of consumers (Maron and Vilà 2001, Duffy 2002). Biotic resistance remains controversial (Simberloff 1995), and quantitative population-level studies are urgently needed to evaluate the generality of the concept (Goeden and Louda 1976, Simberloff and Von Holle 1999).

In the chapter, I report experimental evidence of biotic resistance to invasion by an exotic species in a forest ecosystem. Exclusion of a guild of generalist insectivorous birds led to an unexpected irruption of an introduced spider. Several experimental examples of invasion resistance in natural terrestrial animal communities now come from oceanic islands, often considered intrinsically less resistant to invasion (e.g., Elton 1958, Pimm 1991).

Methods

For almost 3 years (Aug. 1998 to May 2001), I conducted a factorial experiment to test the community-wide impacts of resources and bird predators in a forest ecosystem. The site was located on the historical basaltic lava flow of 1881 on Mauna Loa, Island of Hawai'i. *Metrosideros polymorpha* Gaudichaud-Beaupré (Myrtaceae) dominates this montane (1280 m a.s.l.), early-successional wet forest (~4000 mm a.a.p.), along with ferns (e.g., *Dicranopteris linearis* [Burm.] Underw. [Gleicheniaceae]), sedges (e.g., *Machaerina angustifolia* [Gaud.] T. Koyama [Cyperaeae]) and low shrubs (e.g., *Coprosma ernodeoides* A. Gray [Rubiaceae]). Thirty-two 20 x 20 m plots grouped in eight blocks were established in a randomized block design. Sixteen plots were fertilized at six month intervals ("NPT" of Raich et al. 1996). A randomly selected clump of 1-6 individual *M. polymorpha* trees within the central 8 x 8 meters were either left open or caged using sheer agricultural polypropylene mesh (2 x 2 cm, Easy Gardener Inc., Waco, TX), supported by a frame of aluminum conduit piping 4 meters tall (cages ~20 m circumference). The experimental design is described in detail elsewhere (Chapter 3).

Birds are the only diurnally active, canopy-foraging vertebrate insectivores in the Hawaiian Islands. The dominant birds at this site are Japanese white-eye (*Zosterops japonicus*) and native ʻapapane (*Himatione sanguinea*). Native ʻomaʻo (*Myadestes obscurus*), ʻiʻiwi (*Vestiara coccinea*), ʻamakihi (*Hemignathus virens*), and ʻelepaio (*Chasiempis sandwicensis*), respectively, are present at decreasing frequency. *Zosterops japonicus* and *C. sandwicensis* are predominantly insectivorous, *H. sanguinea* and *V. coccinea* are principally nectarivorous and *M. obscurus*, frugivorous. All take arthropods opportunistically, especially while provisioning nestlings in the spring (Perkins 1903, Baldwin 1953, Ralph et al. unpublished data).

I sampled the entire arthropod fauna of focal trees, but in this paper I focus on an introduced spider, *Achaearanea* cf. *riparia* (Blackwall) (Theridiidae). Like other theridiids, these spiders build small tangle webs between leaves and branches. All three *Achaearanea* species recorded from Hawaiʻi are exotic. The cosmopolitan common house spider (*A. tepidariorum*), present in the islands for at least a century (Kirkaldy

1908), is strictly associated with anthropogenic habitat. *Achaearanea* cf. *riparia* and *A. acorensis* were reported recently as new state introductions (Beatty et al. 2000). Although their current distributions are poorly understood (Nishida 2002), contemporary sampling and comparison to historical record suggest *A. riparia* is expanding within Hawai'i Volcanoes National Park and possibly other areas on the island of Hawai'i (Gagné 1979, Gruner unpublished data).

I sampled tree clumps at experimental outset and conclusion by clipping 5-10 branches, shaking and beating branches onto a lab table, and collecting all arthropods with an aspirator. I scored and identified them to species, measured body length to the nearest millimeter, and estimated dry biomass using length-mass regressions (Gruner 2003). I dried clippings at 70 °C to constant mass and weighed both foliar and woody components. Arthropod densities and biomass were summed per plot and calculated as loads per 100 g foliar dry mass.

Final *A. riparia* density and biomass were log transformed (ln [x +1]) and analyzed using a mixed general linear model in SAS 8.02 (SAS Institute, Cary, NC). Bird exclusion and fertilization were treated as fixed factors, with blocks and their 2-way interactions as random effects.

Results

At the start of the experiment, only 18 *A. riparia* spiders were collected from 9 of 32 plots (28%). In contrast, at the end of the study, 1336 individuals were collected from 25 of 32 plots (78%).

Caging significantly increased both density and biomass of *A. riparia* (Table 4.1, Figure 4.1). Average density in caged, unfertilized plots (17.09 spiders / 100 g foliage ±

Table 4.1. Analysis of final *Achaearanea* cf. *riparia* density and biomass. Response variables were transformed [ln (x + 1)] prior to analysis. Boldface *P*-values are significant at α = 0.05. Italicized effects are random; others are fixed.

Source	df	MS	F	*P*
Density				
Fertilization (F)	1	3.023	4.343	0.076
Cage (C)	1	21.402	20.738	**0.003**
F X C	1	0.999	1.346	0.284
Block (B)	7	1.966	2.649	0.111
F X B	7	0.696	0.937	0.533
C X B	7	1.032	1.391	0.337
Error	7	0.742		
Biomass				
Fertilization (F)	1	1.208	5.780	**0.047**
Cage (C)	1	4.914	15.120	**0.006**
F X C	1	0.775	5.366	**0.054**
Block (B)	7	0.387	2.679	0.108
F X B	7	0.209	1.448	0.319
C X B	7	0.325	2.247	0.154
Error	7	0.144		

6.51 SE) was approximately 25-fold higher relative to control plots (0.60 ± 0.26) and almost 80 times higher than in fertilized, uncaged plots (0.21 ± 0.12; Figure 4.1A). No individuals longer than 3 mm were collected on uncaged plots, compared to 37 larger (4-5 mm) spiders within cages. Fertilization led to a significant reduction in spider biomass, even more so when plots were also caged (significant fertilization X cage interaction, Table 4.1). This negative effect may be due to dilution across increased habitat, as fertilization led to a dramatic increase in vegetative biomass (Chapter 3).

It is possible that presence and density of spiders were underestimated in the initial collections. As destructive sampling was necessarily more conservative at the experimental outset, foliage samples were smaller than at the conclusion of the

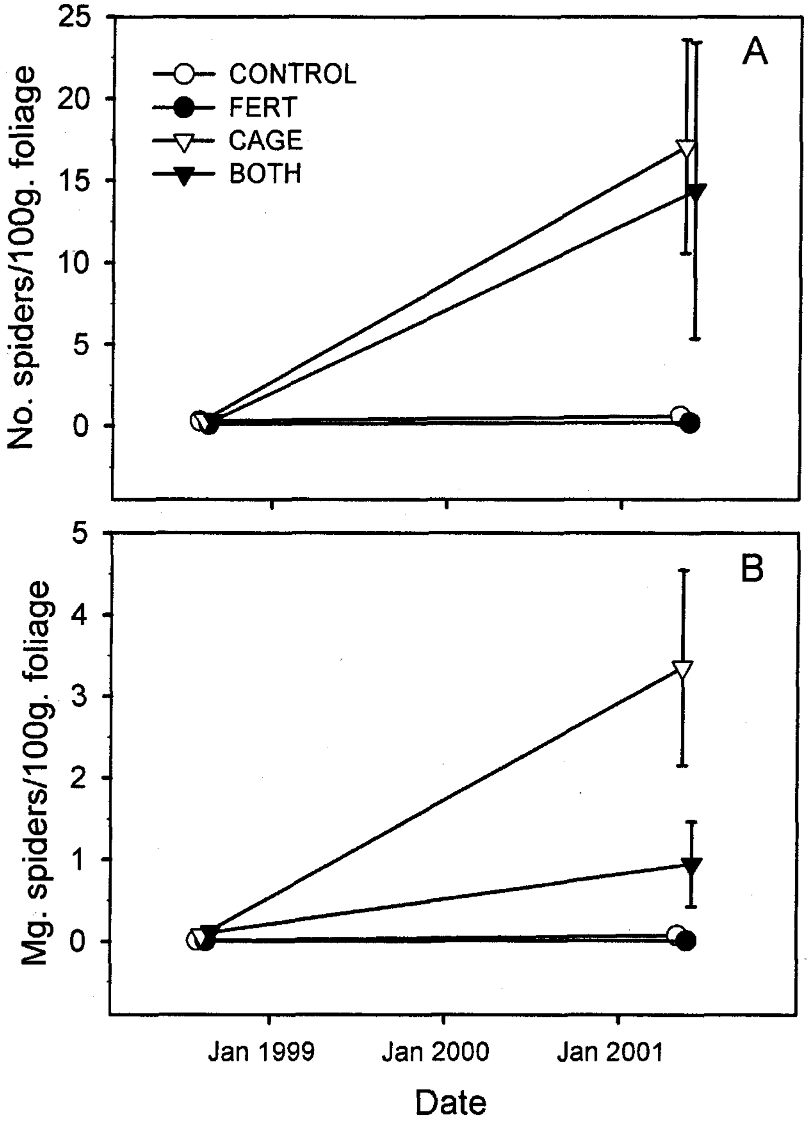

Figure 4.1. Response of *Achaearanea* cf. *riparia* A) density and B) biomass to fertilization and bird exclusion cages over 33 months of manipulation. Shaded symbols (✯, θ) represent fertilized treatments, and upside down triangles (σ, θ) represent bird exclusion treatments. Error bars are ± 1 SE.

experiment (overall foliage means ± SE, n = 88; initial: 81.05 g ± 5.57; final: 238.28 g ± 8.18; one-sided paired t = -20.39, df = 138, $P < 0.0001$). Smaller foliage collections result in a lower probability of sampling rare individuals potentially present on some plots. A higher preponderance of null values may explain the lower density of individuals found initially (control plot means [no. spiders/100 g foliage] ± SE, n = 8; initial: 0.30 ± 0.25; final: 0.68 ± 0.28), but this does not account for the large difference in caged plots. Thus, exclusion of birds had a very strong effect on this single introduced spider species.

Discussion

Crawley (1987) defines a successful invasion as when an invader is able to increase from rarity. By this definition, *A. riparia* was present but not invasive until birds were excluded. Not only was this spider rare in my initial samples (Figure 4.1), but it also was absent from *Metrosideros* at a site less than 15 km away (F.S. Fretz, personal communication) and from 5 other extensive quantitative arthropod collections on 3 islands (Gruner and Polhemus 2003, Chapter 2). Although *A. riparia* is expanding its range, this study explains its continued rarity at the present site, and provides the first experimental demonstration of community resistance mediated by generalist birds. While anecdotes describing biotic resistance are abundant, particularly in highly modified biological control situations (Goeden and Louda 1976, Luck et al. 1999), I am aware of only one other study that demonstrates this phenomenon in a natural terrestrial animal community. On Christmas Island in the Indian Ocean, red crabs (*Gecarcoidea natalis*) prey on introduced African snails (*Achatina fulica*) in undisturbed native forests (Lake and O'Dowd 1991). Interestingly, another invasive species, the long-legged, or yellow crazy ant (Formicidae: *Anoplolepis gracilipes*), preys on red crabs, negating the resistance and indirectly facilitating the invasion of snails (O'Dowd et al. 2003).

In the present case, one introduced species may enhance biotic resistance to other invasive species. *Zosterops japonicus,* the most abundant bird at the site and throughout the Hawaiian Islands overall, thrives both in highly modified habitats and in native forests from sea level to 2000+ m in elevation (Scott et al. 1986). Comparative evidence suggests *Z. japonicus* competes for resources with native birds (Mountainspring and Scott 1985), which implies food resources are limiting for birds at some times or places. Spiders are among the most important prey for five of the six commonest passerines at this site, including *Z. japonicus* (Perkins, 1903, Baldwin 1953, Ralph et al. unpublished data). Nevertheless, these birds forage predominantly within tree canopies, leaving many microhabitats where these spiders and other introduced species may gain a foothold and persist in novel environments.

The observed effect of local invasion resistance thus results from predation by generalist, opportunistic predators. Biotic resistance is predicted to be strong where omnivores or generalists are abundant (Crawley 1986). Theoretical models predict that mobile generalist predators can also confer ecosystem stability (McCann et al. 1998), which has been linked, although controversially, to ecological resistance and diversity (Elton 1958, Pimm 1991). In case studies of mollusks in terrestrial (Lake and O'Dowd 1991) and aquatic systems (e.g., Reusch 1998, Miller et al. 2002), resistance also was attributable to generalist predators. In terrestrial plant communities, where there are more positive examples of biotic resistance (e.g., Hector et al. 2001), the potential effects of consumers remain unclear (Louda and Rand 2003).

Patterns of establishment of introduced birds worldwide are not consistent with the biotic resistance hypothesis but instead are related to abiotic conditions at introduction sites (Blackburn and Duncan 2001). More than 80% of the world's climatic regimes are found in the Hawaiian Islands (Juvik et al. 1978). As invading organisms would be less constrained by abiotic factors, failure to invade may be more related to biotic factors if they can colonize the most conducive microhabitats. Patterns of bird introduction, distribution and local extinction are consistent with the hypothesis that competitive exclusion is responsible for failure of introduced species to establish in Hawai‘i (Moulton and Pimm 1983), but without direct evidence of biotic interactions (Simberloff and Boecklen 1991).

Since prehistoric times, extinction rates of birds on oceanic islands have vastly exceeded rates on continents (Steadman 1995). This study suggests that further loss of insectivorous birds or changes in species composition, as with forest fragmentation (Sekercioglu et al. 2002) and global climate change (Benning et al. 2002), may have a ripple effect altering invasibility of island communities. The complete evolutionary absence or disproportionate loss of functional groups, such as top predators (Duffy 2002), may predispose habitats to decreased biotic resistance or increased ecological impact of introduced species. However, although islands may be more susceptible to the negative impacts of biological invasions (Levine and D'Antonio 1999), it clearly is premature to dismiss islands as less resistant (D'Antonio and Dudley 1995, Simberloff 1995). Further additions of introduced species to island faunas may accelerate ‘invasional meltdown’ (Simberloff and Von Holle 1999, O'Dowd et al. 2003), or may slow the invasion of additional species by augmenting functional diversity and ecological resistance.

CHAPTER 5

TOP-DOWN AND BOTTOM-UP CONSTRAINTS ON SPECIES DIVERSITY AND COMPOSITION OF AN ARBOREAL ARTHROPOD FOOD WEB

Abstract

A longstanding goal for ecologists is to understand the processes that maintain biological diversity in communities. Few studies have investigated the interactive effects of predators and resources on biodiversity in natural ecosystems. I fertilized nutrient limited plots and excluded insectivorous birds in a randomized block design, and examined the impacts on arthropods associated with the dominant tree in the Hawaiian Islands, *Metrosideros polymorpha* (Myrtaceae). After 33 mo, the species load (per foliage mass) of herbivores and carnivores increased with fertilization, but richness (standardized to abundance) did not change. Fertilization depressed species richness and diversity of detritivores, and carnivore richness and diversity dropped in caged, unfertilized plots, both because of the increased dominance of common species with treatments. Herbivore species abundances were more equitable than other trophic levels, and fertilization added individuals and species without changing relative diversity. Plot-level ordinations by nonmetric multidimensional scaling (NMDS) and canonical analysis of principal coordinates weakly discriminated communities from these *a priori* groups. However, tree-level NMDS ordinations ordered samples by host foliar pubescence as strongly as by treatment levels. Overall, the independent and interactive effects of birds and nutrient resources on arthropod diversity were weak, driven primarily by shifts in composition to several highly responsive alien species, and on a par with bottom-up effects of leaf traits.

Introduction

Theory and empirical evidence demonstrate that both resources ("bottom-up") and predators ("top-down") can influence species richness and community composition. Increasing productivity from low levels is expected to increase diversity by: (1) allowing rare species to colonize new resources (MacArthur 1969, Abrams 1995), or (2) persist in larger populations (Hutchinson 1959, Wright 1983, Siemann 1998, Srivastava and Lawton 1998), or by (3) increasing intraspecific density dependence (Abrams 1995, Siemann 1998) or (4) increasing population growth rates and resilience after disturbance (De Angelis 1980, Huston 1994). However, diversity may decline at high productivity creating a unimodal pattern at local to regional scales (Rosenzweig and Abramsky 1993, Rosenzweig 1995, Waide et al. 1999). The relationship of diversity to productivity is still controversial, although it is known to depend on spatial scale, taxonomic affiliation, and perhaps trophic level (Rosenzweig and Abramsky 1993, Abrams 1995, Waide et al. 1999, Mittelbach et al. 2001, Chase and Leibold 2002, Mittelbach et al. 2003, Whittaker and Heegaard 2003). Positive, monotonic patterns appear more common for animal communities at any scale (Waide et al. 1999, Mittelbach et al. 2001).

Experimental manipulation of top predators has been shown to influence the diversity of prey (e.g., Paine 1966, Schoener and Spiller 1996), but impacts vary depending on factors such as diet breadth, temporal and spatial scale, and food web structure (Sih et al. 1985, Holt and Lawton 1994). Generalist predators can depress diversity directly by extirpating rare species or those that occur in small ephemeral populations renewed by immigration (Schoener and Spiller 1996, Spiller and Schoener 1998). In contrast, keystone predators can prey preferentially on dominant competitors or the most frequent prey, thereby mediating prey coexistence and indirectly increasing community richness (Paine 1966, Tilman 1986, Holt et al. 1994, Leibold 1996).

Graphical and mathematical multivariate models predict the effects of consumers will interact with productivity to determine community diversity (Menge and Sutherland 1987, Huston 1994, Leibold 1996, Kondoh 2001). For instance, Leibold's (1996) graphical model hypothesized maximum species coexistence at intermediate levels of both resources and predation. However, qualitative predictions at more extreme bottom-up or top-down parameters were contingent upon species traits, species turnover, and food web complexity. Empirical support for these models has been mixed: while top-down and bottom-up effects are often strong and opposing, they are not always interactive (Proulx and Mazumder 1998, Kneitel and Miller 2002, Worm et al. 2002, Dyer and Letourneau 2003, Hillebrand 2003). To my knowledge, Dyer and Letourneau (2003) provide the only multifactor manipulation of the effects of resources (light and nutrients) and consumers (predatory beetles) on terrestrial arthropod diversity. There is a clear continuing need for more research on top-down and bottom-up constraints on diversity of underrepresented taxa (e.g., terrestrial invertebrates) in multifactor experimental designs.

I experimentally investigated the combined effects of productivity and bird predation pressure on the diversity and composition of a species-rich arboreal arthropod community. The study was carried out for 33 months on a 120 yr-old basaltic lava flow, where nutrients are extremely limited and amenable to experimental treatment through fertilization (Raich et al. 1996, Gruner in press-b). *Metrosideros polymorpha* (Myrtaceae) was the only tree species at the site, and small stature trees could be caged completely to exclude insectivorous birds. The focus on the fauna of a single, dominant plant species controlled confounding impacts of altered plant species composition typically observed with increased productivity (Tilman 1993). Trophic level abundance and biomass responses were reported previously (Gruner in press-b), but this investigation aimed to test the individual and combined effects of resource and predator manipulation on aggregate measures of species density and richness, relative diversity, and species composition. Fertilization was expected to increase diversity and alter species composition across trophic levels. Bird exclusion may increase or decrease diversity, depending on arthropod species composition, prey selectivity of bird species, or ecosystem productivity (and hence the fertilization treatment).

Methods

Site descriptions and study species

The experiments were located on a historical basaltic lava flow of 1881 in the Upper Waiākea Forest Reserve, on the windward slope of Mauna Loa, Island of Hawai‘i (Gruner in press-b, in press-c). The site is a montane (~1280 m. a.s.l.), early successional wet forest (4000 mm aap, Giambelluca et al. 1986, Juvik and Nullet 1994) dominated by ‘ōhi‘a lehua (*Metrosideros polymorpha* Gaudichaud-Beaupré [Myrtaceae]). *Metrosideros polymorpha* is by far the most abundant woody species in these areas and a key contributor to ecosystem biomass and productivity (Raich et al. 1997). Three morphological forms, roughly corresponding to the described varieties *glaberrima*, *polymorpha*, and *incana*, are sympatric at the site (Dawson and Stemmerman 1999). Other common plants included native ferns (e.g., *Dicranopteris linearis* [Burm.] Underw. [Gleicheniaceae]), sedges (e.g., *Machaerina angustifolia* [Gaud.] T. Koyama

[Cyperaeae]) and low shrubs (e.g., *Coprosma ernodeoides* A. Gray [Rubiaceae]). A more comprehensive vegetation description was presented elsewhere (Gruner in press-b).

The fauna associated with *Metrosideros* in Hawai'i is limited to arthropods and birds. Leaf chewing lepidopteran larvae, phloem and xylem feeding Heteroptera and Homoptera, and gall-forming psyllids (Homoptera: Triozidae) are the most common herbivorous taxa at this site (Stein 1983, Gruner in press-a). Invertebrate carnivores (e.g., Araneae, some Heteroptera and Coleoptera), hymenopteran parasitoids (Ichneumonidae, Bethyliidae and Chalcidoidea) and litter processors and detritivores (e.g., Psocoptera, Isopoda, Collembola, some Coleoptera) are diverse. A complete list of arthropods sampled from *M. polymorpha* in these studies is listed in Appendix B.

Six passerines were observed in the region with regularity, three of which are considered insectivorous (*Hemignathus virens virens*, *Chasiempis sandwichensis*, *Zosterops japonicus*). Two nectarivorous (*Himatione sanguinea* and *Vestiaria coccinea*) and one frugivorous (*Myadestes obscurus*) species also take arthropods to a varying degree, especially in the spring while provisioning nests (Perkins 1903, Baldwin 1953, van Riper and Scott 1979, Ralph et al. unpublished data). Spiders, psocopterans and all major phytophagous insect taxa are common prey items from gut and fecal samples (Baldwin 1953, Ralph et al. unpublished data). Aside from bats (*Lasiurus cinereus semotus*), which hunt nocturnally in flight (Jacobs 1999), no mammals have been observed at the site, and the only other vertebrate is an introduced skink (*Lampropholis delicata*), found occasionally in the litter.

Experimental design

Fertilization and avian predator exclusion treatments were established in a 2 x 2 randomized block design. I laid out 20 x 20 m plots, each separated at minimum by 10 m buffer strips, in pairs along an elevational transect at a 245° compass bearing. Before assigning treatments to plots, a clump of 1-6 trees was selected randomly from all possible clumps within the central 8 x 8 m of each plot. Clumps were defined by 1 or more trees at least 2 m tall, but not taller than 3.5 m. Trees taller than 4 m were unusual, but were excluded from consideration because they could not be caged (see below). There were a total of 88 focal trees randomly distributed among 32 plots. Foliar pubescence class (P = pubescent, G = glabrous, GP = intermediate) was noted for each tree (see Chapter 6 for more details).

Eight blocks each consisted of 4 adjacent plots (two pairs). Within each block, plots were randomly assigned to the following treatments: 1) control, 2) fertilization only, 3) bird exclusion cage only, and 4) fertilization and cage. Plots were hand fertilized at six-month intervals with a broad spectrum of granular nutrients following the "NPT" protocol of Raich et al. (1996, Gruner in press-b). The initial application in September 1998 was double that of all future fertilizations; the final fertilization occurred in October of 2000.

Sixteen bird exclosure cages (4 m tall x 4-6 m each side) were constructed in August 1998. Lightweight electrical conduit pipes were affixed onto steel rebar driven into the basalt substrate. Galvanized wire strung between poles supported sheer UV-resistant polypropylene mesh (2 x 2 cm, Easy Gardener Inc., Waco, TX) draped over this frame, and guy wires stabilized cages to additional rebar anchors. Openings in the mesh were stitched together and secured to the ground to minimize gaps. Insects passed freely through this mesh, but birds were excluded.

Arthropod sampling and analysis

I sampled arthropods by branch clipping (Basset et al. 1997, Johnson 2000). I haphazardly selected 5-10 branches from each focal plant and clipped and bagged the terminal (~50 cm) twigs and foliage, the primary microhabitat exploited by many insectivorous birds in the Hawaiian Islands and the site of highest arthropod concentrations (Fretz 2000). Reproductive structures (seeds, flowers) were avoided. Extreme care was exercised in avoiding disturbance of branches and arthropods before branches were quickly collected. However, most arthropod taxa were reluctant to disperse from foliage even when disturbed (Gruner personal observation), and escape from bags in the field was observed rarely.

Foliage samples were collected in the morning hours, one block per day, and transported it to the laboratory at Kilauea Field Station, Hawai‘i Volcanoes National Park, for immediate processing. Foliage was shaken, beaten and sifted over a white cloth, and arthropods were collected with an aspirator and stored in 70% ethanol. Branch shaking and detritus sifting continued until no additional arthropods were observed. I separated foliage from woody material, dried both components to constant mass, and weighed them to within 0.001 g.

To limit the impact of destructive sampling, arthropods were collected from focal trees only before applying experimental treatments (August 25-28, 1998) and at the conclusion of the 33-mo study (April 16-May 3, 2001). The initial samples were taken after delimiting plots but before establishing randomized treatments. The final collection period coincided with the nesting and fledging period of the most common passerines at the site (Baldwin 1953, Scott et al. 1986, Ralph and Fancy 1994), a time when avian demand for arthropods should be high, but before summer declines in arthropod numbers (Gruner unpublished data).

All arthropods collected were counted and identified to species or assigned to operational taxonomic units (OTU), or morphospecies, based on morphological evidence and advice of taxonomists. I classified arthropods by trophic levels (carnivores, detritivores, herbivores and tourists) using evidence from personal observation, literature review, and communication with systematists. Carnivores include all spiders, cursorial hunters and parasitoids; detritivores comprise saprophagic arthropods and grazers of litter, fungi and microbes; herbivores consist of sap feeders, gall-formers (mostly free living adults), wood-borers, and foliage chewers; and tourists include species known to be incidental or non-feeding on *Metrosideros*, or with unknown or highly omnivorous feeding habits.

Specimen data were managed using biodiversity collections database software (Colwell 1997a). I used a taxonomic checklist (Nishida 2002) to classify species as introduced, native (including endemic and indigenous forms) or undetermined in cases where identification was impossible or a group's status was unknown. A complete list of species collected in this study is presented in Appendix B, and vouchers and bulk collections are deposited at the B.P. Bishop Museum, Honolulu.

Species richness and relative diversity

I report three indices of total and trophic level arthropod biodiversity: species load, species richness, and relative diversity. Each index emphasizes different components of community diversity while controlling for possible sampling bias. Although every effort was made to collect similar sized clipping samples, this was impossible in practice. Species load is analogous to species density, which records the number of species per unit area, except that observed species richness was standardized by the dry foliage biomass collected with each sample (per 100 g dry foliage mass). Plot level species load was obtained by averaging trees within plots.

Fertilization and bird exclusion led to increased density of some *Metrosideros* arthropod groups (Gruner in press-b), and increased species number is expected as a random consequence of larger pools of individuals (Gotelli and Colwell 2001). Therefore, rather than report raw species number, I used rarefaction to estimate "expected species richness" (hereafter, "richness") at constant total abundance (Gotelli and Colwell 2001). Species abundances were pooled across trees within plots, and Monte Carlo simulations were run for 1000 iterations on each plot using EcoSim freeware (Gotelli and Entsminger 2002). Plots were compared across a standard abundance threshold for each trophic group in initial (all arthropods only: 40 individuals) and final samples (all arthropods: 130 individuals; detritivores: 75; herbivores: 14; carnivores: 18). Thresholds were selected to include 90% of the plots; there were up to three outlying plots with lower abundances within each trophic comparison. For these outlying plots, the observed species number was used (Kneitel and Miller 2002). Examination of rarefaction plots revealed no changes in trends (e.g., crossing lines) across the higher abundance ranges observed in some plots.

Fisher's α was used to measure relative species diversity. Although other indices are used more widely and frequently (e.g., Shannon H'), α has superior discriminant ability and robustness at even small sample sizes (Magurran 1988, Rosenzweig 1995). Fisher's α was computed for individual trees using PRIMER software (Clarke 2001) and averaged within plots.

Diversity statistics were analyzed with a series of mixed general linear models (GLM) using type III sums of squares in PROC MIXED (SAS 2001). The fertilization and bird exclusion factors were treated as fixed, and the random block term accounted for spatial environmental heterogeneity. All two-way interactions were included in the GLM in accordance with model 1 of Newman at al. (1997). The main fixed effects were tested using the mean square of the corresponding block interaction term as the denominator of the F-ratio, rather than the mean squared error. This had a conservative effect on *P*-values, as the mean squares of the block interactions were usually larger than the error terms in these models.

Initial collections and final collections were analyzed with separate GLMs because initial samples contained fewer branches and were separated in time by > 2.5 yrs. Response data were natural log transformed when necessary to meet assumptions of normality and homoscedasticity. For final collections, linear models were tested for species load, expected species richness, and relative diversity of all arthropods and for carnivores, herbivores, and detritivores separately. For initial collections, I tested only aggregate arthropod response variables due to empty cells for some trophic levels. Post hoc multiple comparisons, using the joint significance level of $\alpha = 0.05$, were run for each GLM using the Tukey-Kramer test.

Finally, I expanded the spatial scale of diversity comparisons by pooling individuals in all replicates and creating a single rarefaction curve for each treatment.

Curves were calculated with EcoSim for all arthropods in aggregate and for each trophic level separately. This approach enabled comparisons of within-plot treatment differences to the landscape covered by this experimental design while accounting for species turnover (McCabe and Gotelli 2000).

Species composition

For composition studies, abundance data were pooled across trees within plots and natural log transformed (x+1), which reduced the influence of a few, highly abundant but small-bodied species (Gruner in press-b). Species abundances were then standardized by dividing by plot total abundance sums (relativization), and distance matrices were calculated using the Euclidean distance measure. Relativization further reduced the influence of altered abundances caused in part by treatments, which were reported in a separate paper (Gruner in press-b), and focused instead on compositional differences (McCune and Grace 2002).

I used nonparametric multivariate analysis of variance (NPMANOVA) to test the influence of treatments on community species composition (Anderson 2001a, McArdle and Anderson 2001). This method allows hypotheses tests and analysis of symmetric distance matrices in ANOVA designs using a pseudo-F ratio and *P*-value determined by permutation (Anderson 2001b). The model design matrix described above for GLM analysis was assembled with the same parameterization and tested using DISTLM software (Anderson 2000). For each trophic level, 999 permutations under the reduced model were run to estimate *P*-values for all 2-way factor combinations. I tested the full community and a reduced dataset excluding all species with only a single occurrence (singletons), but results were similar qualitatively and only the former are presented.

I used nonmetric multidimensional scaling (NMDS, Kruskal 1964, Mather 1976) to visualize community composition of plots and trees in species space. As with NPMANOVA procedures, I used Euclidean distance on natural log (x+1) transformed, relativized data for all ordinations. I fit 40 runs of the community matrix and a maximum of 400 iterations in each of 6 dimensions using PC-ORD (McCune and Mefford 1999). The final dimensionality of each ordination plot was chosen by evaluating incremental reductions in stress, which is an inverse measure of fit to the data, using scree plots. The solution was deemed stable if the standard deviation of stress reached 0.0001 for the last ten iterations. In addition, 50 Monte Carlo randomizations of the data set were produced to determine if the NMDS stress values were lower than expected by chance.

I followed unconstrained NMDS ordinations with canonical analysis of principal coordinates ("CAP," Anderson and Willis 2003). While NMDS allows examination of dispersion within and among groups and may identify unanticipated pattern, CAP constrains ordinations by *a priori* hypotheses. The CAP procedure may uncover patterns masked by variability in unconstrained ordinations, but guards against spurious results created by overparameterization (Anderson and Willis 2003). I collapsed factorial treatments into a single variable with 8 replicates in each of 4 levels (control, fertilization only, bird exclusion only, and both fertilization and bird exclusion). Euclidean distance matrices were distilled into orthogonal axes *m* (principal coordinates), the number of which were chosen using misclassification rates to groups in a "leave-one-out" procedure (Anderson and Willis 2003). I tested the null hypothesis of no difference in multivariate location among treatment levels by calculating the trace statistic of canonical discriminant analysis and obtaining a *P*-value with 999 permutations in CAP software (Anderson 2003).

In addition, I explored overall variation in the data set with unconstrained NMDS and constrained CAP ordinations of all 88 trees, which were the subsamples comprising the plot totals, as described above. Principal coordinate axes were characterized by testing explanatory variables in a mixed model, with a structure extended from the aforementioned GLM to incorporate morphology and its two-way interactions as within-subjects effects. Because trees were selected randomly from those available on plots, the model was unbalanced and missing foliar morphology X treatment combinations for some blocks. Thus, I used the residual maximum likelihood procedure of PROC MIXED (SAS 2001) and the Satterthwaite estimation for degrees of freedom, but report only the type III tests of fixed effects.

