

The effects of foliar pubescence and nutrient enrichment on arthropod communities of *Metrosideros polymorpha* (Myrtaceae)

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Abstract. 1. Nutrient resource availability and host-plant foliar pubescence both influence arthropod food webs, but multifactor studies are needed to understand their interdependence and relative importance. Arthropods were sampled by clipping foliage from *Metrosideros polymorpha* (Myrtaceae) trees of pubescent, glabrous, and intermediate leaf forms on fertilised and unfertilised plots.

2. Fertilisation decreased leaf mass per area (LMA) but did not change the relative mass of pubescence within leaf morphological classes.

3. Fertilisation increased densities of individuals in four taxonomic orders, densities of individuals and species of all trophic levels, and the biomass of Collembola and Homoptera. Herbivore relative diversity (Shannon H') also increased with fertilisation, but detritivore diversity declined due to increasing dominance of *Salina celebensis* (Schaeffer) (Collembola).

4. 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 density did not change with leaf morphological class, but relative diversity of all arthropods and of detritivores increased with increasing pubescence.

5. Both resource availability and leaf pubescence affected *Metrosideros* arthropod communities. However, the pervasive positive influence of fertilisation did not translate to compositional shifts, and there were no interactions with leaf morphological class. In contrast, the effects of leaf pubescence on arthropod density, biomass, and diversity were more restricted taxonomically, and non-parametric MANOVA and redundancy analyses demonstrated significant differentiation in community composition on the pubescent morphology.

Key words. Arthropod community structure, bottom-up control, fertilisation, Hawaiian Islands, non-parametric MANOVA, redundancy analysis, species richness and diversity, trichomes.

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

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fundamental importance to plant productivity and to the arthropod populations and communities on plants (White, 1984; Waring & Cobb, 1992; Kytö *et al.*, 1996). Ambient plant nitrogen levels are low in comparison to consumer requirements (Mattson, 1980; White, 1984; Hartley & Crawley, 1997), and a wide variety of herbivore taxa feed preferentially on nitrogen-enriched tissues (Ball *et al.*, 2000; Nakamura *et al.*, 2003; Albrechtsen *et al.*, 2004). The abundance, biomass, and diversity of herbivores or detritivores and their predators often increase in fertilisation experiments in natural systems (e.g. Levine *et al.*, 1998; Scheu & Schaeffer, 1998; Siemann, 1998; Haddad *et al.*, 2000; Ritchie, 2000; Halaj & 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 fertilisation 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 & Jones, 2001; Denno *et al.*, 2002; Langellotto & 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). Other sources of bottom-up heterogeneity, such as soil salinity (Moon & Stiling, 2002), water supply (Huberty & Denno, 2004), and intraspecific variation in host chemistry (Forkner *et al.*, 2004) or physical morphology (Moon *et al.*, 2000; Hare & Elle, 2002), can also interact with nutrient supply to affect arthropod communities.

Leaf pubescence – the presence of trichomes – may act as a chemical or mechanical defence to herbivores (Levin, 1973; Juniper & Southwood, 1986; Gruenhagen & Perring, 1999). Trichomes can secrete secondary chemicals (Stipanovic, 1983), or they may be composed of inert lignins and cellulose that inhibit digestion (Levin, 1973; Juniper & 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 & 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; Gruenhagen & Perring, 1999; Andres & Connor, 2003; but see van Dam & 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 & 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*, characterised by growth form, leaf size, and shape and the density of trichomes on the leaves and stems (Dawson & 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 & Hiesey, 1973; Kitayama & 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 dead wood and litter of *M. polymorpha* (Gruner, 2004a). 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 *M. polymorpha* appear more resistant to, or less favoured by, most of these herbivores (Lee, 1981; D. S. Gruner, unpublished data).

This study sought to disentangle the community-wide responses of arthropods to nutrient resources and foliar pubescence of *M. 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. Two primary questions were addressed with this study. 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 mass, per area individual 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 fertilisation and leaf pubescence on arthropod communities? Positive effects of fertilisation and negative effects of increasing pubescence on arthropod density and diversity were predicted, but interactive effects of these factors on species and community composition are virtually unexplored.

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 (19.664 °N, 155.284 °W). As in many other native ecosystems throughout the archipelago (Dawson & Stemmerman, 1999), *M. polymorpha* Gaudichaud-Beaupré (Myrtaceae) dominates this early successional wet forest (\approx 4000 mm mean annual precipitation). Ferns [e.g. *Dicranopteris linearis* (Burm.) Underw. (Gleicheniaceae)], sedges [e.g. *Machaerina angustifolia* (Gaud.) T. Koyama (Cyperaceae)],

and low shrubs [e.g. *Coprosma ernodeoides* A. Gray (Rubiaceae)] are also present (Gruner, 2004b).