Results

Sampling considerations

In total, 119 species from 14 arthropod orders were collected from *Metrosideros polymorpha* in initial and final collections, 68 of these in 1998 and 108 in 2001 (Appendix B). Of these species, 25 were classified as herbivorous, 24 were detritivorous, 55 were carnivorous (29 parasitoids, 26 predators), and 15 were tourists or undetermined. Over half of these species (65) were considered native, 33 were introduced, and 21 were of undetermined origin. The distribution of species in trophic levels and taxonomic orders is presented in Figure 5.1.

Sampling effort contributed to the species diversity observed. Initial foliage collections were smaller than final collections because of the need to minimize destructive sampling at the outset. Although average density and biomass were similar among sampling periods (Gruner in press-b), absolute dry mass of foliage collections was lower in initial collections (Gruner in press-c), as was absolute arthropod abundance (mean plot abundance ± SE, initial: 178.2 ± 14.1; final: 510.6 ± 73.3; paired $t = -4.45$, df $= 33$. $P < 0.0001$). These smaller samples probably account for lower total richness observed in August 1998 compared to the final collections.

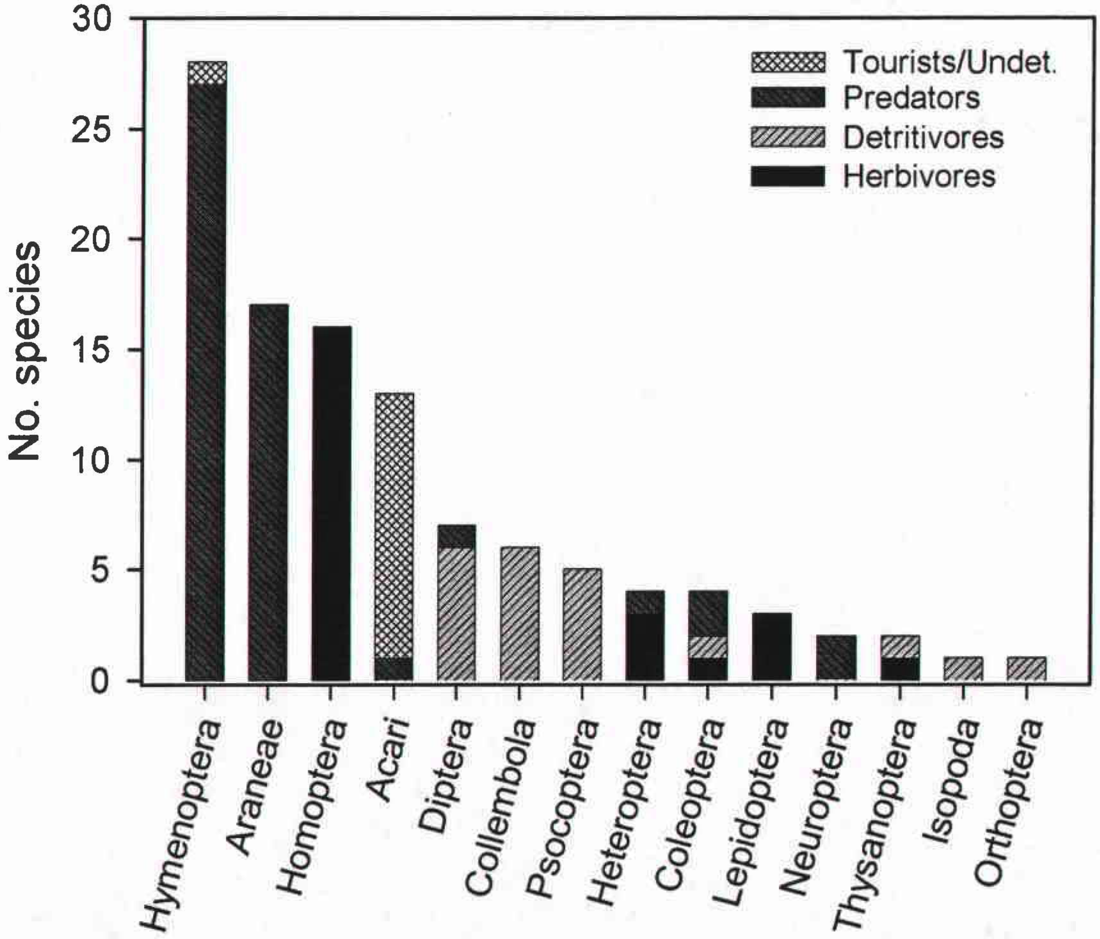

Figure 5.1. Total species richness within taxonomic orders, by trophic level assignment. A total of 119 species were collected in initial and final collections, 68 from August 1998 and 108 from April/May 2001. At least 135 species have been collected from *Metrosideros polymorpha* at this site.

In addition, there was a minor difference in the amount of foliage collected per tree from plots of each treatment in 2001 (one-way ANOVA, $F_{3,84} = 3.67$, $P = 0.015$). Post-hoc comparisons demonstrated a slightly larger foliage sample in caged treatments relative to controls (least-squares means [g] ± 16.0 SE, control: 211.2; cage: 260.0; Tukey's HSD, adjusted $P = 0.021$). There was a significant positive relationship between the dry mass of foliage sampled and the total number of species observed, but the significance was weak ($R^2 = 7.0\%$; df = 87; $P = 0.012$). One sample from a small tree in a control plot yielded only 41 g of foliage and 4 arthropod species (mean foliage mass (g) ± SE = 221.3 ± 6.5; mean species observed 16.9 ± 0.6). When this leverage point is removed, the regression is no longer significant ($R^2 = 3.9\%$; df = 86; $P = 0.068$). Nevertheless, I present three indices for species diversity to account for variable effort in sampling both substrate and individual arthropods.

Species richness and relative diversity

Mixed model GLM analysis of initial collections showed virtually no significant differences in species load, richness or relative diversity. In the sole exception, rarefied total species richness was significantly higher only in fertilized and caged plots (fert. X cage: $F_{1,7} = 10.51$, $P = 0.014$).

Total species load was elevated in fertilized plots (Figure 5.2A; Table 5.1), although this effect was spatially variable (significant fert. X block interaction). No other factors had significant effects on total species load, and no effects were significant for richness or relative diversity when all species were analyzed together (Figure 5.2B; Table 5.1). Detritivore species load was not affected by experimental factors (Figure 5.2C), but

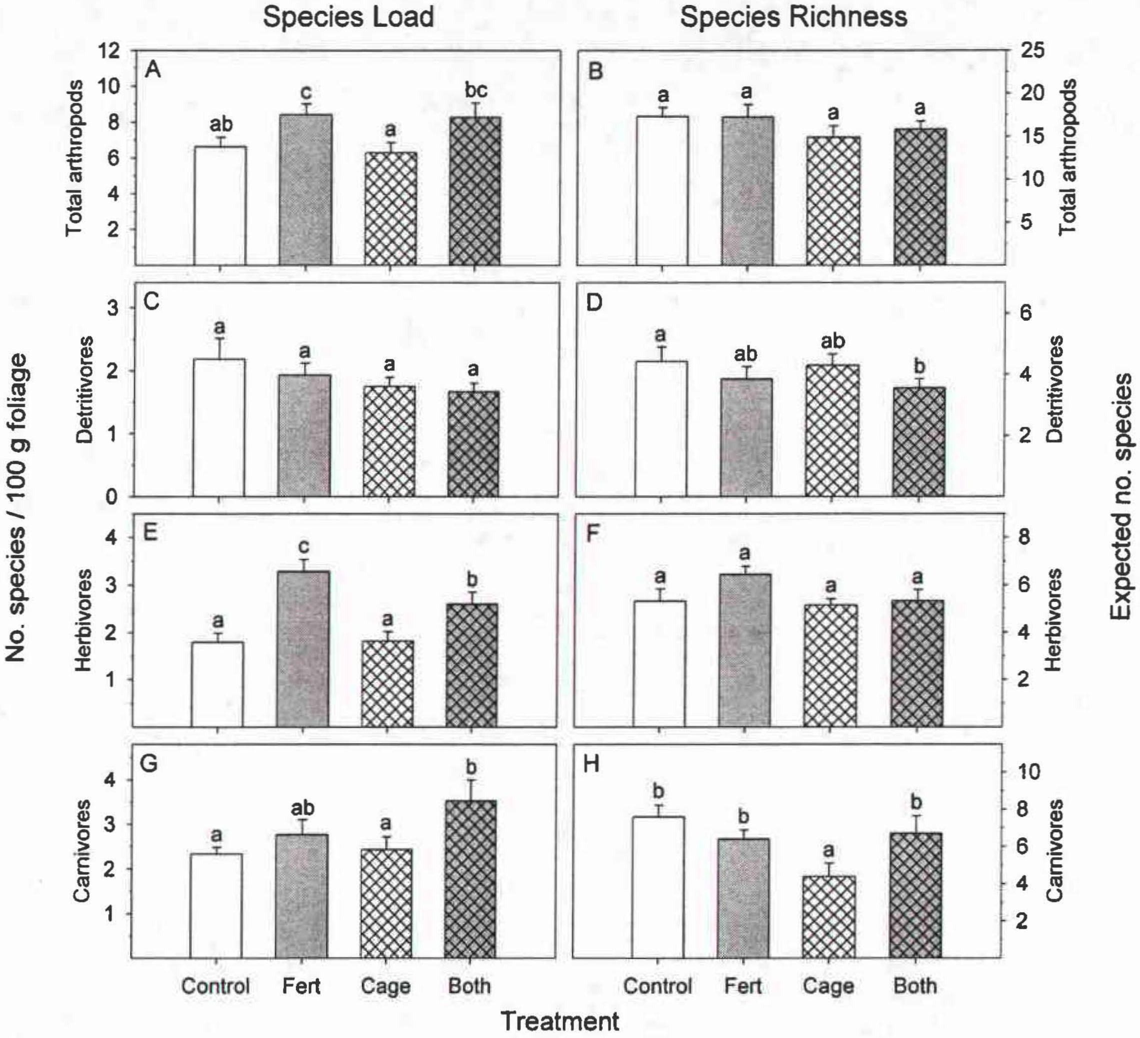

Figure 5.2. Means (± 1 SE) of arthropod trophic level species load and richness in response to experimental fertilization and cage treatments. Species load was the average number of species observed per 100 g dry foliage biomass. Species richness was computed by Monte Carlo individual-based rarefaction at uniform abundance thresholds at the plot level (Gotelli and Entsminger 2002). Results for Fisher's α (not shown) were qualitatively similar to those observed for species richness. Shaded bars are fertilized treatments, and hatched bars represent bird exclusion treatments. Lowercase letters denote significantly different comparisons tested by Tukey's HSD (joint α = 0.05).

Table 5.1. Results from general linear models for arthropod trophic a) species load [number of species / g dry foliage], b) expected species richness from individual-based rarefaction, and c) relative diversity (Fisher's α) from the final sampling in April and May 2001. Boldface *P*-values are significant at $\alpha = 0.05$. Italicized effects were treated as random; others were fixed.

Source	df[a]	All		Carnivores		Herbivores		Detritivores	
		F	*P*	F	*P*	F	*P*	F	*P*
a) Species Load									
Fertilization (F)	1,7	7.54	**0.029**	5.94	**0.045**	13.10	**0.009**	0.87	0.383
Cage (C)	1,7	0.18	0.686	1.63	0.243	2.44	0.162	2.22	0.180
F X C	1,7	0.09	0.776	7.11	**0.032**	4.92	0.062	0.38	0.559
Block (B)	7,7	0.97	0.499	1.06	0.442	0.28	0.945	1.12	0.439
F X B	7,7	5.25	**0.022**	6.60	**0.012**	3.79	**0.050**	1.65	0.263
C X B	7,7	3.48	0.061	7.49	**0.008**	1.74	0.241	2.79	0.100
b) Expected Richness									
Fertilization (F)	1,7	0.08	0.782	0.92	0.369	2.18	0.183	15.50	**0.006**
Cage (C)	1,7	3.21	0.116	3.72	0.095	1.39	0.277	0.41	0.543
F X C	1,7	0.21	0.658	60.43	**<0.001**	1.93	0.207	0.03	0.877
Block (B)	7,7	0.48	0.818	1.30	0.332	0.16	0.987	*	*
F X B	7,7	2.04	0.185	6.74	**0.011**	1.77	0.235	0.12	0.995
C X B	7,7	1.03	0.483	11.00	**0.003**	2.58	0.117	0.45	0.844
c) Relative Diversity									
Fertilization (F)	1,7	4.91	0.062	0.05	0.828	0.04	0.847	14.17	**0.007**
Cage (C)	1,7	0.18	0.685	1.10	0.329	0.50	0.501	1.01	0.348
F X C	1,7	0.18	0.687	16.16	**0.005**	0.03	0.867	0.00	0.948
Block (B)	7,7	0.61	0.736	1.28	0.382	0.57	0.761	*	*
F X B	7,7	1.19	0.413	1.31	0.364	0.45	0.842	0.06	0.999
C X B	7,7	1.61	0.273	2.95	0.089	1.51	0.301	0.54	0.786

a numerator, denominator degrees of freedom.
* not tested

both richness and Fisher's α were depressed with fertilization (Figure 5.2D). In contrast, fertilization also influenced herbivore diversity, but species load increased (Figure 5.2E), while both richness and relative diversity were unchanged (Figure 5.2F). No other factors influenced the diversity of primary consumers, with the exception of a marginally significant interaction of blocks with the fertilization effect on herbivore species load. Carnivore species load was elevated significantly in fertilized treatments (Figure 5.2G), but neither the rarified richness nor α were different (Figure 5.2H). Although the cage factor was not significant for any diversity index, carnivore diversity increased more than additively when both fertilized and caged, and this significant interaction was evident for all three indices. The block factor interacted with both fertilization and bird exclusion for species load and richness, but relative diversity did not change with either factor.

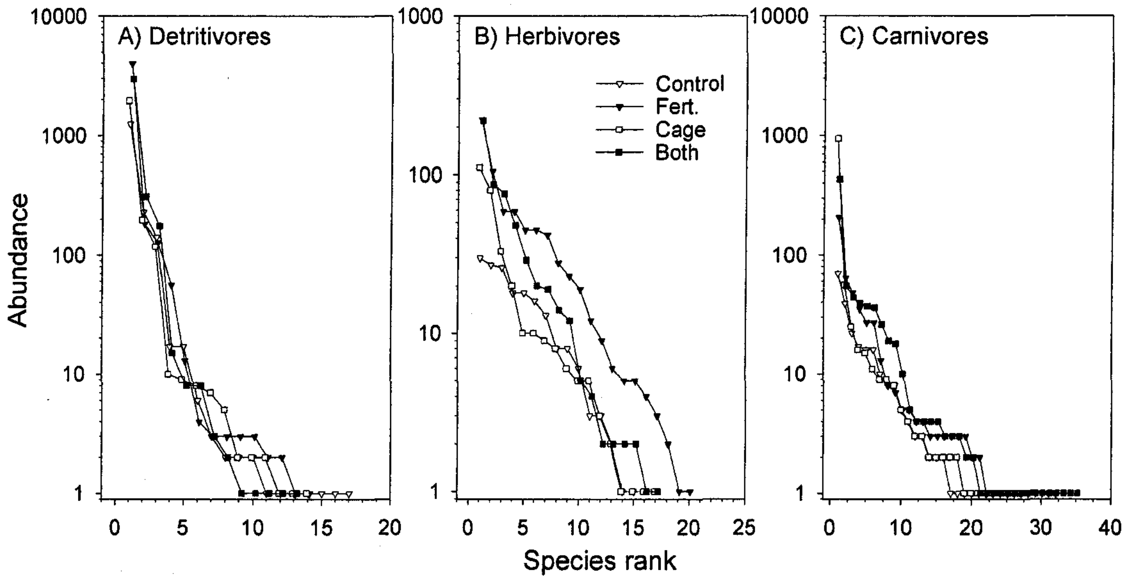

Figure 5.3. Rank abundance curves for trophic level subsets under each treatment: A) detritivores, B) herbivores, and C) carnivores. The plotted points are the pooled abundances of species from all replicates of each treatment, ranked in descending order of abundance. Symbols are as follows: control (σ), fertilization only (θ), caged only (□), and both fertilized and caged (■).

Rank abundance plots for relative abundance of species within trophic levels and across treatments (Magurran 1988) generally were consistent with expectations of the log-series distribution (χ^2, $P > 0.05$), but were distinct from geometric series, lognormal, and broken-stick models (χ^2, $P < 0.001$). However, herbivore dominance relationships were more equitable across species than either detritivores or carnivores (Figure 5.3), with assemblages from control, fertilized only, and caged only treatments not appreciably different than the broken-stick model (control: $\chi^2 = 4.08$, $P = 0.944$; fert.: $\chi^2 = 8.56$, $P = 0.575$; cage: $\chi^2 = 18.47$, $P = 0.048$; both: $\chi^2 = 32.43$, $P = 0.0003$).

Individual-based rarefaction curves, pooling collections from all plots within treatments, showed that control treatments were more diverse than all other treatments on large spatial scales (Figure 5.4). Fertilized, caged, and crossed treatments, all of which had significantly higher densities (Gruner in press-b), showed similar richness levels as a function of individuals. The aggregate result was driven primarily by detritivores, which comprise the majority of individual arthropods and showed a similar response to totals.

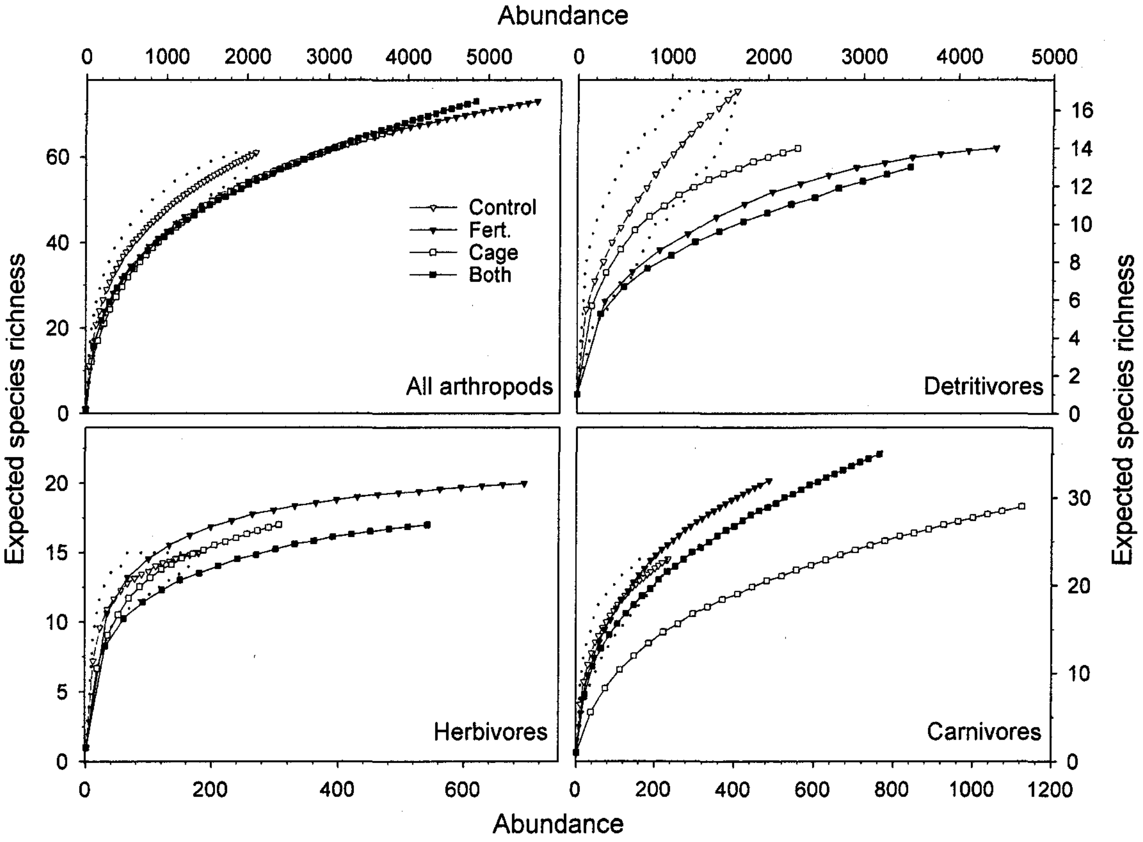

Figure 5.4. Species rarefaction curves for all specimens pooled within treatments. Symbols are as follows: control (σ), fertilization only (θ), caged only (□), and both fertilized and caged (■). Curves for the control treatment (unfertilized and uncaged) are delimited as dotted lines by 95% confidence intervals.

Herbivore richness levels were similar across all treatments, whereas the cage treatment displayed distinctly lower richness of carnivores.

Species composition

Nonparametric MANOVA analyses of Euclidean distances revealed no significant differences in initial community composition. However, both fertilization and cage treatments altered final arthropod species composition (Table 5.2). These effects were driven in part by changes in the carnivore assemblage, which also responded significantly to fertilization and cage treatments. In addition, the carnivore assemblage varied across blocks. There were no significant changes in species composition of detritivores or herbivores in isolation.

Table 5.2. Results of nonparametric MANOVA for species composition of arthropod trophic levels from a) initial sampling before treatments were installed (August 1998) and b) final sampling in April and May 2001. Boldface *P*-values were significant at α = 0.05.

Source	df[a]	All Guilds		Carnivores		Herbivores		Detritivores	
		F	*P*	F	*P*	F	*P*	F	*P*
a) Initial (1998)									
Fertilization (F)	1,7	1.162	0.414	1.162	0.311	0.863	0.682	1.612	0.309
Cage (C)	1,7	0.782	0.761	1.160	0.310	0.841	0.554	0.259	0.933
F X C	1,7	0.690	0.820	0.752	0.710	0.580	0.900	2.103	0.105
Block (B)	7,7	1.240	0.097	1.107	0.299	0.757	0.941	2.272	0.075
F X B	7,7	1.004	0.488	0.973	0.555	0.809	0.890	1.055	0.450
C X B	7,7	1.325	0.068	0.896	0.698	0.845	0.807	2.275	**0.028**
b) Final (2001)									
Fertilization (F)	1,7	3.149	**0.003**	4.140	**0.005**	0.619	0.800	1.930	0.145
Cage (C)	1,7	2.851	**0.013**	5.118	**0.005**	1.862	0.096	0.621	0.738
F X C	1,7	1.476	0.113	1.515	0.166	0.820	0.595	0.980	0.428
Block (B)	7,7	1.531	**0.014**	1.982	**0.013**	1.005	0.490	1.437	0.129
F X B	7,7	0.998	0.504	1.027	0.474	1.173	0.262	0.794	0.762
C X B	7,7	1.126	0.268	1.420	0.128	1.271	0.167	0.767	0.794

[a] numerator, denominator degrees of freedom.

Data manipulations of species abundance matrices were intended to reduce inordinate influence of highly abundant species as well as the species rarely observed. SIMPER analysis, which ranks the importance of each species in analytic outcomes (Clarke 2001), indicated that standardizations and log transformations had their intended effect. Before adjustments, the most abundant five species accounted for an average of 79.2% of the plot-level dissimilarity among treatments in 2001 (n = 6 comparisons). After standardization, these same five species accounted for 28.0% of the dissimilarity, whereas an average of 26 species accounted for the same 79%. Furthermore, standardizations produced conservative results. Without standardization, for example, both the fertilization and cage main effects for carnivores were more strongly significant ($P < 0.001$), as was the fertilization effect for herbivores ($P = 0.010$).

I explored the effects of rare species by removing all singletons (29 species observed only once in 2001) and repeating nonparametric analyses. Singleton removal did not alter qualitative treatment differences in species composition, thus these results are not discussed further. However, removal of the most abundant species had variable effects on statistical results. The collembolan *Salina celebensis* Schaeffer (Entomobryidae) was an order of magnitude more abundant than the next most abundant species, but it was ubiquitous, and its removal had no effect on total arthropod or detritivore-only statistical trends. However, the most abundant carnivore was the spider *Achaearanea* cf. *riparia* Blackwall (Theridiidae), primarily in caged plots. When this species was removed from carnivore-level analyses, all previously significant

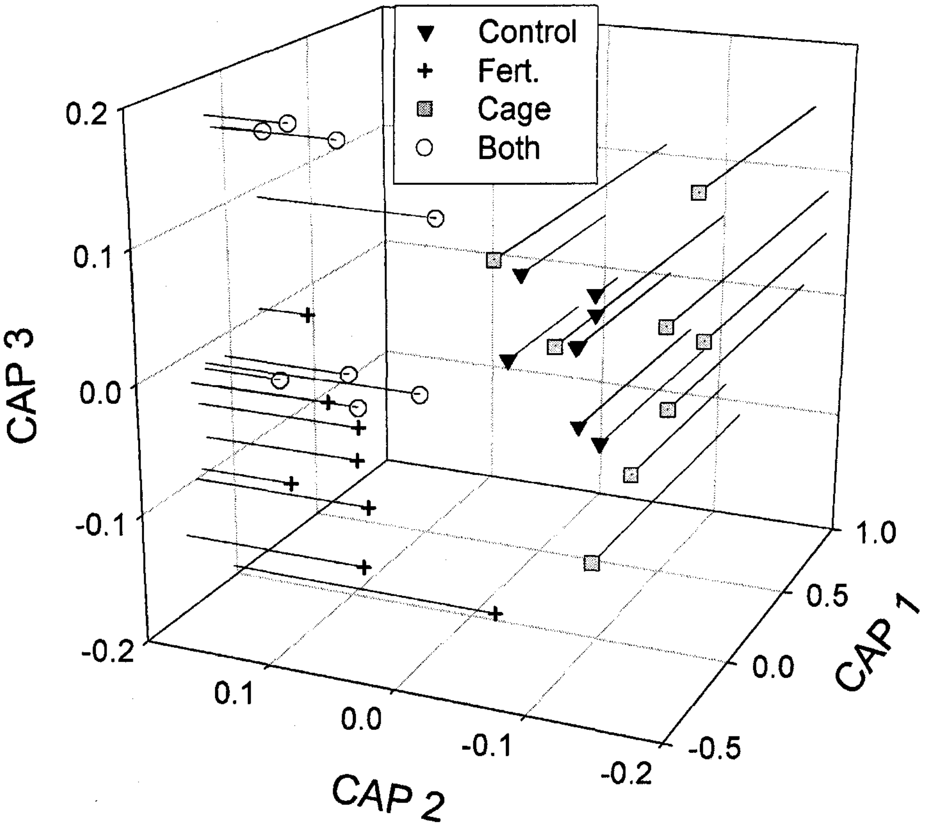

Figure 5.5. Ordination diagram of the first three axes from canonical analysis of principal coordinates. Species data were first transformed (ln X+1) and standardized by plot sums, then all Euclidean distances were calculated. The distance matrix was reduced to nine orthogonal principal coordinates and analyzed through a generalized discriminant analysis, constrained by collapsing fertilization and cage treatments into one factor with four levels.

compositional differences disappeared, although the fertilization effect remained a strong trend (fert.: pseudo-$F_{1,7}$ = 2.53, P = 0.069). Similarly, *A. riparia* accounted for the significant cage effect in total arthropod composition and fertilization remained significant upon its removal (fert.: pseudo-$F_{1,7}$ = 2.70, P = 0.003).

On the level of plots, NMDS ordination diagrams did not reveal strong grouping within treatment combinations for all arthropods, or within any trophic level individually.

The total community (3-D solution) and detritivores (2-D) were grouped non-randomly, but herbivores and carnivores were not significantly different from shuffled communities. However, strong clumping of plots within treatments emerged when the noise and redundancy of 108 species were reduced to principal coordinates (all arthropods: m = 9 axes, 76.17% explained variation) and analyzed with a generalized discriminant analysis (Figure 5.5; trace = 2.783, P = 0.004). The first axis explained the most variation and separated control plots from all treatment plots ($\delta_1^2 = 2.191$), the second axis divided the levels of fertilization ($\delta_2^2 = 0.341$), and the third axis separated the bird exclusion treatments ($\delta_3^2 = 0.250$).

The relatively weak separation of treatments in unconstrained ordinations prompted further exploration into variation at the level of subsamples, the 88 individual trees within plots. Ordinations by NMDS of tree assemblages from initial collections revealed no grouping of trees assigned to treatments in a 2-dimensional solution (Figure 5.6A; stress = 13.2; P = 0.020). However, glabrous and pubescent leaf classes grouped more strongly, although with considerable overlap with the intermediate class (Figure 5.6B). In final collections, a 3-dimensional solution was preferred (stress = 14.04; P = 0.020), but the 2-dimensional solution was also nonrandom and is presented for ease of comparison (stress = 20.1; P = 0.020). Compared to initial collections, more segregation among treatments was observed (Figure 5.6C), consistent with canonical discriminant analyses on plots (Figure 5.5). However, clumping among morphological classes was even more distinct than in initial collections and was stratified with minimal overlap among glabrous and pubescent forms (Figure 5.6D). Principal coordinates analysis

Table 5.3. Fixed effects from mixed model analyses of the first three principal coordinates of arthropod species relative abundance from a) initial sampling before treatments were installed (August 1998) and b) final sampling in April and May 2001. Percentage of total variation explained by each coordinate is listed. F-ratios were estimated for fixed effects by the residual maximum likelihood procedure; random effects involving the block term were not tested, but were included in the model. Boldface *P*-values are significant at $\alpha = 0.05$.

Source	df[a]	PCO1 (38.6%)		PCO2 (16.3%)		PCO3 (9.4%)	
		F	*P*	F	*P*	F	*P*
a) Initial (1998)							
Fertilization (F)	1,7	5.38	**0.032**	0.99	0.322	0.19	0.667
Cage (C)	1,7	0.00	0.948	0.73	0.395	0.08	0.785
F X C	1,7	1.78	0.198	0.03	0.873	0.53	0.480
Morph (M)	2,48	4.80	**0.011**	1.24	0.296	1.40	0.253
F X M	2,48	1.03	0.365	0.59	0.555	0.98	0.379
C X M	2,48	1.24	0.298	0.20	0.816	1.35	0.266
F X C X M	2,48	0.48	0.623	1.92	0.154	1.03	0.361

		PCO1 (23.3%)		PCO2 (12.0%)		PCO3 (10.4%)	
		F	*P*	F	*P*	F	*P*
a) Final (2001)							
Fertilization (F)	1,7	0.03	0.864	29.50	**<0.0001**	35.56	**<0.0001**
Cage (C)	1,7	5.38	**0.051**	19.23	**0.003**	3.45	0.074
F X C	1,7	0.08	0.785	8.87	**0.009**	0.79	0.382
Morph (M)	2,48	29.63	**<0.0001**	6.11	**0.004**	11.75	**<0.0001**
F X M	2,48	3.31	**0.044**	0.02	0.983	1.49	0.233
C X M	2,48	0.11	0.897	1.91	0.156	1.21	0.303
F X C X M	2,48	0.33	0.717	0.47	0.630	0.31	0.735

[a] numerator, denominator degrees of freedom. Denominator degrees of freedom are idealized; actual values estimated by the Satterthwaite procedure varied depending on variance components of expected mean squares.

yielded similar clumping patterns, and leaf morphology was significant for initial samples on the first principal coordinate, and for final samples, highly significantly related to each of the first three principal coordinates (Table 5.3). Fertilization interacted significantly with morphology on the first axis, and was significantly related to the second and third axes. Both the cage factor and its interaction with fertilization were significant on the second coordinate only. Thus, both unconstrained ordinations methods lead to the conclusion that leaf morphology was the primary factor discriminating groups on tree-level assemblages, followed by treatment factors and their interactions (Table 5.3). Leaf morphology did not change with any treatment combination (see Chapter 6).

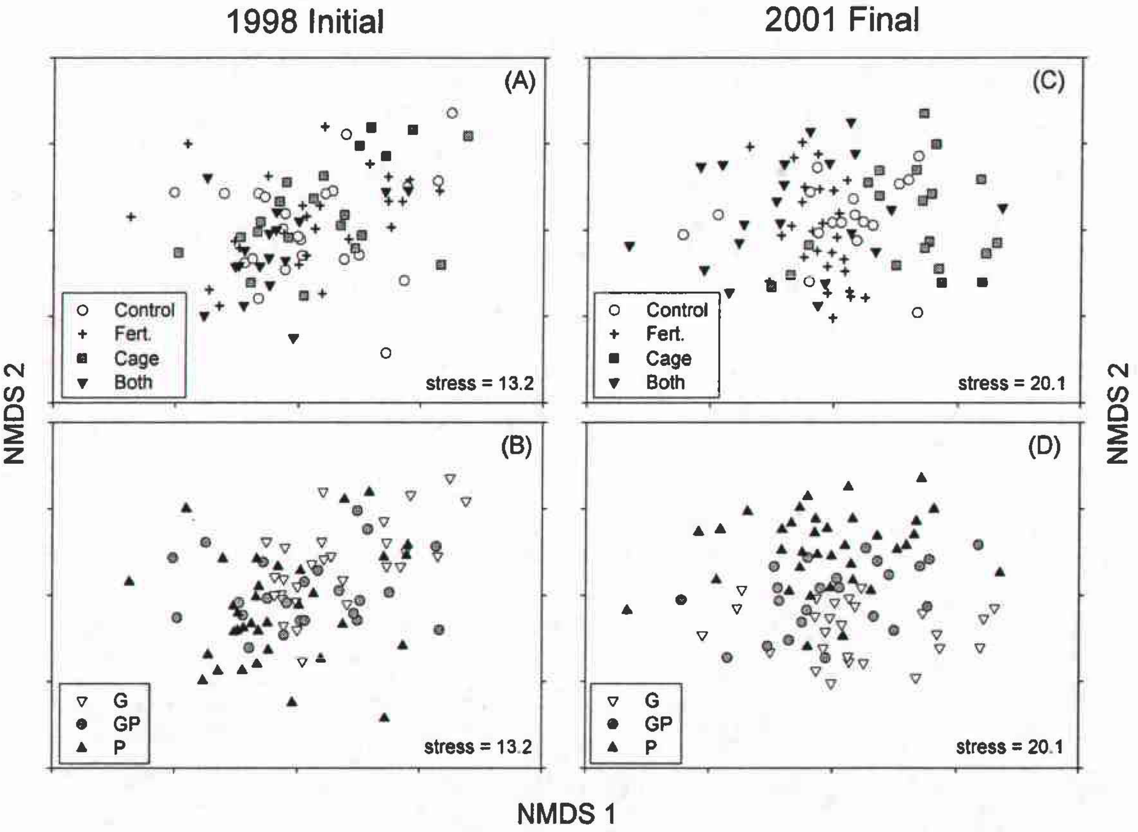

Figure 5.6. Nonmetric multidimensional scaling ordinations of total arthropod communities for initial (A-B) and final (C-D) arthropod collections. For each assemblage, paired diagrams are shown for all individual trees that were subsamples within plots. Experimental treatments are coded on the top row (A, C), and foliar morphology codes for the same data are presented on the bottom row (B, D), where G = glabrous, P = pubescent, and GP = intermediate. Stress values are shown.

Discussion

Top-down and bottom-up constraints and indices of diversity

Previous studies have shown increased arthropod abundance across all trophic levels on fertilized *Metrosideros polymorpha* (Gruner in press-b, Chapter 6). This study demonstrated that fertilization also increased the species load of herbivores, enemies, and all arthropods in aggregate (Figure 5.2, Table 5.1). However, neither the individual-based rarefaction estimates of species richness, nor the relative diversity index (Fisher's α) increased with fertilization for any trophic group (Figure 5.2, Table 5.1). In general, qualitative patterns revealed by Fisher's α and by individual-based rarefaction of species richness did not differ (Table 5.1). This suggests that Fisher's α effectively controls for relative abundance as an index to sample diversity (Magurran 1988), and that increases in species load were driven by increases in densities of individuals. Numerous studies have examined the diversity response of herbivorous or other arthropods to fertilization, but generalizations have been elusive, and may depend on the choice of diversity measures (e.g., Hurd and Wolf 1974, Kirchner 1977, Kajak 1981, Vince et al. 1981, Prestidge 1982, Strauss 1987, Sedlacek et al. 1988, Siemann 1998, Haddad et al. 2000). Several studies observed higher abundance of sap-sucking Auchenorryncha and other herbivorous groups, but evenness and diversity decreased as a small number of species emerged as dominant (Prestidge 1982, Sedlacek et al. 1988, Haddad et al. 2000).

This observation may be relevant for detritivorous species on *M. polymorpha.* Although detritivore species load did not change with fertilization (Figure 5.2C: Table 5.1), richness and relative diversity decreased, and the accumulation of species as a function of overall abundance was less steep than in unfertilized treatments (Figure 5.4).

In particular, one collembolan (*Salina celebensis*) responded numerically to fertilization, although it was so ubiquitous that it did not translate to a compositional change (Table 5.2, see also Chapter 6). Although autecological data for this species is lacking, the congeneric species *Salina banksi* MacGillivray was also an ecological dominant in tree canopies of humid Mexican forests, as it was 30 times more abundant on average than other collembolans (Palacios-Vargas and Castaño-Meneses 2003).

A similar result was evident for carnivores, but as a consequence of the top-down manipulation. The exclusion of insectivorous birds did not directly alter species load of any trophic group (Figures 5.2); however, carnivore evenness and relative diversity decreased with the increased dominance of a single outbreaking species released from bird predation, the introduced theridiid spider *Achaearanea* cf. *riparia* (Gruner in press-c). Within trophic levels, dominant species depressed the rarefied species richness because they reduced the probability of finding other species in random draws of fixed sample size (Figures 5.2D, 5.2H). Effects of birds on diversity were not broadly evident because they do not prey on many of the arthropod species in this community (Baldwin 1953, Ralph et al. unpublished data, Peck et al. unpublished data).

No similar depression of richness or proportional diversity of herbivores was observed, even though fertilization also increased the species load (Figure 5.2E-F, Table 5.1). Equitability of herbivores was greater than that observed for either detritivores or carnivores, and rank abundance distributions were consistent with the broken-stick model for three of four treatment combinations (Figure 5.3). As herbivore abundance increased with fertilization, additional rare species were able to colonize or persist, but without altering equitability patterns within treatments (Figure 5.3, Pielou's J' overall mean ± SE:

0.83 ± 0.02, all F-tests n.s.). These herbivorous species are known to be *Metrosideros* feeders, so it is unlikely they are transients feeding on other plant resources in the community (Gruner in press-a). Thus, increased species load in this case is consistent with the hypothesis that productivity increases diversity by allowing rare species to exist in larger local populations ("consumer rarity hypothesis" *sensu* Siemann 1998, "more individuals hypothesis" *sensu* Srivastava and Lawton 1998, see also Chapter 6).

Foliar pubescence as another bottom-up constraint

Fertilization or nitrogen deposition often alters plant diversity and species composition (Tilman 1993, Naeem et al. 1996, Waide et al. 1999, Stevens et al. 2004), but many arthropod community studies have been unable to disentangle plant productivity from diversity (but see Siemann 1998). In this study, I concentrated on the fauna of a single dominant tree species to control for changes in plant community composition that occur with fertilization. Intraspecific variation in leaf traits, such as foliar pubescence or chemistry, however, can exercise strong bottom-up control on arthropod species composition even while host species is held constant (Fritz and Price 1988, Dickson and Whitham 1996, Stiling and Rossi 1996, Cronin and Abrahamson 2001). *Metrosideros polymorpha* is highly variable in foliar morphology along altitudinal, edaphic, and successional gradients, and multiple pubescence classes are found even within populations (Corn and Hiesey 1973, Stemmermann 1983, James et al. 2004). Evidence indicates that fertilization does not alter foliar pubescence level in *Metrosideros polymorpha* over the short-term, and these factors have independent effects on arthropod abundance and diversity, but interact to create emergent species composition (Chapter 6).

Both herbivores and detritivores may be affected as much by leaf morphology as by fertilization treatments (Figure 5.6; Table 5.3; Chapter 6). The first axis of tree-level NMDS loosely separated fertilization and cage treatment combinations (Figure 5.6C), but the second axis placed communities from glabrous (G) and pubescent (P) forms at opposite ends, with communities on intermediate (GP) phenotypes bridging those clusters (Figure 5.6D). Intriguingly, principal components analysis of *M. polymorpha* leaf morphological traits showed analogous clustering, with described varieties *glaberrima* (corresponds to G) and *polymorpha* (corresponds to P) at opposite ends of the ordination, and *incana* (corresponds to GP) overlapping in between (James et al. 2004).

Although both Collembola and Homoptera increased in density with fertilization (Collembola: $F_{1,7} = 12.94$, $P = 0.0084$; Homoptera: $F_{1,7} = 23.30$, $P < 0.0001$), both were also more abundant on trees with less pubescent leaves (Collembola: $F_{2,48} = 41.85$, $P = 0.0002$; Homoptera: $F_{2,48} = 16.43$, $P < 0.0001$). Concentrations of phenolic compounds differ across pubescence levels (Forkner and Gruner unpublished data), and glabrous leaves may decompose more rapidly (Austin and Vitousek 2000). Parallel studies showed higher herbivore attack rates on glabrous plants, especially by the stem galler *Trioza hawaiiensis* Crawford and bud-mining caterpillars (*Carposina* spp.: Carposinidae; Gruner unpublished data). Stem galls and bud mines often kill apical tissues in place, leaving both a higher amount of dead tissue as a resource and more heterogeneous habitats with the excavated galleries present. However, other taxonomic orders were more dense on pubescent trees (Araneae: $F_{2,48} = 3.46$, $P = 0.038$; Heteroptera: $F_{2,48} = 3.89$, $P = 0.026$; Psocoptera: $F_{2,48} = 25.37$, $P < 0.0001$).

These countervailing results for different taxonomic groups may have diluted the responses from aggregate indices of richness and diversity, which will not account for species turnover. Local dynamic equilibria may hold the number of species relatively constant as a function of basic energetic controls or physical constraints, while species identities change (Whittaker et al. 2001). A well documented top-down mechanism demonstrates that predator-resistant prey within a trophic level may compensate for decreased abundance of less resistant prey (Leibold 1989, Schmitz 1994, Leibold et al. 1997, Chase et al. 2000). Similarly, different arthropod species on one plant species may show positive, negative or no response to foliar pubescence qualities, leading to weak overall effects at the guild or trophic level (Hare and Elle 2002).

Conclusions

Individual-based rarefaction and sample-based accumulation curves in this study did not reach asymptotes (Figure 5.4, Gruner unpublished data). It is a hallmark of insect diversity studies, especially in the tropics, that rare species are commonplace, and that sampling is rarely complete (Fisher et al. 1943, Stork et al. 1997, Basset and Novotný 1999, Basset et al. 2003, but see Longino et al. 2002). In tropical insect communities, regional colonization and metacommunity dynamics may dictate diversity more than biotic interactions (Stirling and Wilsey 2001). Large percentages of migrant species can obscure real biotic interactions of core species within community samples (Magurran and Henderson 2003). However, the removal of singletons had no effect on treatment differences in composition in this study; instead, compositional changes from the top-down and the bottom-up were each driven primarily by abundant species.

The results of this experiment indicate that local mechanisms can explain local diversity in *M. polymorpha* arthropods. Both plant resources and insectivorous birds influenced the diversity and composition of arthropod communities. Fertilization effects were more prevalent across trophic levels, but species additions with higher productivity were mediated by increased overall abundance. The effects of birds on diversity were contingent on one introduced spider species, further highlighting the importance of species traits in creating community pattern (Leibold 1996). Moreover, ordination demonstrated that intraspecific variation in foliar morphology poses an additional bottom-up constraint on arthropod species composition; the role of this heterogeneity in promoting arthropod species coexistence in metacommunities deserves further exploration.

CHAPTER 6

THE EFFECTS OF FOLIAR PUBESCENCE AND NUTRIENT ENRICHMENT ON ARTHROPOD COMMUNITIES OF *METROSIDEROS POLYMORPHA* (MYRTACEAE)

Abstract

Nutrient resource availability and host foliar pubescence both influence arthropod food webs, but multifactor studies are needed to understand their relative and interactive importance. I utilized ongoing experimental fertilizations on a nutrient-limited, recent basaltic lava flow where pubescent to glabrous morphologies of *Metrosideros polymorpha* (Myrtaceae) are sympatric in comparable frequencies. I sampled arthropods by clipping foliage from trees of glabrous, pubescent, and intermediate classes on fertilized and unfertilized plots. Fertilization decreased leaf mass per area but did not change the relative mass of pubescence within leaf morphological classes. Fertilization increased the density and species load of diverse arthropod orders and all trophic levels, and increased the biomass of Collembola and Homoptera. Herbivore relative diversity (Shannon H') also increased with fertilization, but detritivore diversity declined due to increasing dominance of *Salina celebensis* (Collembola). Detritivore density, driven again by *S. celebensis*, increased with decreasing leaf pubescence, but Heteroptera and Acari were most abundant on the intermediate pubescence class, and Psocoptera density and biomass increased with increasing pubescence. Trophic level species load did not change with leaf morphological class, but relative diversity of all arthropods and of detritivores generally increased with increasing pubescence. Both resource availability

and leaf pubescence affected *Metrosideros* arthropod communities. Pubescence class did not interact with fertilization treatments in effects on arthropod density, biomass, or diversity, but these factors interacted to create emergent patterns of species composition.

Introduction

The search for factors that regulate community level properties has identified a suite of bottom-up forces that constrain relative abundance and diversity within food webs. The supply of limited nutrient resources is of fundamental importance to plant productivity and to the arthropod populations and communities on plants (White 1984, Waring and Cobb 1992, Kytö et al. 1996). Ambient plant nitrogen levels are low in comparison to consumer requirements (Mattson 1980, White 1984, Hartley and Crawley 1997), and a wide variety of herbivore taxa feed preferentially on nitrogen enriched tissues (Ball et al. 2000, Nakamura et al. 2003, Albrectsen et al. 2004). The abundance, biomass and diversity of herbivores or detritivores and their predators often increase in fertilization experiments in natural systems (e.g., Levine et al. 1998, Scheu and Schaeffer 1998, Siemann 1998, Haddad et al. 2000, Ritchie 2000, Halaj and Wise 2002).

Bottom-up effects also can arise from variation in resource attributes other than simply the supply of nutrients, and these may interact with nutrient levels to produce emergent impacts on insect communities. For example, the response of arthropods to fertization may be mediated by plant architecture, and increased resources can alter plant physical structure, habitat complexity or species composition (Siemann 1998, Haddad et al. 2000, Orians and Jones 2001, Denno et al. 2002, Langellotto and Denno 2004). Changes in abiotic factors, such as shading, may alter host plant morphology in ways that influence herbivore attack and the success of their enemies (Craig 1994, Moon et al.

2000). Additional sources of bottom-up heterogeneity may include soil salinity (Moon and Stiling 2002a), water supply (Huberty and Denno 2004), or intraspecific variation in host chemistry (Forkner et al. 2004) or physical morphology (Moon et al. 2000, Hare and Elle 2002).

Leaf pubescence—the presence of trichomes—may act as a chemical or mechanical defense to herbivores (Levin 1973, Juniper and Southwood 1986, Gruenhagen and Perring 1999). Trichomes can secrete secondary chemicals (Stipanovic 1983), or they may be composed of inert lignins and cellulose that are of little or inhibit digestion (Levin 1973, Juniper and Southwood 1986). Trichomes can prevent herbivores from coming into contact with a leaf without first removing or consuming the pubescence, or may be directly harmful or fatal to insects (Pillemer and Tingey 1976, Eisner et al. 1998). Mattson et al. (1988) predicted that herbivores can evolve to escape pubescence by reducing their "intimacy of association:" by avoidance or reduction of contact time with pubescence, or by growing larger relative to hair size or density. Numerous studies have shown decreased herbivory or arthropod abundance on pubescent phenotypes relative to glabrous forms (Levin 1973, Turnipseed 1977, Schoener 1987, 1988, Gruenhagen and Perring 1999, Andres and Connor 2003, but see van Dam and Hare 1998, Roda et al. 2001). However, few studies have investigated how resource availability influences plant trichomes and the effects of pubescence on arthropod populations or communities (Wellso and Hoxie 1982, Wilkens et al. 1996, Roy et al. 1999).

Metrosideros polymorpha Gaudichaud-Beaupré (Myrtaceae) is a morphologically variable tree dominant in numerous ecosystem types throughout the Hawaiian Islands.

There are eight described varieties of *M. polymorpha*, characterized by growth form, leaf size and shape and the density of trichomes on the leaves and stems (Dawson and Stemmerman 1999). The distribution of morphological types generally follows broad abiotic gradients that may be associated with nutrient resource supply, with thick-leaved pubescent forms dominant at higher elevation and on young volcanic substrates (Corn and Hiesey 1973, Kitayama and Mueller-Dombois 1992, Geeske et al. 1994). However, multiple phenotypes, ranging from completely glabrous to densely tomentose forms, often coexist in sympatric populations on young basalt lava flows at intermediate elevations (Stemmermann 1983). A diversity of arthropods attack or process the litter of *Metrosideros polymorpha* (Gruner in press-a). Many of the herbivorous species attack buds before leaf hairs are well developed and avoid contact with pubescence through endophagous habits. Nevertheless, pubescent forms of *Metrosideros polymorpha* appear more resistant to these herbivores (Lee 1981, Gruner unpublished data).

I sought to disentangle the community-wide responses of arthropods to nutrient resources and foliar pubescence of *Metrosideros polymorpha.* A multifactor approach allowed an assessment of the lability of foliar morphology in response to variation in resource supply, and of the separate and combined impacts of leaf morphology and resource levels on the arthropod food web. I addressed the following questions: First, do changes in nutrient resources alter leaf thickness, the quantity of pubescence on leaves, or both? Previous studies of *M. polymorpha* suggest that, although leaf thickness is responsive to nutrient levels on young soils (Vitousek 1998), leaf pubescence may be a fixed trait within trees (Cordell et al. 1998). Second, what are the separate and interactive effects of fertilization and leaf pubescence on arthropod communities? I hypothesized positive effects of fertilization and negative effects of increasing pubescence on arthropod density, diversity and composition.

Methods

Study system and experimental design

This study was situated at 1280 m elevation on an 1881 pāhoehoe lava flow in the Upper Waiākea Forest Reserve, windward slope of Mauna Loa, Island of Hawai‘i (19.6642°N, 155.2836°W). As in many other native ecosystems throughout the archipelago (Dawson and Stemmerman 1999), *Metrosideros polymorpha* Gaudichaud-Beaupré (Myrtaceae) dominates this early-successional wet forest (~4000 mm mean annual precipitation). Ferns (e.g., *Dicranopteris linearis* [Burm.] Underw. [Gleicheniaceae]), sedges (e.g., *Machaerina angustifolia* [Gaud.] T. Koyama [Cyperaeae]), and low shrubs (e.g., *Coprosma ernodeoides* A. Gray [Rubiaceae]) are also present (Gruner in press-b).

This experiment took place as part of a larger study investigating the relative importance of birds and resources on the *Metrosideros* arthropod community (Gruner in press-b). In August of 1998, 32 20 x 20 m plots were assigned fertilization and avian predator exclusion treatments as crossed factors in a 2 x 2 randomized block design; the caged treatments were ignored in the present study. Sixteen plots were fertilized twice yearly from September 1998 to October 2000 with a broad spectrum of nutrients (Gruner in press-b). Buffer strips, 10 m wide at minimum, separated all plots. Within each of 8 blocks, there were 2 replicates of the fertilized treatment and 2 of the unfertilized control. Leaf morphology was investigated within each plot in a repeated-measures design.

Pubescence and LMA

To characterize *Metrosideros* leaves, I devised an operational classification scale for hairiness. Other classification schemes exist, but they may be less repeatable among investigators and sites (Kitayama et al. 1997). Trees were assigned to one of three categories: glabrous on both adaxial and abaxial surfaces (G); thickly pubescent on stems and both leaf surfaces (P); and pubescence intermediate (GP), found on abaxial, adaxial or both surfaces, but where present, it could be rubbed off easily without damage to the leaf lamina. Although all *M. polymorpha* seedlings begin with glabrous leaves, they attain their final morphological state within two years (S. Cordell, personal communication). I did not observe the characteristics of multiple classes on any single tree or any changes over the duration of the experiment.

Fertilization on nearby young basaltic substrates decreased leaf mass per area (LMA) of *M. polymorpha*, although LMA typically did not change in response to fertilization on older soils in the Hawaiian Islands (Vitousek 1998). LMA also increases with elevation (Geeske et al. 1994, Raich et al. 1997, Melcher et al. 2000), concomitant with increasing pubescence and with decreasing leaf area. LMA is related to leaf toughness (Wright and Cannon 2001), which is among the most important deterrents to leaf herbivory (Coley and Barone 1996).

I evaluated the contribution of trichomes to LMA, and how this contribution might change with fertilization and among leaf morphotypes. Within each plot, two whorls of the youngest fully expanded leaves were taken from two trees of the pubescent and intermediate morphological classes (P and GP). Two leaves were selected randomly from each of the whorls, for a total of 8 leaves from each morphology/plot combination.

Mass of leaf pubescence was determined in a procedure similar to previous work on *Metrosideros polymorpha* (Geeske et al. 1994, Cordell et al. 1998). Instead of using opposite leaves as paired samples, however, leaves were shaved carefully with a razor on one side of the midrib of each leaf. A cork hole borer (disc area = 0.70 cm^2) was used to sample tissue from each side. Leaf plugs were dried to constant mass at 65 °C and weighed to determine leaf mass and LMA (g/m^2). The difference between scraped and unscraped mass from the same leaf was considered the mass of the pubescence.

Arthropod sampling

Arthropods were collected by clipping branches and foliage into white plastic bags (Fretz 2000, Johnson 2000, Gruner in press-b). I clipped the terminal branchlets (~50 cm) of twigs and foliage and avoided reproductive structures (seeds, flowers). Extreme care was exercised in avoiding disturbance of branches and arthropods before branches were quickly bagged and then clipped. Many arthropod taxa are reluctant to disperse from foliage even when disturbed (Gruner personal observation), and I rarely observed arthropods escape from bags in the field.

On each sampling event, I collected 12 samples from a single block: one from G, GP and P morphotypes on each of four plots. Blocks were randomly selected and sampled monthly from July to December of 1999, in May and June 2000. Blocks therefore represent both temporal and spatial variation in arthropod communities. I clipped from 10-20 haphazardly selected trees in the morning hours for each sample, with the goal of sampling branchlets from as many different trees as possible while obtaining a roughly equivalent sample size (200 to 300 g dry foliage mass).

Foliage was transported it to the laboratory at Hawai'i Volcanoes National Park for immediate processing. Foliage was shaken and beaten onto a white cloth and arthropods were collected with an aspirator and stored in 70% ethanol. I continued shaking branches and sifted the detrital remainder until no additional arthropods were observed. Foliage was separated from woody material, oven-dried to constant mass, and both components weighed to mg precision. Arthropod abundance and biomass are reported per 100 g dry foliage mass ("load, " *sensu* Root 1973).

Analysis of arthropod samples

All arthropods collected were recorded, measured for length to the nearest millimeter, and identified to species or assigned to morphospecies based on morphological evidence and advice of taxonomic experts. Regressions of body length to dry mass were used to estimate biomass (Gruner 2003). Specimens data were managed using the biodiversity collections database software, *Biota* (Colwell 1997a). Bulk material and voucher specimens were deposited at the B.P. Bishop Museum, Honolulu.

Arthropods were assigned to one of four trophic levels—carnivores, detritivores, herbivores and tourists—based on personal observation, literature review, and communication with systematists (Figure 6.1). Carnivores included various predatory arthropods (e.g., Araneae, some Heteroptera and Coleoptera) and hymenopteran parasitoids (Ichneumonidae, Bethyliidae and Chalcidoidea); detritivores composed saprophagous arthropods and grazers of litter, fungi and microbes (e.g., Psocoptera, Isopoda, Collembola, some Coleoptera); and herbivores consisted of sap-feeders (Heteroptera and Homoptera), gall-forming psyllids (Homoptera: Triozidae, mostly free living adults), and foliage chewing Lepidoptera. Tourists included species known to be incidental or non-feeding on *Metrosideros* (e.g., adult moths), or with unknown or highly omnivorous feeding habits. Over one hundred arthropod species were recorded from *M. polymorpha* at the site (Chapter 5, Appendix B).

Several indices were used to represent species diversity. To account for differences in the sizes of samples, species load (analogous to species density) was calculated by dividing species number by the mass of the foliage in a given sample. Fisher's α was used to further control for total arthropod abundance in a sample; this measure has high discriminant ability and robustness even with small samples sizes (Magurran 1988, Rosenzweig 1995), and in a related study of *M. polymorpha* arthropod communities, Fisher's α correlated well with expected species richness calculated by rarefaction. Shannon diversity index (H') is presented to measure evenness rather than richness *per se* (Magurran 1988). Fisher's α and the Shannon H' were computed for individual collections using PRIMER software (Clarke 2001).

Statistical analyses

The design of this study (ignoring the bird exclusion treatments) was equivalent to a repeated-measures design. The block term accounted for temporal and spatial environmental heterogeneity. Fertilization (fixed) and block (random) and their interaction were between-subject effects; the random subject factor, plots, was nested within these main effects; and morphology and all its two-way interactions were within-subject effects. The three-way interaction (fert. X morph. X block) was dropped from the model after determining it was uniformly nonsignificant. I used type III sums of squares analyses in SAS PROC MIXED (SAS 2001), with degrees of freedom for error mean squares of random terms estimated by the Satterthwaite approximation. I used the Tukey-

Kramer test for post hoc multiple comparisons of fertilization and morphology main effects, adjusted for type I error (joint $\alpha = 0.05$).

Natural log transformation was sufficient to meet assumptions of normality and homoscedasticity for all arthropod density and biomass variables, but was not necessary for species density or relative diversity. Separate models were run for arthropod variables broken into trophic levels: carnivores, herbivores, and detritivores. Density and biomass of the six most abundant taxonomic orders (Acari, Araneae, Collembola, Heteroptera, Homoptera, and Psocoptera) were also analyzed, and the orders not sufficiently abundant or widespread for separate analyses were lumped into a single variable (Coleoptera, Diptera, Hymenoptera, Isopoda, Lepidoptera, Neuroptera, and Thysanoptera). Results for pubescence mass were also transformed with the natural log, although LMA values were not. Untransformed means (±1 SE) are reported.

I used nonparametric multivariate analysis of variance (NPMANOVA; Anderson 2001, McArdle and Anderson 2001) and canonical analysis of principal coordinates (CAP; Anderson and Willis 2003) to analyze the effects of fertilization and leaf morphology on arthropod community composition. Both methods are based on a matrix of ecological distances (dissimilarity) between samples, and provide permutation tests of factor effects. Prior to calculating the distance matrices, abundances were log (X+1) transformed to reduce the influence of a few highly abundant but small-bodied species. Transformed abundances were then relativized by dividing by their sum for each sample, to reduce the effect of differences among samples in total abundance and therefore to emphasize differences in relative proportions of taxa. Euclidean distances ("distance between species profiles", Legendre and Gallagher 2001) then were calculated; qualitatively similar results were obtained using Bray-Curtis distances.

NPMANOVA in effect partitions the distances in the matrix into parts attributable to the terms in a general linear model, generating pseudo-F statistics for each term; these are tested by comparing them to the distributions of values produced when the data are randomly permuted according to the null hypothesis appropriate for the given term. Because of the multifactor design of this study, the DISTLM (Anderson 2000) implementation of NPMANOVA was used. For each test I used 999 permutations of the raw data, in units defined by the "error" term of the corresponding pseudo-F ratio. Analysis were done both with and without *Salina celebensis* (Collembola), which alone accounted for almost 70% of individuals.

CAP is a two-step analysis. First, metric multidimensional scaling (principal coordinates analysis, PCO) is used to reduce the dimensionality of the data; with the Euclidean distances I used, this is equivalent to principal components analysis (Anderson and Willis 2003) of the relativized, transformed abundances. The second step in CAP is a generalized discriminant analysis of a subset of the PCO axes in relation to a design factor. The number of PCO axes to use in this step was determined to minimize the misclassification rate in a "leave-one-out" cross-validation procedure (Anderson and Willis 2003). The CAP software (Anderson 2003) only allows a single design factor, so I combined leaf morphology and fertilizer treatments into a single factor with 6 levels, ignoring blocks. I tested the null hypothesis of no difference among these "treatments" using the trace statistic of the discriminant analysis (sum of squared canonical

Table 6.1. Results of general linear models comparing mass of pubescent and intermediate morphology leaves. Scraped and unscraped categories test leaf mass per area (g/m^2) for scraped and unmanipulated leaves; the pubescence category analyzes mass of trichomes scraped from leaves. Italicized sources represent random terms. Boldface *P*-values represent statistical significance at $\alpha = 0.05$.

		unscraped			scraped					
					leaf			pubescence		
Source	df[a]	MS	F	*P*	MS	F	*P*	MS	F	*P*
Fert. [F]	1,7	184.442	225.86	**<0.001**	175.315	164.01	**<0.001**	0.068	0.42	0.535
Block [B]	7,[b]	0.800	0.41	0.840	1.154	-2.54	--	0.179	0.52	0.789
F X B	7,16	0.817	0.44	0.864	1.069	0.80	0.602	0.161	0.92	0.516
Plot (F B)	16,23	1.866	0.80	0.671	1.344	0.50	0.919	0.174	0.95	0.533
Morph [M]	1,7	74.552	21.60	**0.002**	2.227	1.95	0.205	30.157	82.74	**<0.001**
M X F	1,23	1.020	0.44	0.515	0.523	0.20	0.662	0.098	0.53	0.472
M X B	7,23	3.451	1.48	0.223	1.141	0.43	0.874	0.365	1.98	0.102
Error		2.329			2.664			0.184		

[a] Numerator, denominator degrees of freedom

[b] Denominator degrees of freedom estimated by Satterthwaite approximation (unscraped = 1.85, scraped leaf = 0.314, pubescence = 4.83).

correlations), obtaining a *P*-value from 9999 random permutations of the data. To interpret differences among the 6 "treatments" in the CAP in terms of morphology and fertilization, I analyzed the plot scores on the CAP axes by GLMs as above.

Results

Foliar characteristics

Fertilization strongly decreased LMA in unscraped leaf discs, and LMA also was greater in pubescent (P) leaves than intermediate (GP) forms (Table 6.1). Leaf scraping allowed decomposition of these two effects into their components: mass of leaf hairs was responsible for the significant morphology effect, and fertilization decreased mass per area of leaf tissue exclusive of trichomes. Fertilization did not affect pubescence, and over the 33 mos of the study none of the 88 marked trees changed morphology.

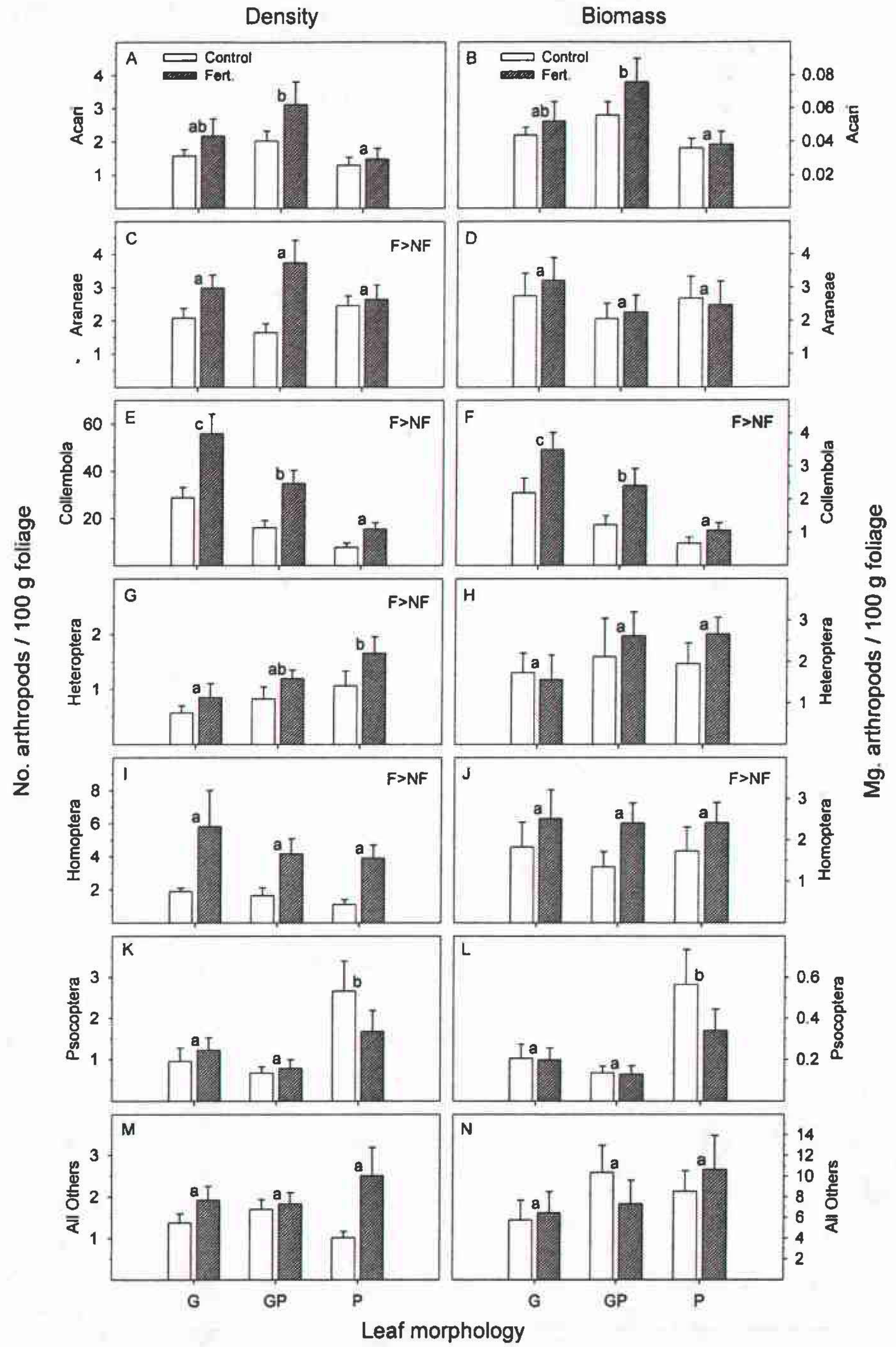

Figure 6.1. Density and biomass of arthropod orders on glabrous (G), pubescent (P) and intermediate (GP) foliar morphologies in fertilized (filled bars) and unfertilized (unfilled) plots. Bars represent treatment means ± 1 SE. The "all other" category combines less abundant orders: Coleoptera, Diptera, Hymenoptera, Isopoda, Lepidoptera, Neuroptera, and Thysanoptera. Lowercase letters denote significant differences in the leaf morphology main effect, and inset notations (F = fert., NF = not fert.) indicate significant differences in the fertilization effect, both tested by the Tukey-Kramer test adjusted for type I error (joint $\alpha = 0.05$).

Table 6.2. F-values from general linear models of a) density, b) biomass loads of taxonomic orders. The "all other" category combines less abundant orders: Coleoptera, Diptera, Hymenoptera, Isopoda, Lepidoptera, Neuroptera, and Thysanoptera. Arthropod density and biomass were natural log transformed prior to analysis. Italicized sources represent random terms. Significance levels of F-values are indicated when significant (* $0.05 > P > 0.01$; ** $0.01 > P > 0.001$; *** $0.001 > P$).

Source	df[a]	Acari	Araneae	Collembola	Heteroptera	Homoptera	Psocoptera	Others
a) Density Load								
Fertilization [F]	1,7	0.58	13.15**	44.63***	5.64*	14.05**	0.71	3.86
Block [B]	7,[b]	0.96	3.00	16.49**	1.26	3.33	5.42	4.03*
F X B	7,16	2.85*	0.83	0.95	0.79	4.49**	0.49	1.47
Plot(F B)	16,46	1.32	0.83	1.82	2.07*	0.86	1.13	1.25
Morph [M]	2,14	3.79*	0.03	65.50***	3.84*	2.01	7.18**	0.49
M X F	2,46	0.36	2.73	0.23	0.49	1.00	2.54	1.94
M X B	14,46	1.92*	0.82	1.08	1.83	1.31	1.22	1.67
b) Biomass Load								
Fertilization [F]	1,7	0.72	0.06	74.09***	1.28	6.73*	1.38	0.85
Block [B]	7,[b]	1.18	2.41	27.15***	1.79	1.91	2.37	7.79**
F X B	7,16	3.31*	0.53	0.27	0.65	1.13	1.27	1.53
Plot(F B)	16,46	1.32	2.03*	3.20**	2.28*	0.85	1.06	0.75
Morph [M]	2,14	4.66*	0.91	47.34***	1.86	0.01	6.21**	1.19
M X F	2,46	0.88	0.34	2.10	2.09	0.12	1.44	0.70
M X B	14,46	1.97*	0.88	1.96	1.79	0.95	1.96*	1.46

a Numerator, denominator degrees of freedom.
b Denominator degrees of freedom estimated by Satterthwaite approximation.

Average foliage mass clipped in arthropod collections was similar among morphologies (overall mean, 244.1 g, ± 4.4 SE; $F_{2,14} = 1.59$, $P = 0.240$), however, the biomass of foliage collected from unfertilized plots was slightly higher than from fertilized plots (fert.: 234.6 g ± 6.0 SE, unfert.: 256.0 g ± 6.1; $F_{1,7} = 10.60$, $P = 0.014$). This did not have marked effects on density or biomass results, as absolute abundance and biomass showed similar patterns as the loads standardized to foliage biomass of collections. To maintain consistency with other studies (Fretz 2000, Gruner in press-b), results based on loads are reported.

Abundance and biomass

The effects of fertilization and leaf morphology on density and biomass differed among arthropod orders, but in no case was there statistically significant interaction between them (Figure 6.1; Table 6.2). Density and biomass of Acari were higher on intermediate morphologies (Figure 6.1A-B) though these effects varied among blocks. Spiders were more abundant on fertilized plots, irrespective of leaf form, but did not differ in biomass (Figure 6.1C-D). Collembola density and biomass, dominated by a single species (*Salina celebensis* Schaeffer > 99% of all Collembola individuals), increased strongly with fertilization, decreased with increasing leaf pubescence, and varied across blocks (Figure 6.1E-F). Fertilization increased the density but not biomass of both Heteroptera and Homoptera, and Heteroptera were more abundant on increasingly pubescent foliage (Figure 6.1G-J); Heteroptera density also showed a significant fertilization X block interaction. Psocoptera density and biomass did not respond to fertilization, but both were significantly elevated on pubescent forms relative to the glabrous and intermediate morphologies (Figure 6.1K-L). The aggregate group of seven less abundant orders did not change with any treatment (Figure 6.1M-N).

Fertilization increased the density of all trophic levels on *Metrosideros polymorpha* (Table 6.3, Figure 6.2). Detritivores, dominated by Collembola (Figure 6.1), were the most abundant trophic group (Figure 6.2C-D). Highly significant effects of fertilization, leaf morphology, and blocks on detritivore density drove the same suite of

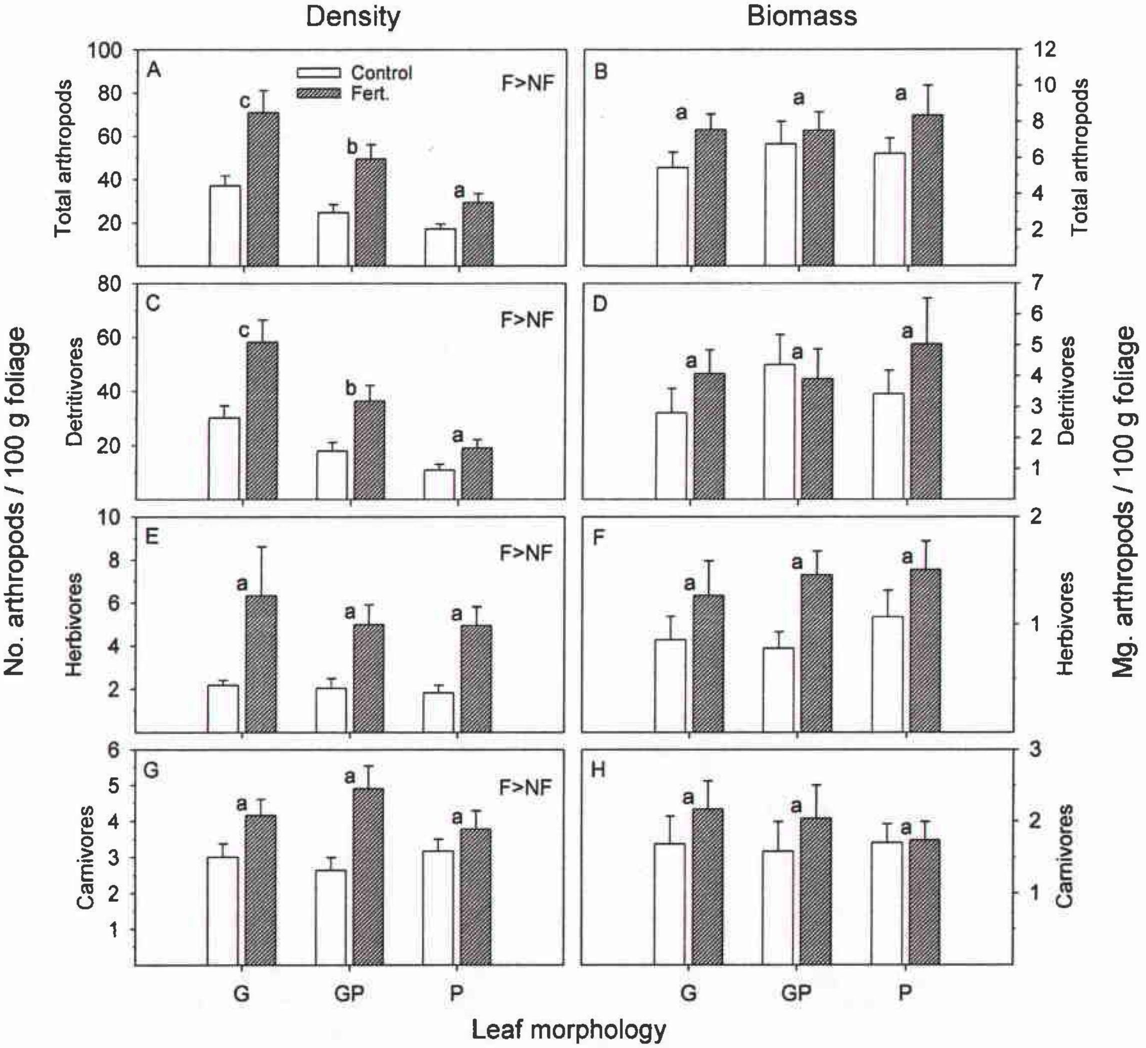

Figure 6.2. Arthropod trophic level density and biomass on glabrous (G), pubescent (P) and intermediate (GP) foliar morphologies in fertilized (filled bars) and unfertilized (unfilled) plots. Bars represent treatment means ± 1 SE. Note the differing scales of arthropod variables, measured as a function of dry foliage biomass, for each trophic level (all arthropods [A, B], detritivores [C, D], herbivores [E, F], carnivores [G, H]). Lowercase letters denote significant differences in the leaf morphology main effect, and inset notations (F = fert., NF = not fert.) indicate significant differences in the fertilization effect, both tested by the Tukey-Kramer test adjusted for type I error (joint $\alpha = 0.05$).

Table 6.3. Results of general linear models for arthropod trophic a) density, b) biomass. Arthropod density and biomass were natural log transformed prior to analysis. Italicized sources represent random terms. Boldface *P*-values are significant at $\alpha = 0.05$.

Source	df[a]	All		Carnivores		Herbivores		Detritivores	
		F	*P*	F	*P*	F	*P*	F	*P*
a) Density Load									
Fertilization [F]	1,7	52.80	**<0.001**	12.12	**0.010**	13.16	**0.008**	22.96	**0.002**
Block [B]	7,[b]	13.64	**<0.001**	1.47	0.330	2.57	0.110	11.30	**0.005**
F X B	7,16	1.15	0.384	1.59	0.208	4.98	**0.004**	1.79	0.158
Plot(F B)	16,46	1.58	0.113	0.67	0.807	0.62	0.855	1.26	0.265
Morph [M]	2,14	37.63	**<0.001**	0.02	0.982	0.18	0.833	40.44	**<0.001**
M X F	2,46	1.19	0.313	2.04	0.141	1.23	0.302	0.73	0.488
M X B	14,46	1.32	0.235	1.25	0.277	1.28	0.255	0.88	0.580
b) Biomass Load									
Fertilization [F]	1,7	3.22	0.116	0.60	0.462	2.73	0.143	1.08	0.333
Block [B]	7,[b]	3.47	0.083	2.06	0.191	0.63	0.722	6.30	**0.011**
F X B	7,16	2.69	**0.048**	0.33	0.928	4.67	**0.005**	3.79	**0.013**
Plot(F B)	16,46	0.75	0.727	2.00	**0.034**	0.37	0.984	0.58	0.883
Morph [M]	2,14	0.02	0.981	0.40	0.679	0.80	0.470	0.15	0.864
M X F	2,46	0.15	0.859	0.28	0.756	0.35	0.709	1.24	0.298
M X B	14,46	0.89	0.570	1.70	0.088	1.08	0.403	1.29	0.248

a Numerator, denominator degrees of freedom.

b Denominator degrees of freedom estimated by Satterthwaite approximation.

results for all arthropods in aggregate. Fertilization effects on herbivore density varied significantly across blocks.

There were no significant effects of morphology or fertilization on trophic level biomass loads (Figure 6.2), except for significant fertilization X block interactions for herbivore, detritivore and total arthropod biomass (Table 6.3). Detritivore biomass varied across blocks, and the plot term was significant for carnivore biomass.

Species diversity

Fertilization increased species load (number of species per unit foliage) for all trophic levels (Figure 6.3, Table 6.4). This fertilization effect also varied significantly

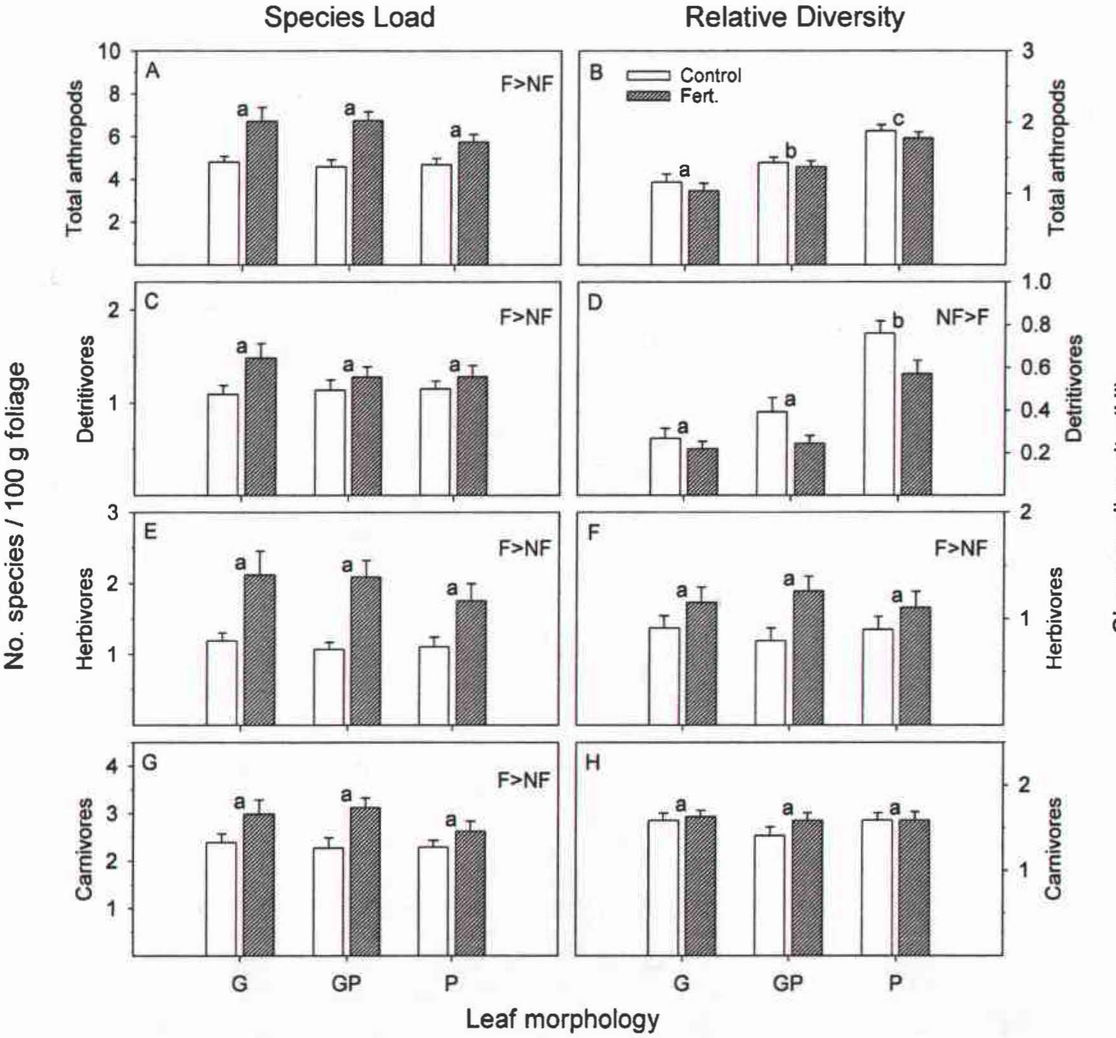

Figure 6.3. Arthropod trophic level species load (richness / 100 g foliage) and relative diversity (Shannon H') on glabrous (G), pubescent (P) and intermediate (GP) foliar morphologies in fertilized (filled bars) and unfertilized (unfilled) plots. Results for Fisher's α were similar to Shannon H', and are not shown. Bars represent treatment means ± 1 SE. Lowercase letters denote significant differences in the leaf morphology main effect, and inset notations (F = fert., NF = not fert.) indicate significant differences in the fertilization effect, both tested by the Tukey-Kramer test adjusted for type I error (joint $\alpha = 0.05$).

across blocks for all trophic levels except detritivores. There were no significant effects of leaf morphology on species load, other than the morphology X block interaction for carnivores.

Behaviors of the two diversity indices (Fisher's α and Shannon H') were comparable to each other, but were distinct from species load results (Figure 6.3, Table 6.4). Relative diversity indices for herbivores alone were higher with fertilization. However, the fertilizer effect varied across blocks for both carnivores and herbivores, and all arthropods in aggregate varied across blocks and plots. Both indices showed increased detritivore diversity with increasing pubescence level, a result paralleled by arthropod totals. Morphology effects also interacted with block effects for all arthropods in aggregate.

Temporal patterns

Although the block factor was significant in tests with various arthropod variables, there were no discernable temporal trends in total arthropod density, biomass, species load (Figure 6.4) or relative diversity (not shown). Fertilization led to higher arthropod numbers relative to unfertilized plots on most sampling dates and across morphological classes. This result was more equivocal for arthropod biomass and for the pubescent morphology. Taxon- and trophic level-specific plots did not reveal appreciably distinct trends across blocks.

Species composition

Nonparametric MANOVA showed no effect of fertilization, nor any interaction involving fertilization on the total community or any of the trophic level assemblages.

Table 6.4. Results of general linear models for arthropod guild a) species density, b) Fisher's α, and c) Shannon H'. Italicized sources represent random terms. Boldface *P*-values are significant at α = 0.05.

Source	df[a]	All		Carnivores		Herbivores		Detritivores	
		F	*P*	F	*P*	F	*P*	F	*P*
a) Species Density									
Fertilization [F]	1,7	12.76	**0.009**	6.53	**0.038**	8.22	**0.024**	21.85	**0.002**
Block [B]	7,[b]	1.38	0.321	0.89	0.543	1.07	0.461	15.49	0.437
F X B	7,16	3.79	**0.013**	3.17	**0.027**	6.83	**0.001**	0.28	0.953
Plot(F B)	16,46	0.85	0.627	0.84	0.636	0.78	0.694	0.98	0.497
Morph [M]	2,14	0.96	0.407	0.58	0.574	0.75	0.490	0.36	0.705
M X F	2,46	1.52	0.230	1.10	0.342	0.73	0.486	0.89	0.418
M X B	14,46	1.60	0.116	2.14	**0.027**	1.36	0.210	0.92	0.541
b) Fisher's α									
Fertilization [F]	1,7	0.10	0.763	0.65	0.447	5.23	**0.056**	2.59	0.152
Block [B]	7,[b]	3.54	0.074	2.93	0.283	0.78	0.633	2.08	0.170
F X B	7,16	0.96	0.490	0.40	0.888	1.16	0.380	0.84	0.573
Plot(F B)	16,46	1.33	0.223	1.05	0.430	0.70	0.783	1.06	0.420
Morph [M]	2,14	6.27	**0.011**	1.95	0.179	0.00	0.995	4.02	**0.042**
M X F	2,46	0.31	0.734	0.11	0.892	1.76	0.184	2.44	0.098
M X B	14,46	1.16	0.336	1.09	0.394	1.18	0.320	1.74	0.080
c) Shannon H'									
Fertilization [F]	1,7	1.47	0.264	0.65	0.445	6.00	**0.044**	6.17	**0.042**
Block [B]	7,[b]	2.96	**0.046**	2.00	0.185	1.61	0.262	1.29	0.361
F X B	7,16	1.31	0.309	4.40	**0.007**	2.69	**0.048**	1.27	0.325
Plot(F B)	16,46	2.09	**0.026**	0.45	0.960	0.60	0.864	1.79	0.063
Morph [M]	2,14	29.13	**<0.0001**	0.87	0.439	0.03	0.973	38.86	**<0.0001**
M X F	2,46	0.17	0.847	0.67	0.519	0.72	0.494	1.44	0.247
M X B	14,46	2.82	**0.004**	1.28	0.258	1.44	0.175	1.45	0.169

a Numerator, denominator degrees of freedom.

b Denominator degrees of freedom estimated by Satterthwaite approximation.

Leaf morphology strongly influenced the composition of the entire community (pseudo-$F_{2,14}$ = 3.808, *P* = 0.001), and of the detritivore assemblage (pseudo-$F_{2,14}$ = 7.950, *P* = 0.001), there was a suggestion of an effect on herbivores (pseudo-$F_{2,14}$ = 2.426, *P* = 0.065). When the most abundant Collembolan species (*Salina celebensis*) was removed from the detritivore and aggregate assemblages, leaf morphology effects remain

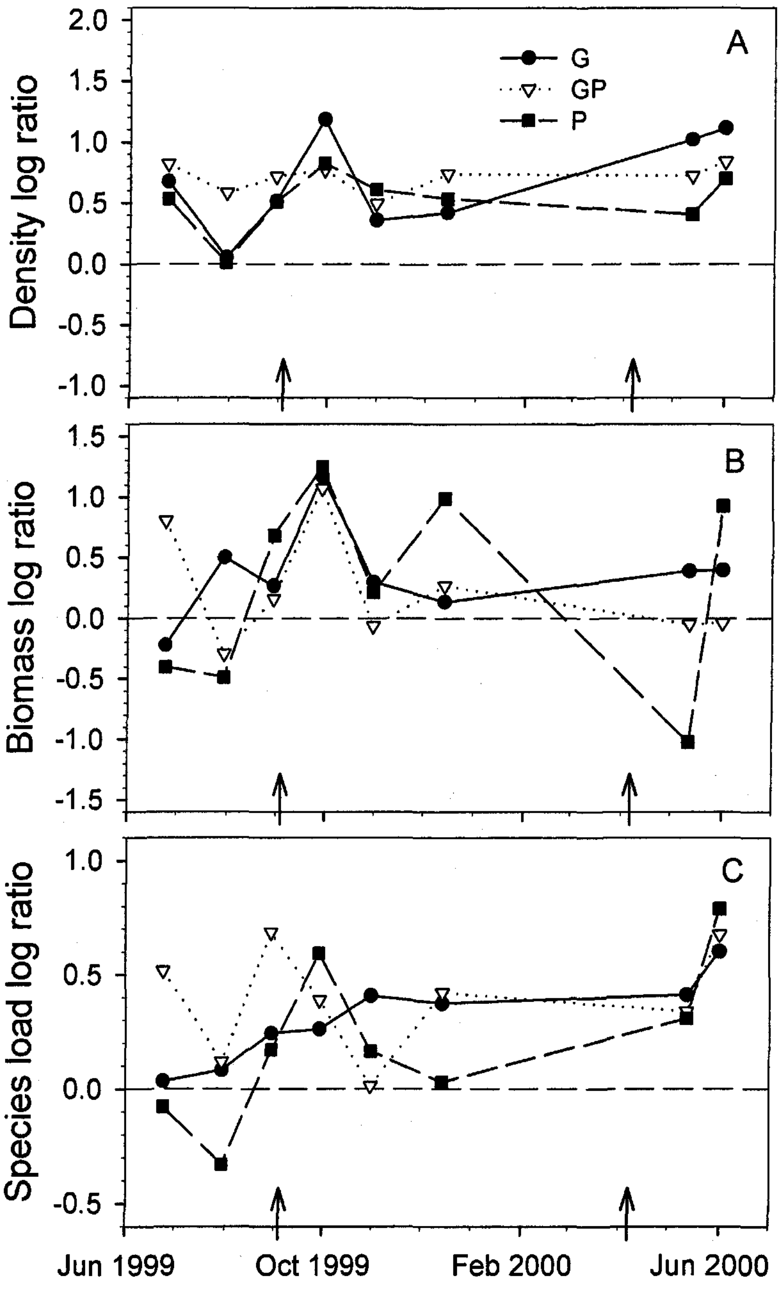

Figure 6.4. Natural log ratios of fertilized plots relative to unfertilized plots for total arthropod A) density, B) biomass, and C) species load by foliar morphology class and sampling date. Each point represents the natural log transformed ratio of the mean of the two fertilized plots for each block divided by the mean of the two unfertilized plots. All variables were standardized by the dry biomass of foliage collections. The dashed control line at Y = 0 represents no net fertilization effect, and arrows show fertilization events.

significant, although less strongly so (total: pseudo-$F_{2,14}$ = 3.770, P = 0.040; detritivores: pseudo-$F_{2,14}$ = 2.753, P = 0.010). There was some indication that the leaf morphology effect was temporally or spatially variable (significant morphology X block interaction, total: pseudo-$F_{14,46}$ = 1.194, P = 0.029; detritivores [no *Salina*]: pseudo-$F_{14,46}$ = 1.169, P = 0.048).

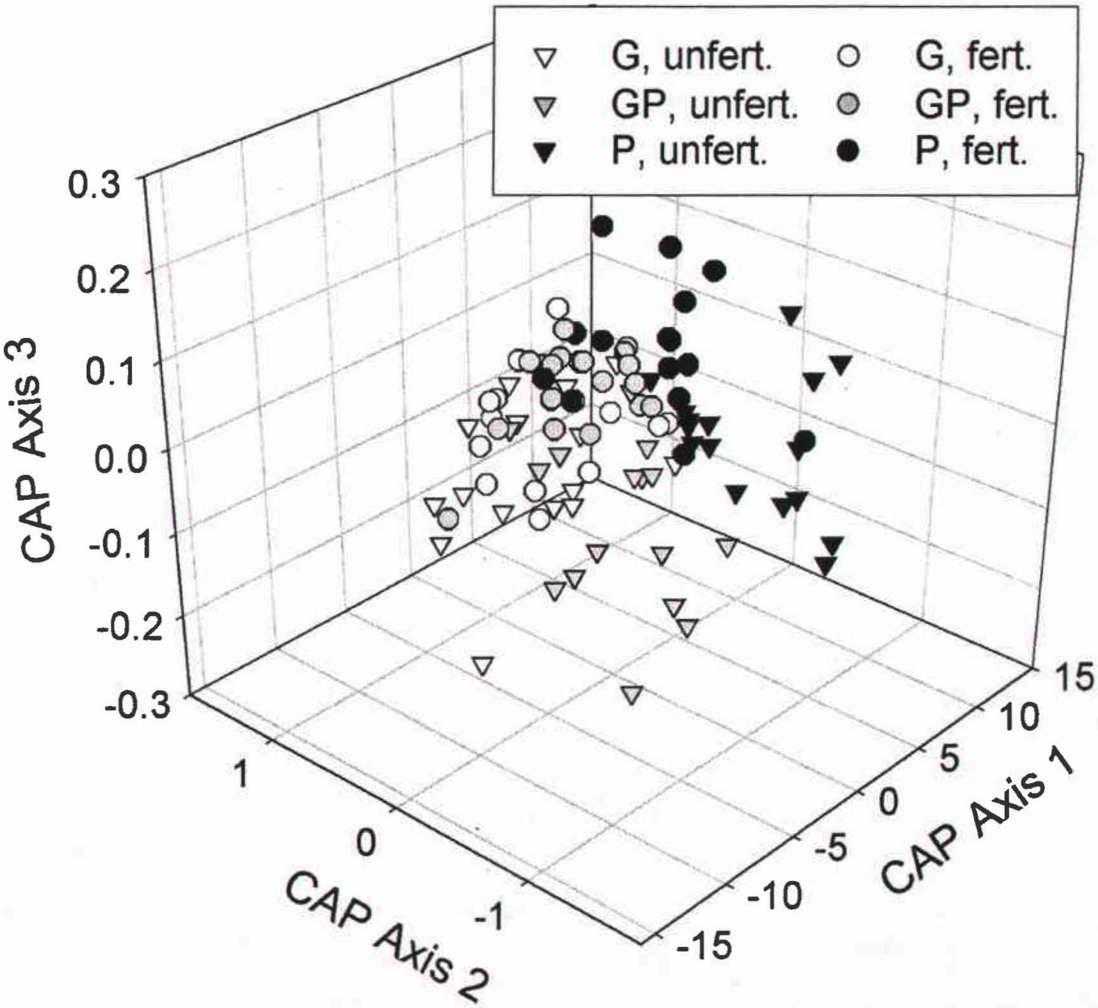

Figure 6.5. Ordination diagram of the first three axes from canonical analysis of principal coordinates constrained by fertilization X morphology treatment combinations. Triangles represent fertilized plots, and circles are unfertilized. Unfilled symbols represent collections from trees with glabrous (G) leaves, black symbols were from the pubescent (P) morphology, and grey symbols represent the intermediate (GP) morphology.

Canonical analysis of principal components revealed significant differences in community composition among the 6 combinations of leaf morphology and fertilization using 3 axes (trace statistic = 2396.3, P = 0.013; Figure 6.5). Plot scores on the first 2 CAP axes differed significantly among leaf morphologies (axis 1: $F_{2,14}$ = 21.01, P < 0.0001; axis 2: $F_{2,14}$ = 20.46, P < 0.0001), but there also were significant morphology X fertilization interactions (axis 1: $F_{2,46}$ = 6.58, P = 0.003; axis 2: $F_{2,46}$ = 5.31, P = 0.008). There were significant main effects of fertilization on the second and third axes (axis 2: $F_{1,7}$ = 13.34, P = 0.008; axis 3: $F_{1,7}$ = 92.48, P < 0.0001).

Discussion

In this highly nutrient-limited environment, LMA decreased but pubescence did not change in response to the experimental fertilizations (Table 6.1). Previous studies of *Metrosideros polymorpha* showed that morphological traits, such as trichome structure and density, have a genetic basis, whereas ecophysiological behavior and anatomical features, such as LMA, are inducible by environmental factors in a common garden setting (Cordell et al. 1998). The independence of morphological and physiological features has been documented in other plant species (Roy et al. 1999, Forkner and Hare 2000). However, increased trichome density may be induced by heavy herbivore defoliation or by intense disturbance events, such as a hurricane (Pullin and Gilbert 1989, Dalin and Björkman 2003, Spiller and Agrawal 2003)—this has not been tested in the present system.

Nutrient additions increased densities of individuals and species of all trophic levels and many taxonomic orders (Figures 6.1-6.3; Tables 6.2-6.4). However, leaf morphology had contrasting effects on different taxonomic orders (Figure 6.1), and effects were more pronounced on the relative diversity and species composition of the community, primarily for detritivorous species. Nutrient resource supply and plant physical morphology had independent bottom-up effects on arboreal arthropod communities, as there were no interactions between pubescence class and the fertilization treatment (Tables 6.2-6.4).

Community responses to fertilization

Increased densities in response to fertilization were observed in most arthropod orders and all trophic levels (Figures 6.1, 6.2; Tables 6.2, 6.3). Reviews of population and community responses to fertilization have shown positive effects on herbivorous arthropod abundance and biomass in many studies (Waring and Cobb 1992, Kytö et al. 1996). This response is attributed generally to increased resource quantity, increased soluble plant tissue N and dissolved amino acids, or reduced allocation to carbon-based chemical or structural defense (Mattson 1980, Strong et al. 1984, Keinanen et al. 1999, Ritchie 2000). Fertilization also decreased LMA (Table 6.1), which is positively related to leaf toughness (Wright and Cannon 2001), an important deterrent to leaf herbivory (Coley and Barone 1996). Detritivores also stand to benefit from these changes, as higher nutrient concentrations decrease lignin concentrations and increase the decomposability of *Metrosideros* litter (Vitousek 1998, Hobbie 2000). Plant nutrient status can cascade up to natural enemies (Forkner and Hunter 2000, Denno et al. 2002), which may suffer even more pervasive nutrient limitation (Fagan et al. 2002). Invertebrate predators, particularly spiders, may respond also to increased structural heterogeneity created in fertilized plots (Langellotto and Denno 2004). Herbivore and detritivore biomass increased in some fertilized blocks, but this effect was highly variable, consistent with results from a companion study (Table 6.3, Gruner in press-b).

Responses of community species richness or diversity in other studies have been more variable and equivocal than abundances (Hurd and Wolf 1974, Kirchner 1977, Sedlacek et al. 1988, Haddad et al. 2000). Discrepancies in the qualitative responses of diversity across systems may be biologically based and system specific, or might vary according to differences in spatial scale (Whittaker and Heegaard 2003), trophic or taxonomic focus (Haddad et al. 2000), diversity metric or standardizations employed (McCabe and Gotelli 2000), or experimental time frame (Haddad et al. 2000). For example, long-term fertilizations frequently decrease plant richness or otherwise alter species composition concomitant with increasing productivity (Siemann 1998, Waide et al. 1999, Haddad et al. 2000). We avoided the confounding from plant community compositional changes with fertilization by isolating the single host, the dominant tree species *Metrosideros polymorpha*. Concerns about scale were addressed by sampling periodically over a one-year time frame, and by reference to a study examining arthropod responses to a productivity gradient across the Hawaiian archipelago (Chapter 2). Moreover, all trophic levels and taxonomic orders were examined to provide a broad understanding of community-wide responses, and multiple diversity metrics were compared within these groups.

Species load of all trophic levels increased with fertilization (Figure 6.3), but this result may be attributable to increased densities. Using indices that account for relative abundance, herbivore diversity alone was elevated with fertilization (Figure 6.3D, Table 6.4), whereas the diversity of detritivores decreased (Figure 6.3F, Table 6.4). Because fertilization increased herbivore abundance but did not change equitability (Pielou's J' overall mean ± SE: 0.89 ± 0.01, all F-tests n.s.), higher herbivore diversity may be an indirect result of rare species becoming abundant enough to persist ("consumer rarity hypothesis" sensu Siemann 1998, "more individuals hypothesis" sensu Srivastava and Lawton 1998). In contrast, detritivore diversity declined with fertilization due to increasing dominance of a single species, *Salina celebensis* Schaeffer, which was by far the most abundant animal on trees (>99% of Collembola individuals in Figure 6.1E). Yet, fertilization produced only modest changes in arthropod species composition, and for the detritivorous component only (Figure 6.5).

Community responses to foliar pubescence

Responses to pubescence classes on *Metrosideros polymorpha* varied with taxonomic order and trophic level (Figures 6.1-6.3). Although previous studies have shown that trichomes can interfere with the foraging behavior of insect predators or parasitoids (Van Lenteren et al. 1995, Eisner et al. 1998), natural enemies did not show sensitivity to leaf pubescence on *Metrosideros polymorpha* (Figures 6.2, 6.3). Herbivore variables also were unchanged across leaf pubescence levels, despite observations that herbivore damage was more frequent on glabrous morphologies at this and nearby sites (Lee 1981, Gruner unpublished data). Cornell (1989) hypothesized that gall formers, leaf miners, and other endophagous insects will avoid leaf defenses through their specialized behavior. Many of the herbivorous lineages that utilize *Metrosideros* in this community are internal feeders, predominantly bud-mining Lepidoptera and gall-forming psyllids. Indeed, some gall-formers can resist or even manipulate the mechanical or chemical defenses of their host plants (Hartley 1998b, Nyman and Julkunen-Tiitto 2000). The abundance of internal-feeding species on manzanita (*Arctostaphylos* spp.: Ericaceae) was not influenced by length, density of glandularity of trichomes although external leaf chewing insects were more abundant on plants with dense pubescence and with glandular trichomes (Andres and Connor 2003). Demographic studies on developing *Metrosideros* leaf cohorts may more effectively assess responses of individual herbivore species in their most actively feeding juvenile stages.

Detritivores as a group increased in abundance (Figure 6.2C) but decreased in diversity (Figure 6.3D) on more glabrous morphologies. Much of the increase in density again can be attributed to *Salina celebensis*; nevertheless, deletion of *S. celebensis* did not erase the significant influence of leaf morphology on detritivore community composition (NPMANOVA pseudo-$F_{2,14} = 2.753$, $P = 0.010$). Higher abundance of detritivores on glabrous forms could arise from several mechanisms. Although nitrogen concentrations did not differ among morphologies (1-way ANOVA from unfertilized trees, $F_{2,30} = 1.42$, $P = 0.257$, see methods in Chapter 3), pubescent leaves may be less palatable tissues for decomposers because of higher levels of cellulose, lignins, or condensed tannins. Alternatively, detritivores may react indirectly to herbivory of phytophagous insects. In particular, the stem galls of *Trioza hawaiiensis* Crawford occurred in higher frequency among glabrous morphotypes, less so on intermediate forms, and never on pubescent morphologies at this site (Gruner unpublished data). These galls sometimes sever and kill stems and leaves with swollen gall tissue. This can provide a direct input of dead organic matter remaining attached to the plant or otherwise suspended in the canopy, and may encourage fungal growth for grazers like Collembola (Gruner personal observation). Insect stem galls also increased the growth of lateral shoots on *Salix*, which were then less tough and had higher nitrogen and water contents (Nakamura et al. 2003). In addition to increased food resources, evacuated galls provide structural heterogeneity on *Metrosideros*, and Collembola and Psocoptera were often observed foraging or residing within excavated gall tissues on leaves or stems.

Arthropod response was heterogeneous among orders, with Psocoptera and some Heteroptera in highest numbers on the most pubescent leaves, and mites most abundant on intermediate forms (Figure 6.1). Some small arthropods also may seek out the habitat heterogeneity offered by trichomes. On bean plants, predatory mites were more abundant on leaves with trichomes, and actually preferred artificial pubescence as habitat structure (Roda et al. 2001). Diametrically opposed responses of different phytophagous taxa has been reported with glandular trichomes of *Datura wrightii* (van Dam and Hare 1998), and across guilds on *Arbutus xalapensis* (Ezcurra et al. 1987). On *Metrosideros*, not all gall types (and their evacuated galls) were more frequent on glabrous morphologies (Gruner unpublished data). Like springtails, psocids are scavengers of dead organic matter and grazers of lichens, fungi, and algae (Thornton 1985, Christiansen and Bellinger 1992). Their distributions could reflect negative competitive outcomes with abundant Collembola, or may be in response to differences in bark structure, tree architecture, or distribution and abundance of microepiphytes or endophytic fungi correlated with foliar pubescence.

Conclusions

The functional significance of pubescence in *Metrosideros polymorpha* is unclear. In addition to possible roles in herbivore resistance, leaf hairs may regulate temperature, water or energy budgets (Ehleringer and Mooney 1978, Meinzer and Goldstein 1985, Grammatikopoulous and Manetas 1994), reduce absorption, reflect, or enhance dissipation of damaging short wave radiation, such as ultraviolet (Johnson 1975, Karabourniotis et al. 1995), or reduce wettability and increase supercooling capacity and freezing resistance (Melcher et al. 2000). The high vagility of seeds (Wright et al. 2000) and the stickiness of pollen for mobile avian pollinators (Carpenter 1976) may allow ecotypes to persist in areas where they are mismatched to local selection pressures.

Although the selective pressures maintaining foliar pubescence in this species are unresolved, this study further supports the hypothesis that pubescence is a genetically determined fixed trait in individuals (Cordell et al. 1998). Leaf thickness changed with nutrient enrichment, but without altering the density of trichomes. Moreover, insect community responses to leaf pubescence were diverse, even within trophic levels on the same taxonomic host plant species, but generally acted independently of resource availability. Leaf morphology may have stronger implications for decomposers than for herbivores, suggesting that trichomes of *M. polymorpha* may be tied functionally to the cycling of nutrients and biomass in this nutrient limited ecosystem.

CHAPTER 7

REGRESSIONS OF LENGTH AND WIDTH TO PREDICT ARTHROPOD BIOMASS IN THE HAWAIIAN ISLANDS

Abstract

Biologists in many fields use published regression equations to predict biomass from simple linear body measurements. Power functions are used with arthropods, facilitating biomass estimation of a sample when destructive techniques are not feasible. Resulting predictive coefficients vary widely depending on region and taxa. There are no published biomass regressions for oceanic island fauna, despite the widely accepted conclusion their arthropod assemblages are unusual in composition. I present a suite of general and taxonomically and morphologically restricted regression equations developed for arthropods in the Hawaiian Islands. General regression equations were highly significant when only length was used to predict biomass, but fits were usually improved by including body width. In regressing restricted sets of taxa, the addition of width did little to improve the fit of the functions. Thus, the choice of regression equations involves a tradeoff in taxonomic resolution: precise biomass estimates will come either from either 1) low taxonomic resolution measured for both length and width, or 2) high taxonomic resolution measured only for body length. These equations have a high predictive capacity for a broad range of arthropod taxa common in the Hawaiian Islands and, in the absence of locally developed equations, the arthropods of other oceanic islands.

Introduction

The sheer abundance and diversity of arthropods in terrestrial ecosystems attest to their importance in ecosystem function. A number of applications require the estimation of arthropod biomass in ecosystems, from testing of classic hypotheses of biomass ratios in trophic groups (Hairston et al. 1960), description of macroecological patterns (Brown and Maurer 1986, Blackburn et al. 1993, Blackburn and Gaston 1997), to the availability of food resources for birds (Hódar 1997) or other vertebrates (Sage 1982). Arthropods can be weighed directly while fresh, or subsequent to freezing. However, fresh biomass measurements are sensitive to the conditioning of the sample, local relative humidity, or any factor that influences the water content of specimens. More often, researchers collect a large quantity of material in a short time and must preserve specimens for identification and analysis at a later date. These specimens can then be dried and weighed in bulk to eliminate the variable influence of body water content, but at the price of destruction of soft-bodied arthropods and any ability to identify and voucher them.

A preferred approach to biomass estimation is to use general or taxonomically restricted regression relationships to predict arthropod biomass from easily obtained length and/or width measurements (Rogers et al. 1976, Rogers et al. 1977, Schoener 1980, Sage 1982, Gowing and Recher 1984, Sample et al. 1993, Hódar 1996). Using power functions, these equations reduce the effort required to estimate biomass of a sample when destructive techniques are not feasible. But which regression coefficients to use? Significant statistical differences among compared equations appear to be rare (Gowing and Recher 1984, Sample et al. 1993). However, Hódar (1996) compared nine published length-weight regression relationships and found their performance highly variable in comparison to the actual known biomass of samples. Several authors emphasized the increased precision obtained with equations specific to lower taxonomic groupings (Gowing and Recher 1984, Hódar 1996). Even among specific groups, Schoener (1980) noticed differences in parameter estimates of tropical versus temperate insects, and suggested hypotheses why there might be systematic differences in the faunas to explain this pattern.

The arthropod fauna of the Hawaiian Islands is widely cited as disharmonic and locally depauperate relative to other tropical areas as a result of its extreme isolation from sources of colonizing lineages (Zimmerman 1948, Howarth 1990). The most common groups in these islands may not be well represented in regression equations developed elsewhere. In addition, shifts to smaller or larger forms are common in the evolution of endemic species on islands (Whittaker 1998). It is not known to what extent these size changes alter the allometric relations of linear measurements to body mass. Thus, it is not at all clear which published length-weight relationships are most applicable to estimation of arthropod biomass on tropical island ecosystems. Recent investigations into the diet of endangered birds required biomass equations but equations specific to Hawai'i were unavailable (Peck 1993, Fretz 2000). As the assessment of the most appropriate published equations may have proven as laborious as generating new ones, I sought to remedy this lack. I present a suite of taxonomically general and specific regression equations developed through the course of ongoing work in the Hawaiian Islands. Beyond their immediate utility, it is hoped that the biomass equations will benefit future work focused on Pacific Island fauna.

Methods

Field and laboratory

I selected specimens as available within incidental or non-quantitative collections obtained over the course of other work in the Hawaiian Islands from 1996 to 2001. With few exceptions, specimens were collected from the endemic tree *Metrosideros polymorpha* Gaudichaud-Beaupré (Myrtaceae). *Metrosideros* is a common genus throughout the Pacific to New Zealand (Mueller-Dombois and Fosberg 1998), but it is particularly abundant and widespread in the Hawaiian Islands (Dawson and Stemmerman 1999). The arthropod fauna of this tree is particularly diverse among Hawaiian trees (Southwood 1960), representing a number of lineages (Stein 1983). Thus it is a reasonable first approximation for arthropod biomass predictions in the Hawaiian Islands, and perhaps, Pacific Islands more generally. I collected arthropods through pyrethrum canopy fogging (Gruner and Polhemus 2003), branch clipping, vegetation beating, malaise trapping, and hand collecting at sites on Hawai'i, Moloka'i, O'ahu, and Kaua'i (Gruner 2003). Several texts provide detail on these collection methods (New 1998, Southwood and Henderson 2000, Toda and Kitching 2002). Most collections were from intact, predominantly native forest ecosystems at elevations above 1000 meters.

All specimens were stored in 70% ethanol, and measured directly upon removal from preservative. Alcohol may distort some specimens, especially in soft-bodied groups such as Lepidoptera and Araneae. Storing of specimens in alcohol also may result in extraction of some body materials (Breymeyer 1967, Rogers et al. 1976). Ethanol is, however, the arthropod preservative of choice for many practitioners in various fields. These regressions, then, will apply to data most easily obtained and widely available. If biomass is indeed lost during ethanol storage, the regression estimates of biomass will be conservative (Gowing and Recher 1984).

Specimens were chosen to represent a range of taxa, sexes, life stages, and sizes as available in the incidental collections. As noted by Hódar (1996), it is of greater importance to represent the full range of variation in the estimation procedure than to randomize specimen selection. Only undamaged specimens were selected. Specimens were identified to species where possible. Otherwise, specimens were assigned to Operational Taxonomic Units (OTU), or "morphospecies" within the finest taxonomic classification obtainable.

Length was measured using a dissecting microscope with an ocular micrometer to 0.05 millimeter precision. Body length included the tip of the abdomen to the end of the head or carapace, excluding mouthparts, genitalia, ovipositors, antennae or spinnerets (spiders). Width was measured at the widest point of the mesothorax. For non-hexapods, width was taken as the widest body segment. After morphometric measurement, specimens were then dried for 24 hours in an oven at 70°C and weighed to the nearest 0.01 milligram. Where possible, at least ten specimens of a particular OTU were measured and weighed, but more than ten often does not improve precision as long as specimens cover the range of variation in the OTU (Hódar 1996). For hemimetabolous arthropods, additional specimens were measured and weighed for life stages that differed appreciably, and for holometabolous species, for each unique life form. Extremely small specimens were weighed in groups of 2-10, lengths and widths averaged, and applied to total group mass divided by the number of individuals used.

Statistical analyses

General and specific linear regressions were created to predict biomass of arthropods from length and width. General equations contained a large number of specimens grouped at the class level or above. Specific equations were created on restricted taxonomic lines, but also on morphological similarities. For instance, *Tetragnatha* spiders, generally long and slender, were calculated separate from other spiders, and several families of beetles and genera of Heteroptera were isolated on the same rationale. Following other authors (Rogers et al. 1977), I used a power model to describe the size-weight relationships. The model takes the form:

$$y = a(x)^b$$

Where y = dry biomass; x = size measurement, whether length, or length*width; a and b are coefficients estimated in the regression procedure. Morphometric and weight data were transformed to natural logarithms for analysis using linear regressions:

$$\ln(y) = \ln(a) + b*\ln(x)$$

Logarithmic transformations reduced heteroscedasticity in the data in accordance with statistical assumptions. Data were analyzed with linear regressions using the Systat statistical software package (Systat 2000). I ran regressions both on length and length*width, and back-transformed the data for parameter estimations. Other authors have applied Bonferroni corrections because of the high number of regression equations developed (e.g., Sample et al. 1993, Hódar 1996). However, because I am not testing the null hypothesis that length (or length and width) is related to mass, I argue it is not necessary to control for the Type I error rate. Nevertheless, I apply the most conservative fixed Bonferroni correction to test the strength of the relationships (overall $\alpha = 0.05$).

Results

I measured length and width of 619 individual arthropods, from which I obtained 488 measures of biomass. Of these specimens, 431 specimens were measured individually for morphometrics and biomass, and 188 additional smaller sized specimens were lumped into 57 groups of 2-10 individuals. Specimens were gathered from 14 arthropod orders in the subphylum Crustacea and in the classes Arachnida and Insecta (Brusca and Brusca 1990). The measured arthropods ranged from lengths of 0.65 (Acari) to 17.6 mm (Coleoptera: Curculionidae), and widths from 0.20 (Diptera: Sciaridae) to 6.45 mm (Isopoda: Porcellionidae). From these specimens I generated regressions at levels running the gamut from phylum-level to single species. For all analyzed groups, I present results from biomass regressions of body length and the product of length and width (Table 7.1). Attempts to create regressions with body width as a separate parameter were less successful and thus not reported here.

The logarithmic length-weight regression of all arthropod taxa was highly significant ($R^2 = 0.773$, $P < 0.0001$; Figure 7.1), as was the regression using the product of length and width ($R^2 = 0.890$, $P < 0.0001$; Figure 7.1). The parameter b, the exponent in the complete power function model, is among the lowest published values for length-only models ($b = 2.191$). Within the most diverse and numerically dominant orders (e.g., Coleoptera, Homoptera), I generated suborder, family and genus level equations (Table 7.1). All equations were highly significant at the alpha level of 0.05, most were significant at the 0.001 level. When the test-wise alpha is adjusted to an overall alpha of 0.05 by dividing by the number of tests, 92% of the 50 length regressions and 96% of the length-width regressions remain statistically significant (test-wise $\alpha = 0.001$).

Table 7.1. Descriptive data and parameter estimates for arthropod length (L, in mm) and length*width (L*W) regressions on dry biomass (mg). Taxa are listed as nested (indented) sets, not necessarily reflecting phylogenetic distance with consistent depth of indentation. The parameters apply to the relation $y = a(x)^b$, where x is L or L*W, and y is mass. N refers to the number of insects measured for length and width, while n is the number used in statistical procedures after lumping of small specimens for weighing. Minimum and maximum lengths are from the statistical n. All regressions are significant below *P* = 0.001 unless otherwise noted.

						L model			L*W model		
Taxon	Stage	N	n	*min*	*max*	a	b	R^2	a	b	R^2
Arthropoda	all	619	488	0.90	17.60	0.0340	2.191	0.773	0.0929	1.330	0.890
Arthropoda	†	596	465	0.90	17.60	0.0288	2.355	0.808	0.0959	1.323	0.889
Insecta	all	591	462	0.90	17.60	0.0350	2.173	0.762	0.0920	1.333	0.884
Insecta	†	570	439	0.90	17.60	0.0291	2.355	0.799	0.0923	1.346	0.888
Crustacea	all	26	26	2.35	13.90	0.0138	2.669	0.918	0.0711	1.322	0.936
Isopoda	all	16	16	2.35	13.90	0.0152	2.770	0.974	0.0578	1.351	0.943
Amphipoda	all	10	10	3.75	10.65	0.0088	2.682	0.989	0.0723	1.419	0.976
Arachnida	all	69	46	0.90	7.40	0.0562	2.332	0.895	0.1377	1.355	0.940
Araneae	all	52	43	1.55	7.40	0.0433	2.532	0.882	0.1261	1.408	0.930
non-Tetragnathidae	all	39	30	1.55	7.40	0.0332	2.924	0.929	0.1241	1.418	0.926
Tetragnathidae (*Tetragnatha*)	all	13	13	2.15	6.20	0.0372	2.406	0.929	0.1379	1.356	0.933
Blattodea	all	18	18	2.55	11.20	0.0313	2.358	0.955	0.0837	1.387	0.963
Hymenoptera	adult	34	22	1.20	7.50	0.0139	2.383	0.918	0.0895	1.298	0.930
Orthoptera	all	21	20	2.65	10.35	0.0180	2.720	0.919	0.1228	1.325	0.945
Psocoptera	all	40	18	1.50	3.15	0.0136	3.115	0.786	0.0877	1.352	0.746
Coleoptera	all	137	130	1.45	17.60	0.0336	2.347	0.771	0.1011	1.358	0.847
Coleoptera	adult	130	123	1.45	17.60	0.0339	2.384	0.801	0.1059	1.355	0.859
Carabidae	adult	16	16	4.10	16.30	0.0168	2.752	0.969	0.1200	1.393	0.970
Ciidae + Scolytidae	adult	18	13	1.45	2.40	0.0313	2.531	0.736	0.1083	1.480	0.898
Ciidae	adult	14	9	1.45	2.45	0.0247	3.102	0.757*	0.1144	1.637	0.875
Coccinellidae	adult	12	12	1.55	4.05	0.0724	2.665	0.651*	0.1873	1.189	0.560
Nitidulidae	adult	22	22	3.00	4.50	0.0679	1.308	0.384*	0.0719	1.103	0.586
(slender beetles§)	adult	21	17	1.65	10.30	0.0138	2.595	0.959	0.1092	1.213	0.962
(all weevils‡)	adult	43	43	2.10	17.60	0.0310	2.641	0.887	0.1363	1.379	0.880
Aglycyderidae (*Proterhinus*)	adult	19	19	2.10	4.05	0.0183	3.144	0.974	0.1295	1.481	0.973
Anobiidae	adult	7	7	3.35	4.45	0.0080	3.463	0.731**	0.0769	1.422	0.820*
Curculionidae	adult	17	17	2.50	17.60	0.0607	2.315	0.781	0.1915	1.298	0.796

Table 7.1. (Continued)

						L model			L*W model		
Taxon	Stage	N	n	min	max	a	b	R^2	a	b	R^2
Heteroptera	all	55	55	2.10	9.55	0.0411	1.934	0.823	0.0843	1.234	0.921
Lygaeidae	all	17	17	2.10	5.25	0.0375	2.065	0.861	0.1046	1.052	0.917
Nabidae (*Nabis*)	all	17	17	2.50	9.55	0.0074	2.749	0.928	0.0855	1.255	0.952
Miridae	all	21	21	2.10	4.45	0.0353	2.185	0.666	0.0771	1.302	0.793
Mirid., no *Nesiomiris*	all	20	20	2.10	4.45	0.0320	2.318	0.762	0.0706	1.360	0.797
Nabis + *Nesiomiris*	all	18	18	2.50	9.55	0.0071	2.764	0.935	0.0904	1.233	0.955
Homoptera	all	119	92	1.10	8.80	0.0234	2.536	0.846	0.0814	1.349	0.880
Homoptera	adult	65	64	1.60	8.80	0.0155	2.835	0.905	0.0848	1.362	0.905
Homoptera	larvae	54	28	1.10	5.20	0.0585	1.670	0.627	0.0911	1.133	0.730
Cicadellidae (*Nesophrosyne*)	all	17	16	3.15	5.25	0.0067	3.141	0.884	0.0328	1.731	0.853
Psyllidae +Aphididae	all	39	19	1.60	3.05	0.0175	2.629	0.839	0.0947	1.260	0.819
Psyllidae	adult	26	14	1.90	3.05	0.0123	2.995	0.752	0.0778	1.592	0.800
Fulgoroidea	all	88	73	1.10	8.80	0.0323	2.338	0.787	0.0661	1.455	0.833
Flatidae (*Siphanta acuta*)	all	18	18	2.45	8.80	0.0088	3.182	0.875	0.0149	2.129	0.895
Native Fulgoroidea•	all	53	38	1.35	5.00	0.0511	2.072	0.809	0.1001	1.240	0.865
Delphacidae	all	21	14	1.90	3.75	0.0206	2.764	0.668	0.0939	1.338	0.644*
Cixiidae	all	24	24	1.10	5.00	0.0691	1.906	0.882	0.0966	1.246	0.923
Lepidoptera	adult	9	9	3.35	8.85	0.0179	2.318	0.922	0.0873	1.184	0.961
Lepidoptera	larvae	14	14	4.25	16.65	0.0271	1.769	0.683	0.0606	1.374	0.877
Diptera	adult	30	19	1.75	8.60	0.0153	2.573	0.850	0.0756	1.338	0.939
Collembola	all	33	9	1.70	3.85	0.0056	2.809	0.924	0.0601	1.374	0.909
Neuroptera	adult	8	8	5.10	6.95	0.0070	2.739	0.911	0.0521	1.467	0.891
All holometabolous	larvae	23	23	1.70	16.65	0.0290	1.730	0.848	0.0534	1.387	0.919

* $0.001 \leq P \leq 0.005$

** $P = 0.014$

† no juvenile holometabolous insects (Neuroptera, Coleoptera, Lepidoptera, and Diptera larvae) in these equations.

‡ All weevils include the families Curculionidae, Anobiidae and Aglycyderidae.

§ Slender beetles include the families Elateridae, Staphylinidae and Silvanidae.

• Includes Delphacidae & Cixiidae only; excludes the adventive flatid *Siphanta acuta*.

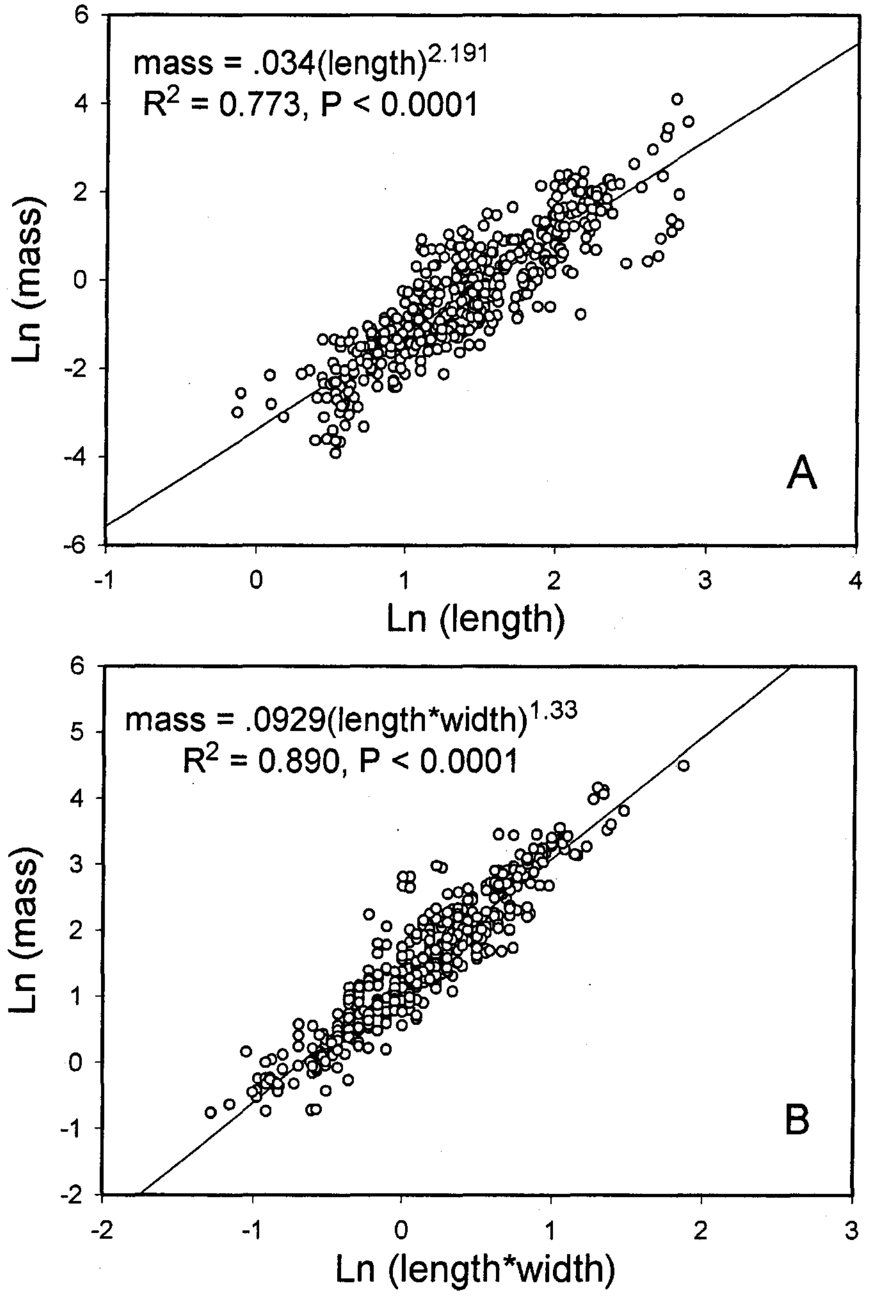

Figure 7.1. General regression relationships of A) length to dry mass, and B) the product of length and width to dry biomass. Data were natural log transformed to reduce heteroscedasticity and to linearize the power function for analysis. Regression equations and the back transformation to the power function are given.

Inclusion of width into the predictor variable x often improved the model fit, with some exceptions (Table 7.1). Incorporating width into the relationship improves the fit in the majority of cases (36/50), but often to a negligible extent. Using an arbitrary but more stringent threshold of 5% change in R^2, less than half of the relationships (22/50) are improved by incorporating width. Part of this result derives merely from the mathematical constraints of percentages; with an upper limit of 100%, a 5% improvement is difficult to achieve if the R^2 is already high. There is, however, a general trend towards more variation explained as taxonomic resolution decreases (Figure 7.2). The less resolved the taxonomic identity of a specimen, the more informative is the additional variable, body width, towards predicting biomass.

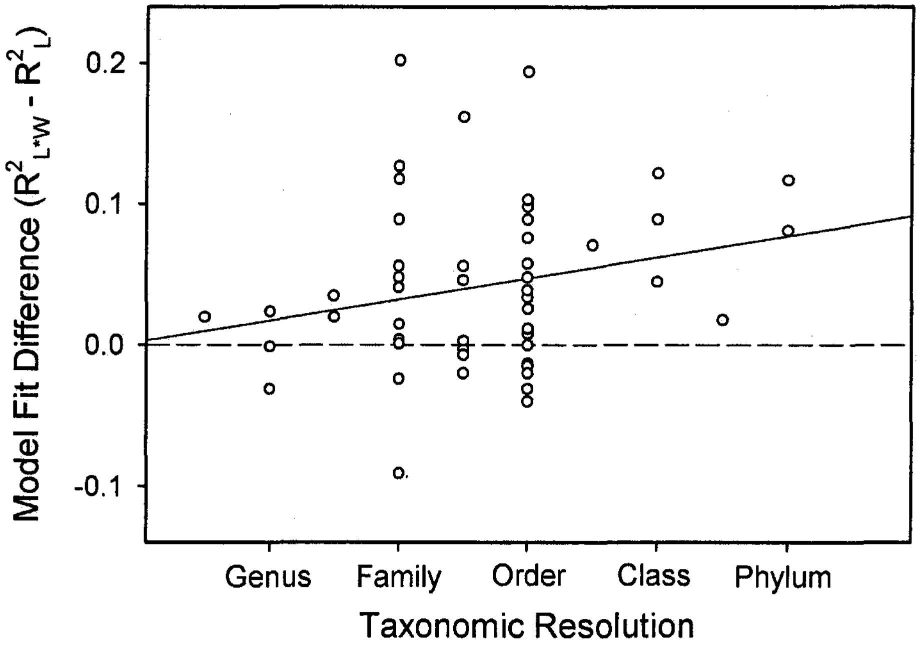

Figure 7.2. Relationship of taxonomic resolution to the relative change in biomass variation explained by length and width (L*W) versus length (L) alone. The dashed line indicates no difference among R^2 fit estimates. The solid line is a simple linear regression of fit difference on taxonomic resolution, where simple integer scores are given to each taxonomic step. The regression is used to illustrate the visual trend, but was not intended for formal analysis.

Discussion

The regression equations presented here provide a tool for the estimation of arthropod biomass in Hawaiian Island ecosystems. Previously, no specific tools were available for Hawaiian arthropods, forcing the use of general relationships constructed for other regions with no shared species. The power *b* of the length-weight relationship derived for Hawaiian arthropods is among the lowest published (Hódar 1996). This probably is due in part to the selection of specimens used. When I remove holometabolous larvae, predominantly long and thin insects such as caterpillars or lacewing larvae, the power rises to 2.355 (Table 7.1), closer to the range found in other studies. Even so, the power is still smaller than the most widely cited, presumably the most-used, general relationship ($b = 2.620$; Rogers et al. 1976).

For regressions involving only length, a uniformly proportional series of insects should have a power *b* in the range of 3, and 1.5, for regressions involving the product of length and width. General regression equations never have powers that high (Hódar 1996), however, and Schoener (1980) noted that tropical insect groups consistently had a lower power than their temperate counterparts. This is due, in part, to greater preponderance of slender insects such as mantids, phasmids, and Orthoptera in the tropical regions. Although there are no mantids or phasmids in the native Hawaiian fauna, long, slender insects are well represented (e.g., Coleoptera: Elateridae, Staphylinidae; Heteroptera: Nabidae, some Miridae). Schoener (1980) suggested a low *b* could be considered an “index of bizarreness”. For example, model fit for beetles in the family Nitidulidae, although still highly significant for both models, was among the poorest for any group (Table 7.1). The parameter *b* is 1.308 for the length model, and

1.103 for the model with both length and width. These insects are highly compressed in the unmeasured dimension, height, so length and width together are incomplete predictors of volume. At the other end of the spectrum, the introduced flatid planthopper (*Siphanta acuta*) holds its broad triangular forewings vertical, roof-like. Their *b* value (3.182) is unusually high, again reflecting the inordinate influence of the unmeasured dimension.

If indeed tropical island insects are less proportional in length and width, there are a number of plausible evolutionary hypotheses that may generate the pattern (Schoener 1980). Predation pressure is hypothesized to be stronger in the tropics (Dyer and Coley 2001). This may select for cryptic taxa resembling twigs, while also favoring the slender body form of many cursorial predators. The Hawaiian Islands fauna is a product of serendipitous colonization history; perhaps disproportional insects are more suited to long distance dispersal on the winds and tides? At present, these alternatives cannot be distinguished from random chance. The lesson in the current application is that species in different biogeographic provinces are subject to differing selection pressures and historical contexts. Thus, it is advisable to generate novel location, and possibly habitat-specific, regression relationships if more than the crudest estimates are necessary.

I am aware of no study of arthropod biomass regressions using a randomized series of insects sampled from their environment and measured for this purpose. Thus, there may be biases inherent in the selection of specimens and the relative number representing each taxon. Most of the specimens in this study were obtained through tree canopy collections, although in some communities there are large numbers of mobile soil organisms in the trees (Chapters 5, 6). Highly mobile, nocturnally active, internally phytophagous and epigeal arthropods are probably underrepresented in these samples. Furthermore, the arthropod fauna of the Hawaiian Islands is highly disturbed or degraded as a result of invasive species or habitat modification (Roderick and Gillespie 1998). Inferences concerning the proportionality of arthropod forms within provincial faunas, and any evolutionary drivers of these patterns, must then be interpreted with caution.

The majority of general relationships, at the phylum, class and ordinal levels, are improved by incorporating body width into the regressions (Figure 7.2). The more taxonomically specific the relationship, the trend is towards less improvement in fits using the combination measure. In the more restricted groupings, fits are no different, or usually perform less well, with width included. It is intuitively pleasing that as a group is narrowed and becomes more homogenous, the more informative is length alone. In the absence of fine taxonomic resolution, the recommendation would be to measure both length and width and apply general equations. If, however, good identifications are possible, specific equations using only body length will yield biomass estimates qualitatively similar to more detailed equations but with less labor. There are exceptions to this generalization, particularly at the family level, where several fits are dramatically improved with inclusion of width. Closer examination reveals families that are either heterogeneous at the family level (e.g., Heteroptera: Miridae), or else are unusually compressed (e.g., Coleoptera: Nitidulidae) or elongate (e.g., Coleoptera: Ciidae & Scolytidae) in the unmeasured dimension, height.

The development of these equations allows a high predictive capacity for biomass of a broad range of arthropod taxa common in the Hawaiian Islands. Moreover, oceanic islands often share suites of common biotic lineages as a result of their disproportionate colonization abilities over large scales. Highly endemic radiations of birds, land snails, and especially arthropods characterize oceanic island faunas, while many groups typical of continents are absent. Ants and termites, for instance, are entirely absent from the native fauna (Wilson 1996a). Small, vagile groups of insects are often found dispersing as aerial plankton on the continents and over the oceans (Holzapfel et al. 1978). These groups are prominent among native Pacific island faunas, along with some relictual taxa no longer present or common on continents (Howarth 1990). Many adventives are widely shared among Pacific Islands, whether as a result of the intrinsic affinity of a species for humankind and associated disturbances, or through replicate introductions of biological control agents for pests of widespread commercial crops. Although other authors recommend the independent development and publication of relationships specific to each region or unique habitat (Hódar 1996), these equations may be the first choice for other Pacific Islands until additional relationships are developed.

CHAPTER 8

CONCLUSIONS

This research integrates local deterministic ecological processes with broad scale patterns assembling communities through evolutionary time. Here, I review major findings, suggest areas that would benefit from further examination, and provide a broad overview of some conservation implications of this work.

Regional and Local Processes

The Hawaiian Islands are the premier example of *in situ* evolutionary change and explosive adaptive and non-adaptive radiation (Whittaker 1998, Ziegler 2002). In this situation, one might expect strong legacies of idiosyncratic colonization history and evolutionary change to manifest themselves in local community properties (Ricklefs and Schluter 1993). Indeed, some lineages were absent from particular sites and islands, and the relative abundance and biomass of orders were varied. However, communities with different geological histories were remarkably convergent in species proportions of trophic structure (Chapter 2), and communities appeared to be structured primarily by resource availability.

Across the chronosequence, productivity variables were positively correlated with arthropod abundance and species diversity (Chapter 2). Increases in site richness and in average α-richness at the finest scale were driven by increases in abundance, as richness standardized by individuals was roughly equivalent across comparisons. This suggests that higher productivity may allow rare species to persist in otherwise suboptimal habitats by supporting more individuals on a limited energy base ("consumer rarity hypothesis" *sensu* Siemann 1998, "more individuals hypothesis" *sensu* Srivastava and Lawton 1998).

More productive sites may also support a higher diversity of resources in the regional area, and may show greater 'mass-effects' or spillover of non-resident or generalist species (Shmida and Wilson 1985, Ødegaard 2004).

Fertilization experiments on an open lava flow showed the same patterns: increased productivity was associated with increased arthropod abundance and richness, but not necessarily diversity (Chapters 5, 6). Furthermore, native herbivorous species drove increases in species density (despite the presence of alien species in the regional pool), further suggesting these rare native species may be excluded by community interactions under low-productivity conditions. Careful work manipulating the insects themselves is needed to verify or reject these hypotheses of community regulation. The assemblage of gall-forming psyllids is tractable for such studies (Hodkinson 1984, Price et al. 1997). Selected species compositions can be introduced to defaunated plants in tightly netted field cages, and galls provide an excellent historical record of resource use, emergence and mortality.

There was no monotonic increase in diversity or species packing in local communities with increased geological age as predicted by the age accumulation hypothesis. Species-genus ratios were higher only on Moloka'i Island. A recent study showed more *Tetragnatha* spider species in local communities in the Maui Nui complex, and overall a humped unimodal pattern with geological age across the archipelago (Gillespie 2004). Combined, these studies suggest that arthropod community development may parallel ecosystem development, and species extinction may outweigh accumulation on older islands as ecosystem productivity declines. To definitively disentangle hypotheses of biogeographical history from ecosystem productivity, studies are needed that use independent climatic and substrate gradients within and among islands (Vitousek 1995), and with vastly improved local site replication. In addition, more phylogenetic and autecological data are needed for key lineages to determine both their diversification histories and modes of resource use in these communities.

Top-Down and Bottom-Up Processes

The strong effect of bird predation on arthropods was surprising considering the low density of birds on the recent lava flow (Chapters 3, 4). Birds primarily impacted invertebrate predators, particularly one invasive species of spider. When the latter was excluded from analysis, the effect of bird exclusion was apparent only in fertilized plots. A lingering question is whether these insectivorous birds spent more time foraging in fertilized plots, and if they recruited in response to higher prey availability or because of enhanced vegetation structure. Answers to this question speak directly to the possibility of arthropod population regulation by birds versus passive donor-control (Zheng et al. 1997), and in turn, whether birds are regulated by arthropod food supply (Fretz 2000). With the broad array of *Metrosideros*-dominated forests throughout the islands, comparative studies of bird foraging behavior in different resource combinations should be possible. Observational studies of bird foraging in experimentally defaunated canopy trees would isolate the food availability hypothesis. Moreover, bird exclusion at this low density site must be viewed as a conservative test of top-down control; further studies are needed from higher elevation sites supporting endemic densities of native specialist insectivores, such as the Hawai‘i ‘akepa, *Loxops coccineus* (Scott et al. 1986).

Top-down impacts were apparent primarily on large-bodied higher-order consumers, and did not cascade to indirectly affect primary consumers, let alone producers (Chapter 3). Conversely, bottom-up factors consistently controlled basal consumers, of which detritivores composed the largest fractions of arthropod density and biomass. As in many forested systems (Scheu and Setälä 2002), most production shunts directly to decomposition rather than herbivory. Moreover, fertilization elevated spider densities, but not other invertebrate predators and parasitoids. An important unresolved question concerns the relatives roles of habitat structure and prey abundance in this indirect bottom-up effect on spiders (Rypstra 1983, Denno et al. 2002). Recent studies suggest that changes in habitat structure, such as the accumulation of litter and detritus, drive the increases in spider abundance with fertilization (Langellotto and Denno 2004), but this hypothesis remains untested in the current system.

As mentioned in the previous section, detailed studies of *M. polymorpha* herbivore dynamics would allow a mechanistic understanding of community regulation in this system. I investigated the individual and interactive effects of birds and resources on relative abundance of sessile herbivores and their damage to *M. polymorpha*, and further attempted to identify the specific resource-mediated mechanisms for these effects. Within the top-down and bottom-up experimental design, I tagged over one thousand terminal buds and monitored their growth, leaf development and senescence, and herbivore attack rates at monthly intervals over multiple years (Gruner unpublished data). I also investigated condensed tannins and total phenolics within this design (Forkner and Gruner unpublished data).

Early results from these herbivory studies suggest that psyllid gall-formers and *Carposina* caterpillars were more sensitive to foliar morphology and host identity than to changing nutrient resources. Fertilization altered *M. polymorpha* growth and foliar nutrient levels (Chapter 3), but had moderate impacts on phenolic chemistry (Forkner and Gruner unpublished data) and no effect on pubescence level (Chapter 6). *Metrosideros polymorpha* has high levels of phenolic compounds in both green leaves and leaf litter, and previous studies showed variation among populations in allocation levels was stronger than plasticity to local resource availability (Hättenschwiler et al. 2003). Thus, host genetical effects may explain herbivory variation and segregation of arthropod communities among foliar morphological classes (Chapter 6). Future studies are also needed on the host selection and oviposition behavior of adult psyllids and *Carposina* moths. The identification of chemical and physical cues for (mobile) female oviposition may help to resolve the mechanisms for variation in (sessile) herbivory on *Metrosideros*.

Implications for Conservation

Metrosideros polymorpha (ʻōhiʻa lehua) is found on all the main Hawaiian Islands, naturally occurring from sea level to tree line (>2000 m), in dry, mesic and wet forests. It is the canopy dominant in old growth and the first woody colonist on recent basaltic lava flows (Dawson and Stemmerman 1999). Throughout all these habitats, ʻōhiʻa lehua trees are extremely important resources for native animals. Numerous arthropod species use *M. polymorpha* for either food or habitat space and it may host the largest fauna of any native plant (Swezey 1954, Southwood 1960, Stein 1983, Appendix B). Out of this large pool of ʻōhiʻa arthropods, specialized herbivorous and saprolyxic insects have evolved within at least 14 lineages (Table 8.1). *Metrosideros* is a year-round nectar resource for native bees, moths, thrips, and other insects (Zimmerman 1978, Daly and Magnacca 2003), and for native nectarivorous birds, such as the ʻapapane (*Himatione sanguinea*), ʻiʻiwi (*Vestiara coccinea*) and ʻakohekohe (*Palmeria dolei*) (Carpenter 1976, Carothers 2001, VanGelder and Smith 2001). ʻŌhiʻa lehua also provides important habitat for birds that forage for arthropod prey in its foliage (e.g., ʻakepa [*Loxops coccineus*]) and bark (e.g., Hawaiʻi creeper [*Oreomystis mana*]) (Baldwin 1953, Conant 1981, Fretz 2000). It can be argued that *M. polymorpha* is the backbone of Hawaiian

Table 8.1. Arthropod lineages with specialist feeders on *Metrosideros* species. Host tissue refers to plant organs fed upon by a lineage. The total richness of endemic species from each genus is listed, followed by the total number recorded from *Metrosideros* and the number hypothesized as specialists. Sources of these data are listed. All published sources predating 1954 are cited in Swezey (1954).

Order	Family	Genus	Host Tissue	Total no. spp.	No. spp. *Metrosideros* feeders	No. spp. specialists	Source†
Coleoptera	Cerambycidae	*Plagithmysus*	wood	139	10	7	3, 8
Heteroptera	Lygaeidae	*Glyptonysius*	seeds	4	2	2	2
Heteroptera	Lygaeidae	*Oceanides*	seeds	29	4	3	1, 2, 3, 4, 10, 11
Heteroptera	Miridae	*Orthotylus*	mesophyll	12	4	2	2
Heteroptera	Miridae	*Sarona*	mesophyll	40	1	1	5, 11
Homoptera	Cicadellidae	*Nesophrosyne*	phloem	62	5	4	1, 3, 4
Homoptera	Cixiidae	*Oliarus*	roots	66	6	5	3, 4, 9
Homoptera	Delphacidae	*Leialoha*	phloem	11	8	7	1, 2, 3, 4
Homoptera	Pseudococcidae	*Gallulacoccus*	galls	1	1	1	4
Homoptera	Pseudococcidae	*Ohiacoccus*	phloem	1	1	1	4
Homoptera	Triozidae	*Kuwayama*	galls	11	6	5	1, 2, 3, 4, 7
Homoptera	Triozidae	*Trioza*	galls	12	8	7	1, 2, 3, 4, 7, 11
Lepidoptera	Carposinidae	*Carposina*	bud mines	49	5	3	1, 6
Lepidoptera	Gracillaridae	*Philodoria*	leaf mines	30	2	2	4, 6
				467	63	50	

† Literature sources: 1 = Gruner unpublished data and personal observations; 2 = Gruner & Polhemus unpublished data, Gruner & Polhemus 2003; 3 = Swezey 1954; 4 = Stein 1983; 5 = Asquith 1994; 6 = Zimmerman 1978; 7 = Nishida et al. 1980; 8 = Gressitt & Davis 1969; 9 = Hoch & Howarth 1999; 10 = Polhemus 2002; 11 = Gagné 1976.

forests and one of the most vital resources for the long-term sustainability of watersheds and their biodiversity in the islands.

This research has increased our knowledge of the distribution and abundance of native and introduced arthropods. More than 50,000 individual arthropods from 23 orders, 130 families, and approximately 700 species in 280 genera were reported from *Metrosideros* collections in these studies. Although morphospecies designations were necessary for the mites (order Acari) and for several large endemic radiations not recently revised (e.g., *Proterhinus* weevils [Aglycyderidae]), I pursued species-level identifications in every arthropod group encountered. At least nine new introductions to the Islands were discovered, and new island range extensions were recorded for over 40 other introduced and endemic species (Gruner in press-a, Appendix B). Furthermore, an estimated 5-10% of the taxa are new to science and are now available for further taxonomic study and description (e.g., Polhemus 2002).

These studies may have predictive value for understanding resource availability of *Metrosideros* forests for canopy-foraging native birds. I showed that arthropod abundance, diversity, and often biomass were elevated in more productive forests (Chapter 2). Furthermore, I established the direct link between nutrient resources, trees, and arthropod numbers in fertilization studies (Chapter 3-6). These results showed that resource availability cascades up the food chain to increase the numbers of detritivores, herbivores, and even spiders, a favored food item for birds in Hawaiian forests (Perkins 1903, Baldwin 1953, Ralph et al. unpublished data). Management plans of many endangered bird species in Hawai‘i involve reintroduction and translocation of forest birds to former or novel ranges (Banko et al. 2001). My findings provide information on one of the variables to consider when choosing locations for releases.

These studies also demonstrated the ecosystems impacts of forest birds. Even at the low densities at the Mauna Loa site, birds altered the relative abundances of arthropods, especially spiders, and subdued the irruption of a previously rare introduced spider (Chapters 3-5). Mobile generalist predators, such as insectivorous birds, may stabilize food webs through many weak interactions across food web compartments (McCann et al. 1998, Neutel et al. 2002), and by regulating potentially dominant species at endemic levels (Holmes 1990). In this sense, the possibility that generalist insectivores maintain community stability and arthropod diversity deserves further investigation.

However, top predators often are the most prone to extinction due to their comparative rarity and higher range size requirements (Duffy 2002). Since prehistoric times, extinction rates of birds on oceanic islands have vastly exceeded rates on continents (Steadman 1995). This study suggests that further loss of insectivorous birds or changes in species composition, as with forest fragmentation (Sekercioglu et al. 2002) and global climate change (Benning et al. 2002), may have ripple effects altering invasibility of island communities. Invasive birds spread non-native seeds (Woodward et al. 1990), may compete with native birds (Mountainspring and Scott 1985), and serve as reservoirs for disease vectors (Tripathy et al. 2000); however, they may also fill functional roles in ecosystems vacated by extinct or declining native birds. This dissertation research exposes the functional interdependencies of *Metrosideros polymorpha*, arthropods and birds in Hawaiian forests.

APPENDIX A

LOCALITIES, DATES, METHODS AND COLLECTORS FOR *METROSIDEROS POLYMORPHA* ARTHROPOD STUDIES

Two-letter site codes are used to identify sites listed in Appendix B. The first six sites, all sampled in 1996, were located in Hawai‘i Volcanoes National Park and were sampled qualitatively only (presence/absence). Beginning with the second sampling near Thurston Lava Tube in 1997, all remaining localities were sampled with quantitative methods.

Site	Locality	Lat. (N)§	Long. (W)§	Elev. (m)	Date(s)	Method	Collector(s)‡
Hawai‘i							
HP	Hilina Pali & Chain of Craters	19.3790°	155.2379°	1055	21-22.x.96	fogging	DSG,DAP,DF
KI	Kīpuka Kī, Mauna Loa Road	19.4438°	155.3190°	1305	24-25.x.96	fogging	DSG,DAP,DF
ML	Keōmoku flow, Mauna Loa Road	19.4764°	155.3647°	1725	24.x.96	fogging	DSG,DAP
OL	‘Ōla‘a tract, Wright Road	19.4640°	155.2472°	1170	25.x.96	fogging	DSG,DAP,KNM
BP	Near Bird Park, Mauna Loa Road	19.4328°	155.2981°	1200	25.x.96	fogging	DSG,DAP
VO	Thurston Lava Tube & Escape Rd.	19.4156°	155.2354°	1200	23.x.96	fogging	DSG,DAP,DF
VO	Thurston Lava Tube & Escape Rd.	19.4156°	155.2354°	1200	6-8.x.97	fogging	DSG,DAP
TP	Upper Waiākea Forest Reserve, Tree Planting Road, 1881 flow	19.6642°	155.2836°	1280	†	clipping	DSG
LA	Laupāhoehoe Forest Reserve, Blair Road	19.9277°	155.2958°	1220	3-5.vi.97	fogging	DSG,DAP
LA	Laupāhoehoe Forest Reserve, Blair Road	19.9277°	155.2958°	1220	6.xi.97	fogging	DSG,JSF,LSS
KH	Kohala Forest Reserve	20.0519°	155.6812°	1150	12-14.x.97	fogging	DSG,DAP
Moloka‘i							
MO	TNC Kamakou Preserve, Kolekole	21.1053°	156.9000°	1185	22-24.x.97	fogging	DSG,DAP
Kaua‘i							
KA	Nāpali-Kona Forest Reserve	22.1422°	159.6264°	1130	29-30.x.97	fogging	DSG,DAP

§ North American Datum 1983.

‡ Collectors: DSG = Daniel S. Gruner, DAP = Dan A. Polhemus, DF = David Foote, KNM = Karl N. Magnacca, JSF = J. Scott Fretz, LSS = Lou S. Santiago.

† Upper Waiākea Forest Reserve site was sampled on multiple dates: 25-28.viii.98, 24.vi.99, 30.vii.99, 30.viii.99, 29.ix.99, 31.x.99, 14.xii.99, 12.v.00, 1.vi.00, 16-18,24-25.iv.01, 1-3.v.01.

APPENDIX B

LIST OF ARTHROPOD SPECIES COLLECTED FROM *METROSIDEROS POLYMORPHA* DURING 1996-2001

Two-letter site abbreviations refer to quantitative collection localities listed in Appendix A, and "1996" includes all sites in Hawai'i Volcanoes National Park sampled by non-quantitative pyrethrum fogging techniques. Biogeographic origin (adv = adventive; end = endemic; ind = indigenous; pur = purposely introduced; ? = undetermined) and feeding guild (chew = chewer; detr = detritivore; flow = flowers; fung = fungivore; gall = gall-former; omni = omnivore; pred = predator; para = parasitoid; sap = xylem, phloem, or mesophyll feeder; seed = seed feeder; tou = tourist; wood = wood- or twig-borer; ? = undetermined) are listed. Quantitative sites are scored by presence (+) or absence (-). Site codes are listed for 1996 when positively recorded, but absence is not noted because of the qualitative nature of these collections. New state (NSR) or island (NIR) records are listed in place of (+) where appropriate; questionable range extensions are noted (?). Determiners were: AMMR = Alastair M.M. Richardson, AV = Amy Vandergast, BRK = Bernarr R. Kumashiro, CAT = Catherine A. Tauber, CPE = Curtis P. Ewing, DAP = Dan A. Polhemus, DMP = Diana M. Percy, DSG = Daniel S. Gruner, ELM = Ed L. Mockford, GAPG = Gary A.P. Gibson, GAS = G. Al Samuelson, GWB = George W. Byers, JAB = Joe A. Beatty, JEG = Jessica E. Garb, JKL = Jim K. Liebherr, JSN = John S. Noyes, JTH = John T. Huber, KTA = Keith T. Arakaki, KYK = Ken Y. Kaneshiro, LM = Lubomir Masner, MA = Manfred Asche, MAA = Miquel A. Arnedo, MLG = M. Lee Goff, MWG = Michael W. Gates, NJR = Neil J. Reimer, NLE = Neal L. Evenhuis, RGG = Rosemary G. Gillespie, RJG = Ray J. Gagné, SLM = Steve L. Montgomery, TAB = Todd A. Blackledge.

Appendix B. List of *Metrosideros* arthropod species.

Taxon	**Origin**	**Guild**	**1996**	**VO**	**TP**	**LA**	**KH**	**MO**	**KA**	**Det.**
CLASS **ARACHNIDA**										
Order **Acari**										
Family **Anystidae**										
Anystidae g. sp. 1	adv	pred	HP VO	+	+	+	+	+	+	MLG
Families undet.										
Acari g. sp. 2	?	?		-	+	-	-	-	-	DSG
Acari g. sp. 3	?	?		-	+	-	-	-	-	DSG
Acari g. sp. 4	?	?		-	+	+	+	-	-	DSG
Acari g. sp. 5	?	?		-	+	-	-	-	-	DSG
Acari g. sp. 6	?	?		-	+	-	-	-	-	DSG
Acari g. sp. 7	?	?		-	+	+	-	+	-	DSG
Acari g. sp. 8	?	?		-	+	+	-	-	-	DSG
Acari g. sp. 9	?	?		-	+	+	-	-	-	DSG
Acari g. sp. 10	?	?		-	+	-	+	+	+	DSG
Acari g. sp. 12	?	?		-	+	-	-	-	-	DSG
Acari g. sp. 13	?	?		-	+	+	-	-	-	DSG
Acari g. sp. 14	?	?		-	+	-	-	-	-	DSG
Acari g. sp. 15	?	?		-	+	-	+	-	+	DSG
Acari g. sp. 16	?	?		+	-	+	+	+	-	DSG
Acari g. sp. 17	?	?		-	-	+	-	-	-	DSG
Acari g. sp. 18	?	?		-	-	+	-	-	-	DSG
Acari g. sp. 19	?	?		-	-	+	+	+	-	DSG
Acari g. sp. 20	?	?		-	-	+	-	-	-	DSG
Acari g. sp. 21	?	?		-	-	-	+	-	-	DSG
Acari g. sp. 22	?	?		-	-	-	+	-	-	DSG
Acari g. sp. 23	?	?		-	-	-	+	-	-	DSG
Acari g. sp. 24	?	?		-	-	-	+	-	-	DSG
Acari g. sp. 25	?	?		-	-	-	+	-	-	DSG
Acari g. sp. 26	?	?		-	-	-	+	-	-	DSG
Acari g. sp. 27	?	?		+	-	-	-	-	-	DSG
Acari g. sp. 28	?	?		+	-	-	-	-	-	DSG
Acari g. sp. 29	?	?		-	-	-	-	+	+	DSG
Acari g. sp. 30	?	?		-	-	-	-	+	-	DSG

Appendix B. (Continued) List of *Metrosideros* arthropod species.

Taxon	Origin	Guild	1996	VO	TP	LA	KH	MO	KA	Det.
Acari g. sp. 31	?	?		-	-	-	-	+	-	DSG
Acari g. sp. 32	?	?		-	-	-	-	+	-	DSG
Acari g. sp. 33	?	?		-	-	-	-	+	-	DSG
Order **Araneae**										
Family **Araneidae**										
Araneus emmae Simon, 1900	end	pred		+	+	+	+	+	+	JAB
Araneus kapiolaniae Simon, 1900	end	pred		+	+	-	-	-	-	JAB
Araneus sp. 1	end	pred		-	+	-	-	-	-	JAB
Argiope trifasciata (Forskal, 1775)	adv	pred		-	+	-	-	-	-	JAB
Cyclosa perkinsi Simon, 1900	end	pred		-	+	-	-	-	-	TAB
Cyclosa simplicicauda Simon, 1900	end	pred		-	-	-	-	-	NIR?	TAB
Cyclosa sp. 2	end	pred		-	-	-	-	+	+	DSG
Family **Dysderidae**										
Dysdera crocota C.L. Koch, 1838	adv	pred		-	-	-	-	+	-	JAB
Family **Linyphiidae**										
Erigone autumnalis Emerton, 1882	adv	pred		+	+	+	+	NIR?	+	JAB
Linyphiidae g. sp. 1	adv	pred		-	NSR?	-	-	-	-	DSG
Linyphiidae g. sp. 2	adv	pred		+	+	-	-	-	-	DSG
Tenuiphantes tenuis (Blackwall, 1952)	adv	pred		-	-	-	-	NIR	-	JAB
Cheiracanthium mordax L. Koch, 1866	adv	pred		-	+	-	-	-	-	DSG
Family **Philodromidae**										
Pagiopalus atomarius Simon, 1900	end	pred		+	+	+	+	+	+	JAB
Family **Salticidae**										
Havaika navatus (Simon, 1900)	end	pred		-	-	-	-	-	+	JAB
Havaika pubens (Simon, 1900)	end	pred		-	-	-	-	+	-	JAB
Havaika sp. 3	end	pred		+	+	+	+	-	-	JAB
Family **Tetragnathidae**										
Tetragnatha "golden dome"	end	pred		+	-	+	+	-	-	AV
Tetragnatha "long clawed"	end	pred		-	-	-	+	-	-	RGG
Tetragnatha "small spiny"	end	pred		-	-	+	-	-	-	RGG
Tetragnatha acuta Gillespie, 1992	end	pred		+	+	-	-	+	-	DSG
Tetragnatha anuenue Gillespie, 2002	end	pred		+	+	+	+	-	-	AV
Tetragnatha brevignatha Gillespie, 1991	end	pred		-	-	+	+	-	-	AV

Appendix B. (Continued) List of *Metrosideros* arthropod species.

Taxon	Origin	Guild	1996	VO	TP	LA	KH	MO	KA	Det.
Tetragnatha hawaiiensis Simon, 1900	end	pred		+	+	+	-	-	+	AV
Tetragnatha kauaiensis Simon, 1900	end	pred		-	-	-	-	-	+	DSG
Tetragnatha kea Gillespie, 1994	end	pred		-	-	+	-	-	-	RGG
Tetragnatha maka Gillespie, 1994	end	pred		-	-	-	-	-	+	DSG
Tetragnatha perkinsii Simon, 1900	end	pred		-	+	-	-	-	-	AV
Tetragnatha quasimodo Gillespie, 1991	end	pred		+	+	+	+	+	-	AV
Family **Theridiidae**										
Achaearanea cf. *riparia* (Blackwall, 1834)	adv	pred	KI	-	+	-	-	-	-	JAB
Argyrodes argentatus Cambridge, 1880	adv	pred		-	-	-	-	NIR	-	JAB
Argyrodes corniger (Simon), 1900	end	pred		-	-	+	-	-	-	JAB
Argyrodes sp. 1	end	pred		+	-	+	-	-	-	DSG
Argyrodes sp. 2	end	pred		+	-	+	-	-	-	DSG
Theridiidae g. sp. 4	?	pred		-	-	-	+	-	-	DSG
Theridion grallator Simon, 1900	end	pred		+	-	+	+	+	-	DSG
Theridion mauiense Simon, 1900	end	pred		-	-	-	-	NIR	-	MAA
Theridion melinum Simon, 1900	end	pred		-	+	+	-	-	-	MAA
Theridion n. sp. 1	end	pred		-	-	-	-	-	+	MAA
Theridion praetextum Simon, 1900	end	pred		-	+	+	-	-	-	MAA
Theridion sp. 6	end	pred		-	-	-	-	-	+	MAA
Family **Thomisidae**										
Mecaphesa naevigerum (Simon), 1900	end	pred		-	-	+	-	-	-	JEG
Misumenops anguliventris (Simon, 1900)	end	pred		-	+	-	+	-	+	JEG
Misumenops discretus (Suman), 1970	end	pred		-	-	-	-	-	+	JEG
Misumenops facundus (Suman, 1970)	end	pred		-	+	+	-	-	-	JEG
Misumenops junctus (Suman), 1970	end	pred		-	-	+	-	-	-	JEG
Misumenops sp. 5	end	pred		-	-	-	+	-	-	DSG
Misumenops sp. 6	end	pred		-	-	-	-	+	-	DSG
CLASS **INSECTA**										
Order **Blattodea**										
Family **Blattellidae**										
Balta similis (Saussure, 1869)	adv	detr	HP VO	+	-	+	+	+	+	DSG

Appendix B. (Continued) List of *Metrosideros* arthropod species.

Taxon	Origin	Guild	1996	VO	TP	LA	KH	MO	KA	Det.
Order **Coleoptera**										
Family **Aglycyderidae**										
Proterhinus arhopalus Perkins, 1900	end	wood		-	-	-	-	+	-	DSG
Proterhinus blackburni Sharp, 1878	end	wood		+	-	+	+	+	+	DSG
Proterhinus similis Sharp, 1885	end	wood		+	-	-	+	-	-	DSG
Proterhinus sp. nr. *simplex* Sharp, 1878	end	wood		-	-	-	+	+	-	DSG
Proterhinus sp. 3	end	wood		-	-	-	+	-	-	DSG
Proterhinus sp. 6	end	wood		-	-	+	+	-	-	DSG
Proterhinus sp. 7	end	wood		-	-	+	-	-	-	DSG
Proterhinus sp. 9	end	wood		-	-	-	-	+	-	DSG
Proterhinus sp. 11	end	wood		-	-	-	-	+	-	DSG
Proterhinus sp. 12	end	wood		-	-	-	-	+	-	DSG
Proterhinus sp. 16	end	wood		-	-	-	-	+	-	DSG
Proterhinus sp. 17	end	wood		-	-	-	-	-	+	DSG
Proterhinus sp. 18	end	wood		-	-	-	-	-	+	DSG
Proterhinus sp. 19	end	wood		-	-	-	-	-	+	DSG
Proterhinus sp. 23	end	wood		-	-	-	-	-	+	DSG
Proterhinus sp. 25	end	wood		-	-	-	-	-	+	DSG
Proterhinus sp. 26	end	wood		-	-	-	-	-	+	DSG
Proterhinus sp. 27	end	wood		-	-	-	-	-	+	DSG
Proterhinus sp. 28	end	wood		-	-	-	-	-	+	DSG
Proterhinus sp. 29	end	wood		-	-	-	-	-	+	DSG
Proterhinus tarsalis Sharp, 1885	end	wood		-	-	+	+	-	-	DSG
Family **Anobiidae**										
Mirosternus sp. 1	end	wood		-	-	-	-	-	+	DSG
Mirosternus sp. 2	end	wood		-	-	-	-	-	+	DSG
Xyletobius collingei Perkins, 1910	end	wood		-	-	-	+	-	-	DSG
Xyletobius proteus proteus Perkins, 1910	end	wood		+	-	-	-	-	-	DSG
Xyletobius sp. 1	end	wood		+	-	-	-	-	-	DSG
Xyletobius sp. 2	end	wood		-	-	-	+	-	-	DSG
Xyletobius sp. 3	end	wood		-	-	-	-	+	-	DSG
Xyletobius sp. 4	end	wood		-	-	+	-	-	-	DSG

Appendix B. (Continued) List of *Metrosideros* arthropod species.

Taxon	Origin	Guild	1996	VO	TP	LA	KH	MO	KA	Det.
Family **Anthribidae**										
Araecerus varians Jordan, 1946	adv	fung		-	-	+	-	-	+	GAS
Family **Carabidae**										
Blackburnia abax (Sharp, 1903)	end	pred		-	-	-	-	+	-	JKL
Blackburnia aterrima (Sharp, 1903)	end	pred		-	-	-	-	-	+	JKL
Blackburnia cheloniceps (Perkins, 1917)	end	pred		-	-	-	-	+	-	JKL
Blackburnia constricta (Sharp, 1903)	end	pred		-	-	-	-	+	-	JKL
Blackburnia fraudator (Sharp, 1903)	end	pred		-	-	-	-	+	-	JKL
Blackburnia hawaiiensis (Sharp, 1903)	end	pred		+	-	-	-	-	-	JKL
Blackburnia kilauea Liebherr & Zimmerman, 2000	end	pred		+	-	-	+	-	-	JKL
Blackburnia kukui Liebherr, 2000	end	pred		-	+	-	-	-	-	JKL
Blackburnia longipes (Sharp, 1903)	end	pred		-	-	-	-	+	-	JKL
Blackburnia pavida (Sharp, 1903)	end	pred		-	-	-	-	-	+	JKL
Blackburnia sphodriformis (Sharp, 1903)	end	pred		-	-	-	-	+	-	JKL
Blackburnia tricolor (Sharp, 1903)	end	pred		-	-	-	-	+	-	JKL
Blackburnia vagans (Sharp, 1903)	end	pred		-	-	-	-	+	-	JKL
Laemostenus complanatus (Dejean, 1828)	adv	pred	VO, OL	+	-	-	-	-	-	JKL
Mecyclothorax deverilli (Blackburn, 1879)	end	pred		-	+	+	+	-	-	JKL
Mecyclothorax molokiae (Sharp, 1903)	end	pred		-	-	-	-	+	-	JKL
Mecyclothorax n. sp. nr. *platysminus* (Sharp, 1903)	end	pred		-	-	-	-	+	-	JKL
Mecyclothorax oculatus Sharp, 1903	end	pred		-	-	-	-	+	-	JKL
Mecyclothorax paradoxus (Blackburn, 1879)	end	pred		-	+	-	-	-	-	JKL
Mecyclothorax variipes (Sharp, 1903)	end	pred		-	-	-	+	-	-	JKL
Family **Cerambycidae**										
Curtomerus flavus (Fabricius, 1775)	adv	wood	HP	-	-	-	-	-	-	DSG
Plagithmysus bilineatus Sharp, 1896	end	wood		-	-	-	+	-	-	DSG
Family **Chrysomelidae**										
Diachus auratus (Fabricius, 1801)	adv	tou	KI	-	-	-	-	-	-	GAS
Family **Ciidae**										
Apterocis ephistemoides (Sharp, 1885)	end	fung		-	-	-	-	+	-	DSG
Apterocis hawaiiensis Perkins, 1900	end	fung		-	-	+	-	-	-	DSG

Appendix B. (Continued) List of *Metrosideros* arthropod species.

Taxon	Origin	Guild	1996	VO	TP	LA	KH	MO	KA	Det.
Apterocis hystrix Perkins, 1900	end	fung		-	-	-	-	NIR?	-	DSG
Apterocis variabilis Perkins, 1900	end	fung		-	-	-	-	-	NIR?	DSG
Apterocis variegatus Perkins, 1900	end	fung		-	-	-	-	NIR	-	DSG
Apterocis nr. *variegatus* Perkins, 1900	end	fung		-	-	-	+	-	-	DSG
Cis calidus Sharp, 1885	end	fung		-	-	-	-	-	+	DSG
Cis evanescens Sharp, 1879	end	fung		-	-	-	-	-	+	DSG
Cis insulicola Dalla Torre, 1911	end	fung		+	-	-	-	-	-	DSG
Cis molokaiensis Perkins, 1900	end	fung		-	-	-	-	+	-	DSG
Cis nigrofasciatus Blackburn, 1885	end	fung		-	-	NIR	NIR	NIR	-	DSG
Cis pacificus Sharp, 1879	end	fung		NIR	-	-	NIR	-	-	DSG
Cis porcatus Sharp, 1879	end	fung		+	+	+	+	NIR	+	DSG
Cis setarius Sharp, 1885	end	fung		-	-	+	+	NIR	-	DSG
Cis signatus Sharp, 1879	end	fung		+	-	+	+	+	+	DSG
Cis sp. 1	end	fung		-	-	-	+	+	-	DSG
Family **Coccinellidae**										
Halmus chalybeus (Boisduval, 1835)	pur	pred	KI OL	-	-	+	+	+	+	DSG
Scymnodes lividigaster (Mulsant, 1853)	pur	pred	KI	-	-	+	-	-	-	DSG
Family **Cucujidae**										
Cryptamorpha desjardinsi (Guerin-Meneville, 1844)	adv	pred		-	-	+	+	-	+	DSG
Psammoechus insularus (Sharp, 1885)	adv	pred	HP OL	-	-	-	-	-	-	GAS
Family **Curculionidae**										
Acalles n. sp. 1	end	wood		-	-	-	-	+	-	GAS
Asynonychus godmanni Crotch, 1867	adv	tou		+	-	+	+	-	+	DSG
Deinocossonus nesiotes Perkins, 1900	end	wood		-	-	-	-	-	+	DSG
Hypera postica (Gyllenhal, 1834)	adv	tou		-	-	-	+	-	-	GAS
Nesotocus munroi Perkins, 1900	end	tou		-	-	+	+	-	-	DSG
Oodemas corticis Perkins, 1900	end	tou		-	-	-	-	+	-	DSG
Oodemas multiforme Perkins, 1900	end	wood		-	-	-	+	-	-	DSG
Oodemas paludicola Perkins, 1933	end	wood		-	-	-	-	+	-	DSG
Stenotrupis prolixa (Sharp, 1878)	end	tou		-	-	-	-	+	-	GAS
Syagrius fulvitarsis Pascoe, 1875	adv	tou		+	-	-	-	-	-	GAS

Appendix B. (Continued) List of *Metrosideros* arthropod species.

Taxon	Origin	Guild	1996	VO	TP	LA	KH	MO	KA	Det.
Family **Dermestidae**										
Labrocerus laticornis Sharp, 1908	end	detr		-	-	+	-	-	-	DSG
Family **Elateridae**										
Conoderus exsul (Sharp, 1877)	adv	pred		-	-	-	+	-	-	GAS
Eopenthes konae Blackburn, 1885	end	pred		-	+	-	-	-	-	DSG
Eopenthes tinctus Sharp, 1908	end	pred		-	+	-	-	-	-	DSG
Family **Eucnemidae**										
Dromaeolus n. sp. nr. *puncticollis*	end	wood		+	-	-	+	-	-	DSG
Family **Histeridae**										
Aeletes subalatus (Scott), 1908	end	detr		-	-	-	-	+	-	DSG
Family **Hydrophilidae**										
Cercyon sp. 1	adv	detr		-	-	NSR	-	-	-	DSG
Family **Lathridiidae**										
Aridius nodifer (Westwood, 1839)	adv	fung		-	-	-	+	-	NIR	GAS
Family **Nitidulidae**										
Epuraea ocularis Fairmaire, 1849	adv	detr		-	-	-	-	NIR	-	CPE
Eupetinus curtus Scott, 1908	end	detr		-	-	-	-	+	-	CPE
Eupetinus impressus (Sharp), 1878	end	detr		-	-	-	-	-	+	CPE
Eupetinus spretus (Blackburn), 1885	end	detr		-	-	-	+	-	-	CPE
Eupetinus striatus (Sharp), 1881	end	detr		+	+	+	-	-	-	CPE
Eupetinus sulcatus Scott, 1908	end	detr		-	-	-	-	+	-	CPE
Gonioryctus molokaiensis Sharp, 1908	end	detr		-	-	-	-	+	-	CPE
Goniothorax inaequalis (Sharp), 1908	end	detr		-	-	+	-	-	-	CPE
Nesopeplus floricola (Blackburn), 1885	end	detr		-	-	-	-	-	+	CPE
Nesopeplus inauratus (Sharp), 1881	end	detr		-	-	+	+	-	-	CPE
Nesopeplus latiusculus Scott, 1908	end	detr		-	-	-	-	+	-	CPE
Nesopetinus rudis Sharp, 1908	end	detr		-	-	-	+	-	-	CPE
Nesopetinus varius (Sharp), 1881	end	detr		-	-	+	-	-	-	CPE
Orthostolus germanus Sharp, 1908	end	detr		-	-	-	-	+	-	CPE
Stelidota geminata Say	adv	detr		-	-	-	+	-	-	CPE
Family **Ptiliidae**										
Acrotrichis discoloroides Johnson, 1969	adv	detr		NIR	-	NIR	-	-	-	DSG
Ptiliodes insignis Scott, 1908	end	detr		-	-	-	+	-	-	DSG

Appendix B. (Continued) List of *Metrosideros* arthropod species.

Taxon	Origin	Guild	1996	VO	TP	LA	KH	MO	KA	Det.
Family **Scolytidae**										
Xyleborinus saxeseni (Ratzeburg, 1837)	adv	wood		+	-	-	+	-	-	GAS
Xyleborus hiiaka Samuelson, 1981	end	wood		-	-	-	+	-	-	DSG
Xyleborus simillimus Perkins, 1900	end	wood		+	-	+	-	-	-	DSG
Xylosandrus crassiusculus (Motschulsky, 1866)	adv	wood	HP	-	-	-	-	-	-	GAS
Family **Staphylinidae**										
Aleochara sp.	adv	pred		-	+	+	-	-	-	DSG
Anotylus sp. 1	adv	pred		-	-	-	+	-	-	DSG
Anotylus sp. 2	adv	pred		-	+	-	-	+	-	DSG
Atheta coriaria (Kraatz, 1856)	adv	pred	HP	-	-	-	-	-	-	DSG
Creophilus maxillosus (Linnaeus, 1758)	adv	pred		-	+	-	-	-	-	DSG
Myllaena sp. 1	end	pred		-	-	-	+	-	-	DSG
Myllaena sp. 2	end	pred		-	+	-	-	-	-	DSG
Oligota glabra Sharp, 1880	end	pred		-	+	-	-	-	-	DSG
Oligota sp. 1	end	pred		-	-	-	+	+	-	DSG
Oligota sp. 2	end	pred		-	-	-	-	-	+	DSG
Oligota sp. 3	end	pred		-	-	+	-	-	-	DSG
Oligota sp. 4	end	pred		+	+	+	+	-	-	DSG
Oligota sp. 5 nr. *glabra*	end	pred		-	-	+	-	-	-	DSG
Oligota sp. 6	end	pred		-	-	-	+	-	-	DSG
Osorius rufipes Motshulsky, 1857	adv	pred		-	-	+	+	-	-	DSG
Sunius debilicornis (Wollaston, 1857)	adv	pred		-	-	-	-	+	-	DSG
Thoracophorus blackburni (Sharp, 1880)	end	pred		+	-	-	-	-	-	DSG
Order **Collembola**										
Family **Entomobryidae**										
Entomobrya laha Christiansen & Bellinger, 1992	end	detr		+	+	+	+	-	+	DSG
Entomobrya mauka Christiansen & Bellinger, 1992	end	detr		-	-	-	-	+	-	DSG
Entomobrya sauteri Borner, 1909	adv	detr		+	-	-	-	-	-	DSG
Entomobrya socia (Denis, 1929)	adv	detr		+	+	+	-	-	-	DSG
Entomobryidae g. sp. 3	?	detr		-	-	-	-	-	+	DSG

Appendix B. (Continued) List of *Metrosideros* arthropod species.

Taxon	Origin	Guild	1996	VO	TP	LA	KH	MO	KA	Det.
Salina celebensis (Schaeffer, 1898)	adv	detr		+	+	+	+	+	+	DSG
Tomocerus minor (Lubbock, 1862)	adv	detr		+	+	-	-	+	-	DSG
Willowsia kahlertae Christiansen & Bellinger, 1992	end	detr		-	-	-	+	-	-	DSG
Family **Isotomidae**										
Isotoma notabilis Schaeffer, 1896	adv	detr		-	+	-	+	-	-	DSG
Isotoma sensibilis Tullberg, 1876	adv	detr		-	+	-	-	-	-	DSG
Family **Sminthuridae**										
Dicyrtoma brevifibra Snider, 1990	end	detr		-	-	-	-	+	-	DSG
Order **Diptera**										
Family **Agromyzidae**										
Phytoliriomyza montana Frick, 1953	end	wood		-	-	-	+	-	-	DSG
Family **Anisopodidae**										
Sylvicola cinctus (Fabricius, 1787)	adv	detr	VO	+	-	+	+	-	-	DSG
Family **Asteidae**										
Asteia apicalis Grimshaw, 1901	end	detr		+	-	-	+	-	-	DSG
Asteia molokaiensis Hardy & Delfinado, 1980	end	detr		-	-	-	-	+	-	DSG
Family **Calliphoridae**										
Calliphoridae g. sp. 1	?	detr		-	-	+	-	-	-	DSG
Calliphoridae g. sp. 2	?	detr		-	-	+	-	-	-	DSG
Calliphoridae g. sp. 3	?	detr		+	-	-	-	-	-	DSG
Family **Cecidomyiidae**										
Porricondylinae g. sp.	adv	?		+	-	-	-	-	-	RJG
Contarinia sp. 1	adv	flow		+	-	-	+	-	-	RJG
Cecidomyiinae g. sp.	?	detr		+	-	-	+	+	-	RJG
Monardia recondita Hardy, 1960	end	detr		+	-	+	+	NIR	-	DSG
Mycophila fungicola Felt, 1911	adv	fung		NIR?	-	-	-	-	-	DSG
Trisopsis oleae Kieffler, 1912	adv	pred		-	-	-	-	NIR	-	DSG
Family **Ceratopogonidae**										
Dasyhelea hawaiiensis Macfie, 1934	end	detr		-	+	+	+	+	+	KTA
Dasyhelea platychaeta Hardy, 1960	end	detr		-	-	-	-	NIR?	-	DSG
Forcipomyia hardyi Wirth & Howarth, 1982	end	detr		+	+	+	+	+	+	KTA

Appendix B. (Continued) List of *Metrosideros* arthropod species.

Taxon	**Origin**	**Guild**	**1996**	**VO**	**TP**	**LA**	**KH**	**MO**	**KA**	**Det.**
Forcipomyia pholeter Wirth & Howarth, 1982	end	detr		+	-	-	-	-	-	DSG
Family **Chironomidae**										
Orthocladius grimshawi Hardy, 1960	end	detr		-	-	-	-	-	NIR?	DSG
Orthocladius membranisensoria Hardy, 1960	end	detr		-	-	-	+	-	-	DSG
Orthocladius sp. 2	end	detr		-	-	-	-	+	-	DSG
Orthocladius williamsi Hardy, 1960	end	detr		+	+	+	+	+	-	DSG
Pseudosmittia paraconjuncta (Hardy, 1960)	end	detr		+	-	-	-	-	-	DSG
Family **Dolichopodidae**										
Campsicnemus bryophilus (Adachi, 1954)	end	pred		-	-	-	-	+	-	DSG
Campsicnemus calcaritarsus Adachi, 1953	end	pred		-	-	-	-	+	-	DSG
Campsicnemus distinctus Hardy & Kohn, 1964	end	pred		-	-	+	-	-	-	DSG
Campsicnemus modicus Hardy & Kohn, 1964	end	pred		+	-	-	-	-	-	DSG
Campsicnemus norops Hardy & Kohn, 1964	end	pred		-	-	-	-	-	+	NLE
Campsicnemus scolimerus Hardy & Kohn, 1964	end	pred	VO	-	-	-	-	-	-	NLE
Campsicnemus sp. 6	end	pred		-	-	-	+	-	-	DSG
Dolichopus exsul Aldrich, 1922	adv	pred		-	-	+	-	-	-	DSG
Eurynogaster argentata Hardy & Kohn, 1964	end	pred		-	-	-	+	-	-	DSG
Eurynogaster hawaiiensis (Grimshaw, 1901)	end	pred		-	-	-	+	-	-	DSG
Eurynogaster maculata Parent, 1940	end	pred		+	-	+	+	-	-	DSG
Eurynogaster n. sp. 1	end	pred		-	-	-	-	+	-	DSG & NLE
Eurynogaster n. sp. 2	end	pred		-	-	-	-	+	-	DSG & NLE
Eurynogaster sp. A	end	pred		-	-	-	-	+	-	DSG
Eurynogaster variabilis Hardy & Kohn, 1964	end	pred		-	+	-	-	-	-	DSG
Family **Drosophilidae**										
Drosophila canipolita Hardy, 1965	end	fung		+	-	+	-	-	-	KYK
Drosophila conformis Hardy, 1965	end	detr		+	-	+	+	-	-	KYK
Drosophila demipolita Hardy, 1965	end	fung		-	-	+	-	-	-	DSG
Drosophila immigrans Sturtevant, 1921	adv	tou		-	-	+	-	-	-	DSG

Appendix B. (Continued) List of *Metrosideros* arthropod species.

Taxon	Origin	Guild	1996	VO	TP	LA	KH	MO	KA	Det.
Drosophila medialis Hardy, 1966	end	detr		-	-	+	+	-	-	DSG
Drosophila melanoloma Hardy, 1965	end	detr		-	-	-	-	+	-	DSG
Drosophila molokaiensis Grimshaw, 1901	end	detr		-	-	-	-	+	-	DSG
Drosophila nr. *musae* Hardy, 1965	end	detr		-	-	-	-	+	-	DSG
Drosophila nr. *paracracens* Hardy & Kaneshiro, 1979	end	detr		-	-	+	-	-	-	KYK
Drosophila paucitarsus Hardy & Kaneshiro, 1979	end	detr		-	-	-	-	+	-	DSG
Drosophila percnosoma Hardy, 1965	end	detr		-	-	+	-	-	-	DSG
Drosophila simulans Sturtevant, 1919	adv	detr		-	+	-	-	-	-	DSG
Drosophila sordidapex Grimshaw, 1901	end	detr		-	-	+	-	-	-	KYK
Drosophila sp. A	end	detr		-	-	+	-	-	-	DSG
Drosophila sp. B	end	detr		-	-	+	-	-	-	DSG
Drosophila sp. C	end	detr		-	-	-	-	+	-	DSG
Drosophila suzukii (Matsumura, 1931)	adv	detr		-	-	+	-	+	-	KYK
Drosophila tanythrix (Hardy, 1965)	end	detr		-	-	+	-	-	-	KYK
Scaptomyza articulata Hardy, 1965	end	detr		-	-	-	-	+	-	DSG
Scaptomyza bryani (Wirth, 1952)	end	para		-	-	+	+	+	-	DSG
Scaptomyza buccata Hackman, 1962	end	detr		-	-	-	+	-	-	DSG
Scaptomyza eurystylata Hardy, 1965	end	detr		+	-	-	-	-	-	DSG
Scaptomyza exigua (Grimshaw, 1901)	end	detr		-	-	-	+	-	-	DSG
Scaptomyza inaequalis (Grimshaw, 1901)	end	detr		+	-	+	+	-	-	DSG
Scaptomyza infurcula Hardy, 1965	end	detr		-	+	+	-	-	-	DSG
Scaptomyza longipecten Hackman, 1959	end	detr		-	-	-	-	+	-	DSG
Scaptomyza longisetosa Hackman, 1959	end	detr		+	-	-	-	-	-	DSG
Scaptomyza mauiense (Grimshaw, 1901)	end	detr		-	-	-	-	+	-	DSG
Scaptomyza neoevexa O'Grady et al., 2003	end	para		-	-	-	-	+	-	DSG
Scaptomyza neokauaiensis O'Grady et al., 2003	end	para		-	-	-	-	-	+	DSG
Scaptomyza neosilvicola O'Grady et al., 2003	end	para		+	-	+	-	-	-	DSG
Scaptomyza setosiscutellum (Hardy, 1965)	end	para		+	-	+	+	+	-	DSG
Scaptomyza sp. A	end	detr		-	-	+	-	-	-	DSG
Scaptomyza sp. B	end	detr		+	-	-	+	-	-	DSG

Appendix B. (Continued) List of *Metrosideros* arthropod species.

Taxon	Origin	Guild	1996	VO	TP	LA	KH	MO	KA	Det.
Scaptomyza swezeyi (Wirth, 1952)	end	para		-	-	-	-	-	+	DSG
Scaptomyza univitta Hardy, 1965	end	detr		-	-	-	-	NIR	+	DSG
Scaptomyza nr. *univitta* Hardy, 1965	end	detr		-	-	-	+	-	-	DSG
Scaptomyza xanthopleura Hardy, 1965	end	detr		-	-	+	-	-	-	DSG
Family **Ephydridae**										
Hydrellia tritici Coquillet, 1903	adv	tou		+	-	+	-	NIR	-	KTA
Family **Hybotidae**										
Chersodromia dissita Collin, 1960	end	detr		-	-	-	-	+	-	DSG
Family **Keroplatidae**										
Trigemma infurcata (Hardy, 1960)	end	detr		-	-	-	+	-	-	DSG
Family **Lauxaniidae**										
Homoneura unguicalata (Kertesz, 1913)	adv	detr		-	-	-	+	-	-	DSG
Lauxaniidae g. sp. 1	?	?		+	-	-	-	-	-	DSG
Family **Limoniidae**										
Dicranomyia hawaiiensis (Grimshaw, 1901)	end	detr		+	-	+	+	-	-	DSG
Dicranomyia kauaiensis (Grimshaw, 1901)	end	tou		-	-	+	-	+	-	DSG
Dicranomyia sp. nr. *pontophila* Tokunaga	?	detr		-	-	+	-	-	-	DSG
Dicranomyia grimshawi (Alexander, 1919)	end	detr		-	-	-	+	-	-	DSG
Dicranomyia spp. (larvae)	end	detr		+	-	+	+	+	+	DSG
Dicranomyia stygipennis (Alexander, 1919)	end	detr		-	-	+	+	+	-	DSG
Dicranomyia swezeyi (Alexander, 1919)	end	detr		-	+	+	+	+	-	DSG
Dicranomyia variabilis (Grimshaw, 1901)	end	detr		-	+	-	-	-	-	DSG
Libnotes n. sp. nr. *trukensis* Alexander	adv	detr	OL(NSR)	-	-	-	NSR	NSR	-	GWB
Family **Muscidae**										
Brontaea quadristigma (Thomson, 1869)	adv	tou		-	-	+	-	-	-	DSG
Lispocephala longipes (Grimshaw, 1901)	end	detr		-	-	+	-	-	-	DSG
Lispocephala sp. 1	end	detr		-	-	-	+	-	-	DSG
Family **Phoridae**										
Diplonevra peregrina (Wiedemann, 1830)	adv	?		-	-	-	-	NIR	-	DSG
Family **Pipunculidae**										
Cephalops holomelas (Perkins, 1910)	end	para		-	-	-	-	+	-	DSG
Cephalops injectivus (Hardy, 1964)	end	para		-	-	+	-	-	-	DSG
Cephalops juvator juvator (Perkins, 1905)	end	para		-	-	+	-	-	-	DSG

Appendix B. (Continued) List of *Metrosideros* arthropod species.

Taxon	Origin	Guild	1996	VO	TP	LA	KH	MO	KA	Det.
Cephalops n. sp. 1	end	para		+	-	+	+	-	-	DSG
Cephalops terryi (Perkins, 1905)	end	para		-	-	-	-	-	+	DSG
Cephalops timberlakei (Hardy, 1953)	end	para		+	-	-	+	-	-	DSG
Family **Psychodidae**										
Psychoda alternata Say, 1824	adv	detr		-	-	-	+	-	-	DSG
Psychoda sp. 1	?	detr		-	-	+	-	-	-	DSG
Trichomyia hawaiiensis Quate, 1954	end	?		+	-	+	+	NIR	NIR	DSG
Family **Scatopsidae**										
Coboldia fuscipes (Meigen, 1830)	adv	detr		-	+	-	-	-	-	KTA
Family **Sciaridae**										
Bradysia impatiens (Johannsen, 1912)	adv	detr		-	-	-	-	+	-	DSG
Bradysia molokaiensis (Grimshaw, 1901)	end	detr		+	-	-	+	+	-	DSG
Bradysia setigera (Hardy, 1960)	end	detr		+	-	+	+	-	-	DSG
Bradysia spatitergum (Hardy, 1956)	adv	detr		-	-	-	+	-	-	DSG
Ctenosciara hawaiiensis (Hardy, 1956)	end	detr		+	+	+	+	+	+	DSG
Hyperlasion magnisensoria (Hardy, 1965)	end	detr		+	+	+	+	+	+	DSG
Lycoriella hoyti (Hardy, 1956)	end	detr		-	-	+	+	-	-	DSG
Platosciara adrostylata Hardy, 1956	end	detr		+	-	-	+	-	NIR	DSG
Scatopsciara nigrita Hardy, 1956	end	detr		+	-	-	+	-	-	DSG
Sciara prominens Hardy, 1956	end	detr		+	-	+	-	NIR	NIR	DSG
Sciaridae g. sp. 1	?	detr		-	-	-	-	-	+	DSG
Sciaridae g. sp. 4	?	detr		-	+	-	-	-	-	DSG
Sciaridae g. sp. 10	?	detr		+	-	-	-	-	-	DSG
Family **Sepsidae**										
Sepsis biflexuosa Strobl, 1893	adv	detr		+	-	-	-	-	-	DSG
Family **Sphaeroceridae**										
Leptocera sp. 1	adv	?		-	-	+	-	-	-	DSG
Opalimosina mirabilis (Collin, 1902)	adv	?		+	-	-	-	-	-	KTA
Family **Stratiomyidae**										
Exaireta spinigera (Wiedemann, 1830)	pur	pred		-	-	-	+	+	-	DSG
Family **Syrphidae**										
Allograpta obliqua (Say, 1823)	adv	pred		-	-	+	+	-	-	DSG

Appendix B. (Continued) List of *Metrosideros* arthropod species.

Taxon	**Origin**	**Guild**	**1996**	**VO**	**TP**	**LA**	**KH**	**MO**	**KA**	**Det.**
Order **Heteroptera**										
Family **Anthocoridae**										
Lasiochilus montivagus Kirkaldy, 1908	end	pred		+	-	-	+	-	-	DAP
Lasiochilus silvicola Kirkaldy, 1908	end	pred		-	-	-	-	-	+	DAP
Family **Lygaeidae**										
Glyptonysius hylaeus (Kirkaldy), 1910	end	seed		-	-	-	-	-	+	DAP
Glyptonysius n. sp. 1	end	seed		-	-	+	-	-	-	DAP
Neseis fasciata Usinger, 1942	end	seed		-	-	+	+	-	-	DAP
Neseis hiloensis interoculatus Usinger, 1942	end	seed		-	-	-	-	+	-	DAP
Neseis sp. KA1	end	seed		-	-	-	-	-	+	DAP
Nysius blackburni White, 1881	end	seed		+	+	-	-	-	-	DAP
Nysius coenosulus Stal, 1859	end	seed		-	-	-	-	+	-	DAP
Nysius lichenicola Kirkaldy, 1910	end	tou		-	+	-	-	-	-	DSG
Nysius nemorivagus White, 1881	end	seed		-	-	-	-	+	+	DAP
Oceanides gruneri Polhemus, 2002	end	seed		-	-	-	-	+	-	DAP
Oceanides ptericolida (White, 1881)	end	seed	HP KI	-	-	-	-	-	-	DAP
Oceanides sp. KA1	end	seed		-	-	-	-	-	+	DAP
Oceanides sp. KA2	end	seed		-	-	-	-	-	+	DAP
Oceanides vulcan (White, 1881)	end	seed	HP VO KI OL	+	+	+	+	-	-	DAP
Remaudiereana nigriceps (Dallas), 1852	adv	seed	VO	-	-	-	-	-	-	DAP
Family **Miridae**										
Hyalopeplus pellucida (Stal,1859)	end	sap		-	+	+	+	-	-	DAP
Kamehameha lunalilo Kirkaldy, 1902	end	pred?		-	-	+	-	-	-	DAP
Koanoa hawaiiensis Kirkaldy, 1902	end	sap	KI	-	+	+	+	+	-	DAP
Nesiomiris ehu Kirkaldy, 1902	end	tou		-	-	-	-	-	+	DAP
Nesiomiris hawaiiensis Kirkaldy (1902)	end	tou	VO OL	+	-	+	-	-	-	DAP
Nesiomiris williamsi Gagne, 1997	end	tou		-	-	+	-	-	-	DAP
Opuna sharpianus luteus (Kirkaldy), 1902	end	sap		-	-	-	-	-	+	DAP
Orthotylus n. sp. "coprosmicola"	end	tou		-	-	-	-	+	-	DAP
Orthotylus kanakanus Kirkaldy, 1902	end	tou		+	-	+	+	-	-	DAP
Orthotylus kassandra Kirkaldy, 1902	end	sap		+	-	-	-	-	-	DAP
Orthotylus n. sp. "metrosideri"	end	sap		+	-	+	+	-	-	DAP

Appendix B. (Continued) List of *Metrosideros* arthropod species.

Taxon	Origin	Guild	1996	VO	TP	LA	KH	MO	KA	Det.
Orthotylus n. sp. "metrosideroides"	end	sap		-	-	-	-	+	-	DAP
Orthotylus n. sp. KA1	end	sap		-	-	-	-	-	+	DAP
Orthotylus n. sp. KA2	end	sap		-	-	-	-	-	+	DAP
Pseudoclerada sp. KA1	end	pred?		-	-	-	-	-	+	DAP
Pseudoclerada sp. KH1	end	pred?		-	-	-	+	-	-	DAP
Pseudoclerada sp. MO1	end	pred?		-	-	-	-	+	-	DAP
Sarona adonias Kirkaldy, 1902	end	sap	VO	+	+	+	+	+	-	DAP
Family **Nabidae**										
Nabis blackburni White, 1878	end	pred	VO KI							
Nabis curtipennis Blackburn, 1888	end	pred		-	+	-	-	-	-	DAP
Nabis morai (Kirkaldy, 1902)	end	pred		-	-	-	-	-	+	DAP
Nabis n. sp. "kilauea"	end	pred		-	+	-	-	-	-	DAP
Nabis oscillans Blackburn, 1888	end	pred	HP VO KI	+	+	+	+	-	-	DAP
Nabis sharpianus (Kirkaldy, 1902)	end	pred		-	-	-	-	-	+	DAP
Nabis silvicola (Kirkaldy, 1908)	end	pred		-	-	-	-	+	-	DAP
Family **Pentatomidae**										
Coleotichus blackburniae White, 1881	end	tou		-	-	-	+	-	-	DSG
Oechalia sp. KA1	end	pred		-	-	-	-	-	+	DAP
Oechalia sp. MO1	end	pred		-	-	-	-	+	-	DAP
Oechalia sp. VO1	end	pred		+	-	-	-	-	-	DAP
Family **Reduviidae**										
Haematoloecha rubescens Distant, 1883	adv	pred		-	NIR	-	NIR	-	-	DAP
Family **Rhyparochromidae**										
Brentiscerus australis (Bergroth)	adv	seed		-	-	-	+	+	-	DAP
Family **Veliidae**										
Microvelia vagans White, 1878	end	tou		-	-	+	-	-	-	DAP
Order **Homoptera**										
Family **Aphididae**										
Greenidea formosana (Maki, 1917)	adv	sap		-	NIR	NIR	NIR	NIR	-	BRK
Idiopterus nephrelepidis Davis, 1909	adv	tou		-	-	-	-	-	NIR	DSG
Toxoptera aurantii (Fonscolombe, 1841)	adv	sap		-	+	+	+	-	-	DSG
Family **Cercopidae**										
Philaenus spumarius (Linnaeus, 1758)	adv	tou		-	-	+	-	-	NIR	DSG

Appendix B. (Continued) List of *Metrosideros* arthropod species.

Taxon	Origin	Guild	1996	VO	TP	LA	KH	MO	KA	Det.
Family **Cicadellidae**										
Nesophrosyne giffardi Kirkaldy, 1910	end	sap		-	+	+	-	-	-	DAP
Nesophrosyne sp. HA1	end	sap		+	-	-	-	-	-	DAP
Nesophrosyne sp. HA2	end	sap		-	-	+	-	-	-	DAP
Nesophrosyne sp. KA1	end	sap		-	-	-	-	-	+	DAP
Nesophrosyne sp. KA2	end	sap		-	-	-	-	-	+	DAP
Nesophrosyne sp. KA3	end	sap		-	-	-	-	-	+	DAP
Nesophrosyne sp. MO1	end	sap		-	-	-	-	+	-	DAP
Sophonia rufofascia (Kuoh & Kuoh), 1983	adv	sap	HP KI	-	+	-	-	-	-	DSG
Family **Cixiidae**										
Iolania perkinsi Kirkaldy, 1902	end	tou	VO	+	+	+	+	-	-	DSG
Oliarus consimilis Giffard, 1925	end	tou?		-	-	-	-	-	+	DSG
Oliarus filicicola Kirkaldy, 1909	end	tou		+	-	+	-	-	-	DSG
Oliarus halemanu Giifard, 1925	end	sap?		-	-	-	-	-	+	DSG
Oliarus inaequalis Giffard, 1925	end	sap		-	+	+	+	-	-	DSG
Oliarus inconstans Giffard, 1925	end	sap		+	+	-	-	-	-	DSG
Oliarus kahavalu Kirkaldy, 1909	end	sap		-	-	-	-	+	-	DSG
Oliarus koanoa Kirkaldy, 1902	end	tou		+	-	-	-	-	-	DSG
Oliarus similis Giffard, 1925	end	sap?		-	-	-	-	+	-	DSG
Family **Delphacidae**										
Leialoha hawaiiensis Muir, 1916	end	sap		+	+	+	+	-	-	DSG
Leialoha kauaiensis Muir, 1916	end	sap		-	-	-	-	-	+	DSG
Leialoha lehuae (Kirkaldy, 1910)	end	sap		-	-	-	-	NIR	-	DSG
Leialoha ohiae (Kirkaldy), 1910	end	sap		-	-	-	-	-	+	DSG
Nesosydne koae Kirkaldy, 1907	end	tou		-	-	+	-	-	-	MA
Family **Flatidae**										
Siphanta acuta (Walker, 1851)	adv	sap	HP	+	+	+	+	-	-	DSG
Family **Pseudococcidae**										
Pseudococcidae g. sp. 1	?	sap		-	+	-	+	-	-	DSG
Pseudococcidae g. sp. 2	?	sap		-	+	-	-	-	-	DSG
Pseudococcidae g. sp. 3	?	sap		-	-	-	-	+	-	DSG
Pseudococcidae g. sp. 4	?	sap		-	-	-	-	-	+	DSG

Appendix B. (Continued) List of *Metrosideros* arthropod species.

Taxon	**Origin**	**Guild**	**1996**	**VO**	**TP**	**LA**	**KH**	**MO**	**KA**	**Det.**
Family **Triozidae**										
Kuwayama minuta Crawford, 1918	end	gall?		+	+	+	+	NIR	+	DMP
Kuwayama n. sp. 1	end	gall?		-	+	-	+	-	-	DSG
Kuwayama nigricapita Crawford, 1918	end	gall?		+	+	+	+	+	-	DMP
Kuwayama sp. 3	end	gall?		-	-	+	+	+	-	DSG
Kuwayama sp. 4	end	gall?		-	-	-	+	+	-	DSG
Kuwayama sp. 5	end	gall?		-	-	-	+	+	-	DSG
Kuwayama sp. 6	end	gall?		-	-	-	-	+	-	DSG
Kuwayama sp. 7	end	gall?		-	-	-	-	-	+	DSG
Trioza hawaiiensis Crawford, 1918	end	gall		+	+	+	+	-	-	DMP
Trioza kauaiensis Crawford, 1925	end	gall		-	-	-	-	-	+	DSG
Trioza molokaiensis Crawford, 1927	end	gall		-	-	-	-	+	-	DSG
Trioza sp. nr. *molokaiensis* Crawford	end	gall		-	-	-	-	+	-	DSG
Trioza ohiacola Crawford, 1918	end	gall		+	+	+	+	+	-	DMP
Trioza sp. 2 nr. *ohiacola* Crawford	end	gall		+	+	+	+	-	-	DMP
Trioza sp. 5	end	gall		-	+	+	+	-	-	DSG
Trioza sp. 6	end	gall		-	-	-	+	-	-	DSG
Order **Hymenoptera**										
Family **Agaonidae**										
Odontofroggatia galili Wiebes, 1980	adv	tou		-	NIR	-	-	-	-	DSG
Family **Aphelinidae**										
Aphytis g. sp. 1	adv	para	KI	+	-	+	+	-	+	DSG
Family **Bethylidae**										
Sierola sp. A	end	para		-	-	-	-	+	+	DSG
Sierola sp. B	end	para		-	+	-	-	-	+	DSG
Sierola sp. C	end	para		-	-	-	-	-	+	DSG
Sierola sp. D	end	para		-	-	-	-	-	+	DSG
Sierola sp. E	end	para		-	-	-	-	-	+	DSG
Sierola sp. G	end	para		-	-	-	-	-	+	DSG
Sierola sp. I	end	para		-	-	-	-	+	-	DSG
Sierola sp. J	end	para		-	-	-	-	+	-	DSG
Sierola sp. K	end	para		-	-	-	-	+	-	DSG
Sierola sp. M	end	para		+	-	+	+	+	-	DSG

Appendix B. (Continued) List of *Metrosideros* arthropod species.

Taxon	Origin	Guild	1996	VO	TP	LA	KH	MO	KA	Det.
Sierola sp. N	end	para		+	+	+	+	-	-	DSG
Sierola sp. O	end	para		-	-	+	+	-	-	DSG
Sierola sp. R	end	para		-	-	-	-	+	-	DSG
Sierola sp. S	end	para		-	-	-	+	-	-	DSG
Sierola sp. T	end	para		-	-	-	+	-	-	DSG
Sierola sp. U	end	para		-	+	-	-	-	-	DSG
Sierola sp. V	end	para		-	+	-	-	-	-	DSG
Sierola sp. W	end	para		-	-	+	-	-	-	DSG
Sierola sp. X	end	para	VO	-	-	-	-	-	-	DSG
Sierola sp. Y	end	para		+	-	-	-	-	-	DSG
Sierola sp. Z	end	para		-	+	-	-	-	-	DSG
Family **Braconidae**										
Apanteles opacus (Ashmead, 1905)	adv	para	KI	-	-	-	-	-	-	DSG
Apanteles trifasciatus Muesebeck, 1946	adv	para	HP	-	-	-	-	-	-	DSG
Aspilota konae Ashmead, 1901	end	para		-	-	+	-	-	-	DSG
Glyptapanteles militaris (Walsh, 1861)	pur	para		-	-	+	-	-	-	DSG
Leiophron sp. 1	adv	para		-	-	NSR	NSR	-	-	JTH
Meteorus laphygmae Viereck, 1913	pur	para	VO	-	-	+	-	+	-	DSG
Ontsira palliatus (Cameron, 1881)	adv	para		-	-	-	+	-	-	DSG
Ontsira syagrii (Fullaway, 1922)	pur	para		+	-	-	-	-	-	DSG
Family **Colletidae**										
Hylaeus coniceps (Blackburn, 1886)	end	tou		-	-	+	-	-	-	DSG
Hylaeus connectens (Perkins, 1899)	end	tou	ML	-	-	-	-	-	-	DSG
Hylaeus pubescens (Perkins, 1899)	end	tou		-	+	-	-	-	-	DSG
Hylaeus unicus (Perkins, 1899)	end	tou		-	-	-	-	+	-	DSG
Family **Diapriidae**										
Trichopria nr. *subtilis* (Perkins, 1910)	end	para		-	NIR	-	-	-	-	DSG
Trichopria soror (Perkins, 1910)	end	para		+	-	+	-	-	-	DSG
Family **Dryinidae**										
Dicondylus perkinsi (Ashmead), 1901	end	para		+	+	+	+	+	+	DSG
Family **Encyrtidae**										
Anagyrus ?nigricans Perkins, 1910	end	para		+	+	+	+	+	-	JSN
Anagyrus sp. 2	end	para		+	-	+	+	+	-	DSG

Appendix B. (Continued) List of *Metrosideros* arthropod species.

Taxon	Origin	Guild	1996	VO	TP	LA	KH	MO	KA	Det.
Anagyrus sp. 3	end	para		+	-	-	+	-	-	DSG
Anicetus annulatus Timberlake, 1919	adv	para		-	+	-	-	-	-	JSN
Cerchysiella ?perkinsi (Timberlake, 1924)	adv	para		-	-	-	-	+	-	DSG
Cerchysiella sp. 2	?	para		-	-	-	-	-	+	JSN
Coelopencyrtus sp. 1	?	para		+	-	-	+	-	-	JSN
Coelopencyrtus sp. 2	?	para		-	-	-	-	+	-	JSN
Coelopencyrtus sp. 3	end	para		-	-	-	-	-	+	JSN
Copidosoma floridanum (Ashmead, 1900)	pur	para		+	-	-	-	-	-	JSN
Encyrtidae g. sp. 22	?	para		-	-	-	-	-	+	DSG
Encyrtidae g. sp. 25	?	para		-	-	-	+	-	-	DSG
Encyrtidae g. sp. 26	?	para		-	-	-	+	-	-	DSG
Hypergonatopus sp. 1	end	para		-	-	+	-	-	-	JSN
Hypergonatopus sp. 2	end	para		-	-	-	-	-	NIR	DSG
Hypergonatopus sp. 3	end	para		-	-	-	-	+	-	DSG
Hypergonatopus sp. 4	end	para		-	+	-	-	-	-	DSG
Metaphycus ?alberti (Howard, 1898)	adv	para		-	+	-	+	-	-	DSG
Metaphycus ?stanleyi Compere, 1940	adv	para		-	-	-	-	+	-	DSG
Microterys flavus (Howard), 1881	adv	para		+	+	+	+	-	+	JSN
Ooencyrtus erionotae Ferriere, 1931	pur	para		+	-	-	-	-	-	JSN
Plagiomeris hospes Timberlake, 1920	adv	para		+	+	+	+	+	+	JSN
Rhopus sp. 1	?	para		-	-	-	-	-	NIR	JSN
Tetracnemoidea brevicornis (Girault)	adv	para		-	-	-	-	-	NIR	JSN
Family **Eucoilidae**										
Eucoilidae g. sp. 1	end	para		-	+	+	-	+	+	DSG
Pseudodiranchis sp. 1	end	para		-	-	+	-	+	-	DSG
Family **Eulophidae**										
Asecodes sp.	pur	para		NSR	-	-	-	-	-	MWG
Elachertus advena Timberlake, 1926	adv	para	KI(NIR)	-	-	-	-	-	-	DSG
Euderinae g. sp. 1	?	para		-	-	-	-	-	+	MWG
Euderus metallicus (Ashmead, 1901)	adv	para		+	+	-	+	+	+	DSG
Eulophidae g. sp. 4	?	para		-	-	-	+	-	-	DSG
Eulophidae g. sp. 8	?	para		-	-	-	+	-	-	DSG
Euplectrus platyhypenae Howard, 1885	pur	para		-	+	-	-	-	-	DSG

Appendix B. (Continued) List of *Metrosideros* arthropod species.

Taxon	Origin	Guild	1996	VO	TP	LA	KH	MO	KA	Det.
Pauahiana metallica Yoshimoto, 1965	end	para		-	+	-	-	-	-	MWG
Pauahiana n. sp. "incenta"	end	para		-	-	+	-	-	-	DSG
Pauahiana swezeyi Yoshimoto, 1965	end	para		+	+	-	+	+	NIR	MWG
Sympiesis hawaiiensis (Ashmead, 1901)	end	para		-	-	-	-	NIR?	-	MWG
Sympiesis konae Ashmead, 1901	end	para		-	-	-	-	NIR?	NIR?	DSG
Family **Eupelmidae**										
Eupelmus axestias Perkins, 1910	end	para		NIR	-	-	-	NIR	-	DSG
Eupelmus chloropus Perkins, 1910	end	para		-	-	-	-	-	NIR	DSG
Eupelmus nr. *chloropus* Perkins, 1910	end	para		-	-	-	-	-	+	DSG
Eupelmus epilampropS Perkins, 1910	end	para		+	-	-	-	-	-	DSG
Eupelmus euprepes Perkins, 1910	end	para	KI	-	-	-	-	-	-	DSG
Eupelmus leptophyas Perkins, 1910	end	para		-	+	-	-	-	-	DSG
Eupelmus leucothrix Perkins, 1910	end	para		-	-	-	NIR?	-	-	DSG
Eupelmus n. sp. 1	end	para		+	-	-	+	-	-	DSG
Eupelmus paraxestops Perkins, 1910	end	para		-	-	-	-	NIR?	-	DSG
Eupelmus xanthotarsus Perkins, 1910	end	para		-	-	-	-	NIR	-	DSG
Eupelmus xestias Perkins, 1910	end	para		-	-	-	-	-	NIR	DSG
Eupelmus xestops Perkins, 1910	end	para	VO	-	-	+	+	-	-	DSG
Family **Formicidae**										
Paratrechina bourbonica (Forel, 1886)	adv	omni	HP	-	-	-	-	-	-	DSG
Pheidole megacephala (Fabricius, 1793)	adv	omni	HP	-	-	-	-	-	-	DSG
Solenopsis papuana Emery, 1900	adv	omni		-	-	-	-	+	-	DSG
Tetramorium bicarinatum (Nylander, 1847)	adv	omni	HP	-	-	-	-	-	-	DSG
Family **Ichneumonidae**										
Diadegma blackburni (Cameron, 1883)	adv	para		+	+	-	-	-	-	DSG
Diadegma insularis (Cresson, 1883)	pur	para	KI	-	-	-	-	-	-	DSG
Enicospilus molokaiensis Ashmead, 1901	end	para		-	-	-	+	-	-	DSG
Pimpla punicipes Cresson, 1873	adv	para	VO	-	-	+	+	+	-	DSG
Pristomerus hawaiiensis Perkins, 1910	end	para		-	+	+	+	-	-	DSG
Spolas spp. (Ashmead), 1906	end	para		+	+	+	+	-	+	DSG
Vulgichneumon diminutus (Matsumura, 1912)	adv	para	VO	-	+	+	-	-	-	DSG

Appendix B. (Continued) List of *Metrosideros* arthropod species.

Taxon	Origin	Guild	1996	VO	TP	LA	KH	MO	KA	Det.
Family **Megaspilidae**										
Dendrocerus sp. 1	?	para	KI	-	-	-	-	-	-	DSG
Family **Mymaridae**										
Alaptus sp. 1	adv	para		-	-	-	-	+	-	JTH
Polynema hawaiiensis Ashmead, 1901	end	para		-	-	-	-	+	-	DSG
Polynema jassidarum Perkins, 1910	end	para		-	-	-	-	+	-	DSG
Polynema n. sp. "waikamoiense"	end	para		-	-	-	-	+	-	DSG
Polynema pyrophila Perkins, 1910	end	para		+	-	-	+	-	NIR	DSG
Polynema sp. 1	end	para		-	+	-	-	-	-	DSG
Family **Proctotrupidae**										
Brachyserphus hawaiiensis (Ashmead, 1901)	?	para	KI	-	+	-	-	-	+	DSG
Family **Platygastridae**										
Aphanomerus rufescens Perkins, 1905	adv	para		-	NSR	-	NSR	-	-	DSG
Family **Pteromalidae**										
Cyrtogaster fuscitarsis (Ashmead, 1901)	adv	para		+	-	+	-	-	+	GAPG
Miscogasterini g. sp. 1	?	para		-	+	-	-	-	+	MWG
nr. *Gastrancistrus* sp. 1	?	para		-	-	-	+	+	-	MWG
Pteromalidae g. spp.	?	para		-	-	-	+	-	-	DSG
Toxeuma affinis Ashmead, 1901	end	para		-	-	-	-	-	+	DSG
Toxeuma ferrugineipes Ashmead, 1901	end	para		+	-	-	-	-	-	DSG
Toxeuma hawaiiensis Ashmead, 1901	end	para		-	-	-	+	-	-	DSG
Toxeuma n. sp. 1	end	para		-	-	+	-	-	-	DSG
Toxeuma n. sp. 2	end	para		+	-	-	+	-	-	DSG
Toxeuma nubilipennis Ashmead, 1901	end	para		NIR	-	-	NIR	NIR	+	MWG
Zolotarewskya n. sp. 1	adv	para	KI(NSR)	-	-	-	-	-	-	GAPG
Family **Scelionidae**										
Baeus persordidus Perkins, 1910	?	para		NIR	NIR	-	NIR	-	-	DSG
Opisthacantha nigricornis (Ashmead), 1901	end	para		NIR?	-	NIR?	NIR?	+	-	DSG
Opisthacantha sp. nr. *oahuensis* (Perkins, 1910)	end	para		NIR?	-	NIR?	-	-	-	DSG
Opisthacantha tarsalis (Ashmead), 1901	end	para		-	-	-	NIR?	-	+	DSG
Telenomus sp. 1	end	para		+	+	+	+	+	-	DSG
Trimorus sp. 1	pur	para		-	-	NSR	-	-	-	LM

Appendix B. (Continued) List of *Metrosideros* arthropod species.

Taxon	**Origin**	**Guild**	**1996**	**VO**	**TP**	**LA**	**KH**	**MO**	**KA**	**Det.**
Family **Signiphoridae**										
Chartocerus dactylopii (Ashmead, 1900)	adv	para		-	NIR	-	-	-	-	DSG
Signiphora aspidioti (Ashmead), 1900	adv	para		NIR	NIR	-	NIR	+	-	DSG
Family **Sphecidae**										
Ectemnius tumidoventris (Perkins, 1899)	end	pred		-	+	-	-	-	-	DSG
Rhopalum sp. 1 [of Beardsley & Perreira, 2000]	adv	pred		+	-	+	+	-	-	DSG
Family **Trichogrammatidae**										
Trichogramma sp. 2	?	para		-	-	-	-	+	-	MWG
Family **Vespidae**										
Vespula pensylvanica (Saussure, 1857)	adv	pred		+	+	-	-	+	-	DSG
Order **Lepidoptera**										
Family **Carposinidae**										
Carposina caterpillar sp. 1	end	chew		-	+	+	-	-	-	DSG
Carposina caterpillar sp. 2	end	chew		+	-	+	-	-	-	DSG
Carposina caterpillar sp. 3	end	chew		-	-	-	+	-	-	DSG
Carposina caterpillar sp. 4	end	chew		-	-	-	+	-	-	DSG
Carposina caterpillar sp. 5	end	chew		-	-	-	-	+	-	DSG
Carposina caterpillar sp. 6	end	chew		-	-	-	-	+	-	DSG
Family **Geometridae**										
Eupithecia monticolens Butler, 1881	end	chew		+	+	+	+	+	-	SLM
Eupithecia n. sp. 2 [Montgomery, 1982]	end	pred		-	-	-	-	-	+	SLM
Eupithecia nr. *niphoreas* (Meyrick, 1899)	end	pred		-	-	+	-	-	-	SLM
Eupithecia orichloris (Meyrick, 1899)	end	pred		-	-	+	+	-	-	SLM
Larentiinae g. caterpillar sp. 1	?	chew		-	-	-	+	-	-	DSG
Larentiinae g. caterpillar sp. 4	?	chew		-	+	-	-	-	-	DSG
Scotorythra caterpillar sp. 1	end	chew		+	-	-	+	+	+	DSG
Scotorythra caterpillar sp. 4	end	chew		+	-	-	+	+	-	DSG
Scotorythra caterpillar sp. 5	end	chew		-	-	-	+	-	-	DSG
Scotorythra caterpillar sp. 7	end	chew		-	-	+	-	+	+	DSG
Scotorythra caterpillar sp. 8	end	chew		-	-	-	-	+	-	DSG
Scotorythra caterpillar sp. 9	end	chew		-	-	+	-	+	-	DSG
Scotorythra caterpillar sp. 11	end	chew		-	-	-	-	+	-	DSG

Appendix B. (Continued) List of *Metrosideros* arthropod species.

Taxon	Origin	Guild	1996	VO	TP	LA	KH	MO	KA	Det.
Scotorythra caterpillar sp. 15	end	chew		-	-	+	+	+	+	DSG
Family **Oecophoridae**										
Thyrocopa caterpillar sp. 2	end	detr		-	-	-	+	-	-	DSG
Thyrocopa caterpillar sp. 3	end	detr		-	-	-	-	+	-	DSG
Thyrocopa caterpillar sp. 4	end	detr		-	-	-	-	-	+	DSG
Thyrocopa caterpillar sp. 11	end	detr		-	-	+	-	-	-	DSG
Family **Pyralidae**										
Pyralidae g. caterpillar sp. 5	?	chew		-	-	+	+	+	-	DSG
Pyralidae g. caterpillar sp. 14	?	chew		-	-	+	-	-	-	DSG
Pyralidae g. caterpillar sp. 17	?	chew		+	-	-	+	-	-	DSG
Pyralidae g. caterpillar sp. 19	?	chew		-	-	-	+	-	-	DSG
Pyralidae g. caterpillar sp. 20	?	chew		-	-	-	+	-	-	DSG
Pyralidae g. caterpillar sp. 21	?	chew		-	-	-	-	+	-	DSG
Family **Sphingidae**										
Hyles wilsoni wilsoni (Rothschild 1894)	end	chew		-	-	+	+	-	-	DSG
Family undet.										
Lep. g. caterpillar sp. 18	?	chew		-	-	-	+	-	-	DSG
Lep. g. caterpillar sp. 22	?	chew		-	-	-	-	-	+	DSG
Order **Mantodea**										
Family **Mantidae**										
Tenodera angustipennis Saussure, 1869	adv	pred		-	+	-	-	-	-	DSG
Order **Neuroptera**										
Family **Chrysopidae**										
Anomalochrysa hepatica McLachlan, 1883	end	pred		-	+	+	-	-	-	CAT
Anomalochrysa maclachlani maclachlani Blackburn, 1889	end	pred		-	+	+	-	+	+	CAT
Family **Hemerobiidae**										
Hemerobius pacificus Banks, 1897	adv	pred		-	+	+	-	-	-	CAT
Micromus brunnescens (Perkins),1899	end	pred		-	-	-	-	+	-	CAT
Micromus longispinosus (Perkins), 1899	end	pred		+	-	-	-	-	-	CAT
Micromus minimus (Perkins), 1899	end	pred		-	-	-	+	-	-	CAT
Micromus rubrinervis (Perkins), 1899	end	pred		+	+	+	-	-	-	CAT
Micromus subochraceus (Perkins), 1899	end	pred		-	-	-	+	-	-	CAT

Appendix B. (Continued) List of *Metrosideros* arthropod species.

Taxon	**Origin**	**Guild**	**1996**	**VO**	**TP**	**LA**	**KH**	**MO**	**KA**	**Det.**
Nesobiella hospes (Perkins), 1899	ind	pred		-	-	+	-	-	-	CAT
Order **Orthoptera**										
Family **Gryllidae**										
Leptogryllus elongatus Perkins, 1899	end	detr		+	-	-	-	-	-	DSG
Leptogryllus kauaiensis Perkins, 1899	end	detr		-	-	-	-	-	+	DSG
Leptogryllus molokai Perkins, 1899	end	detr		-	-	-	-	+	-	DSG
Leptogryllus nr. *forficularis* (Brunner, 1896)	end	detr		-	-	-	+	-	-	DSG
Trigonidium atroferrugineum (Brunner, 1896)	end	detr		-	-	-	-	+	-	DSG
Trigonidium crepitans (Perkins, 1899)	end	detr		-	-	-	-	-	+	DSG
Trigonidium neogrande Otte, 1994	end	detr		+	-	-	-	-	-	DSG
Trigonidium neovarians Otte, 1994	end	detr		-	-	+	-	-	-	DSG
Trigonidium procrustum Otte, 1994	end	detr		-	-	-	-	-	+	DSG
Trigonidium sp. 1	end	detr		-	-	-	-	+	-	DSG
Trigonidium sp. 2	end	detr		-	-	-	-	-	+	DSG
Trigonidium sp. 3	end	detr		-	-	-	-	-	+	DSG
Trigonidium sp. 4	end	detr		-	+	-	-	-	-	DSG
Trigonidium waimea Otte, 1994	end	detr		-	-	-	+	-	-	DSG
Family **Tettigoniidae**										
Banza affinis (Perkins, 1899)	end	tou		-	-	-	-	-	+	DSG
Banza nitida nitida (Brunner, 1896)	end	tou		-	-	+	+	-	-	DSG
Order **Psocoptera**										
Family **Caeciliidae**										
Stenocaecilius analis (Banks, 1931)	adv	detr		+	-	-	+	+	-	ELM
Valenzuela badiostigma (Okamoto, 1910)	adv	detr		-	+	+	+	-	+	ELM
Family **Ectopsocidae**										
Ectopsocus briggsi McLachlan, 1899	adv	detr		-	-	-	NSR	-	-	ELM
Family **Elipsocidae**										
Kilauella micramaura (Perkins, 1899)	end	detr		+	-	-	+	NIR	-	DSG
Kilauella sp. 2	end	detr		-	+	-	+	-	-	DSG
Kilauella sp. 3	end	detr		-	+	+	+	+	-	DSG
Kilauella sp. 4	end	detr		+	+	+	+	-	-	DSG
Kilauella sp. 5	end	detr		+	-	+	-	-	-	DSG

Appendix B. (Continued) List of *Metrosideros* arthropod species.

Taxon	Origin	Guild	1996	VO	TP	LA	KH	MO	KA	Det.
Kilauella sp. 6	end	detr		-	-	+	+	-	-	DSG
Kilauella sp. 7	end	detr		-	-	+	+	-	-	DSG
Kilauella sp. 9	end	detr		+	-	+	-	+	-	DSG
Kilauella sp. 11	end	detr		-	-	-	+	-	-	DSG
Kilauella sp. 12	end	detr		-	-	-	+	-	-	DSG
Kilauella sp. 13	end	detr		-	-	-	-	+	-	DSG
Kilauella sp. 15	end	detr		-	-	-	-	+	-	DSG
Kilauella sp. 16	end	detr		-	-	-	-	+	-	DSG
Kilauella sp. 18	end	detr		-	-	-	-	-	+	DSG
Kilauella sp. 19	end	detr		-	-	-	-	-	+	DSG
Kilauella sp. 20	end	detr		-	-	-	-	-	+	DSG
Kilauella sp. 21	end	detr		-	-	-	+	+	+	DSG
Kilauella sp. 22	end	detr		-	-	-	-	-	+	DSG
Kilauella spp.	end	detr		+	-	+	+	+	+	DSG
Palistreptus hyalinus Thornton, 1990	end	detr		-	-	+	-	-	-	DSG
Palistreptus inconstans (Perkins, 1899)	end	detr		-	-	-	+	-	-	DSG
Palistreptus n. sp. 1	end	detr		-	-	+	-	-	-	ELM
Palistreptus pictifrons Thornton, 1990	end	detr		-	-	-	-	+	-	DSG
Palistreptus setosus Thornton, 1990	end	detr		-	-	-	-	-	+	DSG
Family **Lepidopsocidae**										
Lepidopsocus aureus Thornton, 1981	adv	detr	HP	-	-	-	-	-	-	ELM
Lepolepis pictus Thornton, 1981	adv	detr	HP	-	-	-	-	-	-	ELM
Family **Philotarsidae**										
Haplophallus sp. 1	adv	detr		-	-	-	-	NSR	-	ELM
Family **Pseudocaeciliidae**										
Lobocaecilius monicus Lee & Thornton, 1967	adv	detr		+	+	+	+	+	+	ELM
Family **Psocidae**										
Ptycta apicantha Thornton, 1984	end	detr		+	-	-	+	-	-	DSG
Ptycta dicrosa Thornton, 1984	end	detr		-	-	-	-	+	-	DSG
Ptycta disclera Thornton, 1984	end	detr		-	-	-	-	+	-	DSG
Ptycta distinguenda (Perkins, 1899)	end	detr		+	-	-	-	+	-	DSG
Ptycta haleakalae (Perkins, 1899)	end	detr		-	-	-	-	+	-	ELM

Appendix B. (Continued) List of *Metrosideros* arthropod species.

Taxon	Origin	Guild	1996	VO	TP	LA	KH	MO	KA	Det.
Ptycta hardyi Thornton, 1984	end	detr		+	-	+	+	-	-	DSG
Ptycta hawaiiensis Thornton, 1984	end	detr		+	-	-	-	-	-	DSG
Ptycta kauaiensis (Perkins, 1899)	end	detr		-	-	-	-	-	+	DSG
Ptycta lanaiensis fusca Thornton, 1984	end	detr		-	-	-	-	+	-	DSG
Ptycta n. sp. 1	end	detr		-	-	-	-	-	+	DSG
Ptycta persimilis Thornton, 1984	end	detr		-	-	-	-	-	+	DSG
Ptycta pikeloi Thornton, 1984	end	detr		-	-	-	-	+	-	DSG
Ptycta simulator kilauea Thornton, 1984	end	detr		-	-	-	+	-	-	DSG
Ptycta spp.	end	detr		+	+	-	+	+	+	DSG
Ptycta telma Thornton, 1984	end	detr		-	-	-	-	-	+	DSG
Ptycta zimmermani Thornton, 1984	end	detr		-	-	-	-	-	+	DSG
Order **Thysanoptera**										
Family **Phlaeothripidae**										
Haplothrips davisi Bianchi, 1946	end	fung		-	+	+	+	-	-	DSG
Hoplothrips flavitibia Moulton, 1928	adv	tou		-	-	-	-	-	+	DSG
Hoplothrips swezeyi Moulton, 1928	end	fung		-	-	+	-	-	-	DSG
Karnyothrips flavipes (Jones, 1912)	adv	pred		+	-	-	-	-	-	DSG
Family **Thripidae**										
Asprothrips seminigricornis (Girault, 1926)	adv	tou		-	-	-	+	+	-	DSG
Frankliniella sp. 1	adv	tou		-	+	-	-	-	-	DSG
Heliothrips haemorrhoidalis (Bouche, 1833)	adv	sap		+	+	+	+	-	+	DSG
Neurisothrips sp. 1	?	flow		-	-	+	+	-	-	DSG
Thysanoptera g. sp. 6	?	tou?		-	-	-	-	+	-	DSG
CLASS **CHILOPODA**										
Order undet										
Family undet										
Chilopoda g. sp. 1	?	pred		-	-	-	-	+	-	DSG
Order **Lithobiomorpha**										
Family **Lithobiidae**										
Lithobius sp. 1	?	pred		-	-	-	-	+	-	DSG

Appendix B. (Continued) List of *Metrosideros* arthropod species.

Taxon	Origin	Guild	1996	VO	TP	LA	KH	MO	KA	Det.
CLASS **DIPLOPODA**										
Order **Julida**										
Family **Blanulidae**										
Proteroiulus fuscus (Am Stein, 1857)	adv	detr		-	-	+	-	-	-	DSG
Family **Julidae**										
Cylindroiulus latestriatus (Curtis, 1844)	adv	detr		-	-	-	+	-	-	DSG
Order **Polydesmida**										
Family **Paradoxosomatidae**										
Akamptogonus novarae (Humbert & Saussure, 1869)	adv	detr		-	-	+	-	-	-	DSG
Oxidus gracilis (C.L. Koch, 1847)	adv	detr	VO	-	-	-	-	-	-	DSG
Order **Spirostreptida**										
Family **Cambalidae**										
Nannolene sp. 1	end	detr		-	-	+	-	-	-	DSG
Nannolene sp. 2	end	detr		-	-	-	-	-	+	DSG
CLASS **MALACOSTRACA**										
Order **Amphipoda**										
Family **Talitridae**										
Hawaiorchestia n. sp. nr. *gagnei*	end	detr		-	-	-	-	-	+	AMMR
Platorchestia n. sp. nr. *lanipo*	end	detr		-	-	-	-	NIR	-	AMMR
Order **Isopoda**										
Family undet.										
Isopoda g. sp. 1	?	detr		-	-	-	-	-	+	DSG
Family **Philosciidae**										
Australophiloscia societatis (Maccagno, 1932)	ind	detr		+	-	+	+	+	+	DSG
Family **Porcellionidae**										
Porcellio scaber Latreille, 1804	adv	detr	HP VO KI OL	+	+	+	+	+	+	DSG

APPENDIX C

PUBLICATION RECORD

Some of the chapters in this dissertation are already published or in press with peer-reviewed journals. Each journal granted copyright permission for the use of material in this format.

Chapter 2 (*in part*): D.S. Gruner and D.A. Polhemus. Arthropod communities across a long chronosequence in the Hawaiian Islands. Pages 135-145 *in* Y. Basset, V. Novotný, S. E. Miller, and R. L. Kitching, eds. *Arthropods of Tropical Forests: Spatio-Temporal Dynamics and Resource Use in the Canopy.* Cambridge University Press, London.

Chapter 3: D.S. Gruner. 2004. Attenuation of top-down and bottom-up forces in a complex terrestrial community. *Ecology* 85(12), in press.

Chapter 4: D.S. Gruner. 2004. Biotic resistance to an invasive spider conferred by generalist insectivorous birds on Hawai'i Island. *Biological Invasions* 6(4), in press.

Chapter 6: D.S. Gruner, A.D. Taylor, and R.E. Forkner. The effects of foliar pubescence and nutrient enrichment on arthropod communities of *Metrosideros polymorpha* (Myrtaceae). *Ecological Entomology*, submitted.

Chapter 8: D.S. Gruner. 2003. Regressions of length and width to predict arthropod biomass in the Hawaiian Islands. *Pacific Science* **5**7(3):325-336.

Appendices A & B: D.S. Gruner. 2004. Arthropods from ‘ōhi‘a lehua (Myrtaceae: *Metrosideros polymorpha*), with new records for the Hawaiian Islands. *Bishop Museum Occasional Papers*, in press.

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