The arthropod fauna associated with *Metrosideros* in the Hawaiian Islands is rich with species, but depauperate at higher functional and taxonomic levels because of biogeographic isolation (Howarth, 1990). *Metrosideros polymorpha* is attacked by multiple guilds of herbivorous insects, including several families of leaf-chewing Lepidopteran larvae, phloem- and xylem-feeding Heteroptera and Homoptera, gall-forming psyllids (Homoptera: Trioziidae), and wood-boring coleopteran larvae (Swezey, 1954; Gagné, 1979; Stein, 1983). Invertebrate predators (e.g. Araneae, Heteroptera: Nabidae), hymenopteran parasitoids (e.g. Ichneumonidae, Bethyliidae, and Chalcidoidea), and litter processors, fungal grazers, and scavengers (e.g. Psocoptera, Isopoda, Collembola, some Coleoptera) are abundant within tree canopies.

This experiment took place as part of a larger study investigating the relative importance of birds and resources on the *Metrosideros* arthropod community (Gruner, 2004b). In August 1998, 32 20 × 20 m plots were assigned fertilisation and avian insectivore exclusion treatments as crossed factors in a 2 × 2 randomised block design; the caged treatments were ignored in the present study. Sixteen plots were fertilised twice yearly from September 1998 to October 2000 with a broad spectrum of nutrients (Gruner, 2004b). Buffer strips, 10 m wide at minimum, separated all plots. Within each of eight blocks, there were two replicates of the fertilised treatment and two of the unfertilised control. Leaf morphology was investigated within each plot in a repeated-measures design.

Pubescence and leaf mass per area

An operational classification scale was devised to characterise hairiness of *Metrosideros* leaves, with slight modification to previous schemes (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 appressed and intermediate (GP), found on abaxial, adaxial, or both surfaces, but where present, it could be rubbed off easily without damage to the leaf lamina. These classes correspond roughly to described varieties *glaberrima*, *polymorpha*, and *incana* respectively, but these names were not applied because of taxonomic uncertainties (Dawson & Stemmerman, 1999; James *et al.*, 2004). Although all *M. polymorpha* seedlings begin with glabrous leaves, they usually attain their final morphological state within 2 years (S. Cordell, pers. comm.). Multiple classes were not observed on any single tree in this study, although others have noted epicormic shoots with characteristics corresponding to different varieties (James *et al.*, 2004).

Fertilisation on nearby young basaltic substrates decreased leaf mass per area (LMA) of *M. polymorpha*, although LMA typically does not change in response to fertilisation 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 & Cannon, 2001), which is among the most important deterrents to leaf herbivory (Coley & Barone, 1996).

The contribution of trichomes to LMA, and how this contribution might change with fertilisation and among leaf morphotypes, was evaluated. 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 eight leaves from each morphology – plot combination. Mass of leaf pubescence was determined in a procedure similar to previous work on *M. polymorpha* (Geeske *et al.*, 1994; Cordell *et al.*, 1998). Instead of using opposite leaves as paired samples, however, leaves were shaved with a razor on one side of the midrib of each leaf. A cork hole borer (disc area = 0.70 cm²) was used to sample tissue from each side. Leaf discs were dried to constant mass at 65 °C and weighed to determine leaf mass and LMA (g m⁻²). The difference between unscraped and scraped mass from the same leaf was considered the mass of the pubescence.

Arthropod sampling

Arthropods were collected by clipping branches and foliage into heavy white plastic bags (Fretz, 2000; Gruner, 2004b). The terminal branchlets (≈ 50 cm) of twigs and foliage were clipped while avoiding reproductive structures (seeds, flowers). Many arthropod taxa in this system are reluctant to disperse from foliage even when disturbed (Gruner, pers. obs.). Nevertheless, extreme care was exercised in avoiding disturbance of branches and arthropods before branches were quickly bagged and then clipped.

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

Foliage was transported 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. Branches were shaken and the detrital remainder sifted until no additional arthropods were observed. Foliage was separated from woody material, oven-dried to constant mass, and both components weighed to milligram 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 millimetre, 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, 1997). 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 (see Appendix). Carnivores included various predatory arthropods (e.g. Araneae, some Heteroptera and Coleoptera) and hymenopteran parasitoids (Ichneumonidae, Bethyliidae, and Chalcidoidea); detritivores included 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 100 arthropod species have been recorded from *M. polymorpha* at the site (Gruner, 2004a, 2004b).

Several indices were used to represent species diversity. To account for differences in the sizes of samples, species density was calculated by dividing species number by the mass of the foliage in a given sample. Individual-based rarefaction was not used because of low abundance counts in several samples. Instead, the Shannon diversity index (H') was used a measure of relative diversity, to control for total arthropod abundance, and to incorporate evenness (Magurran, 1988). Shannon H' was 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. Fertilisation (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 (fertilisation \times morphology \times block) was dropped from the model after determining it was uniformly non-significant. Models were analysed with type III sums

of squares in SAS PROC MIXED (SAS, 2001), with d.f. for error mean squares of random terms estimated by the Satterthwaite approximation. Tukey–Kramer tests were used for comparisons of morphology main effects only (joint $\alpha = 0.05$).

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

Several methods based on matrices of ecological distances (dissimilarity) between samples were used to analyse the effects of fertilisation and leaf morphology on arthropod community composition. These methods recognise species identities and treat the community as a multivariate entity. Prior to calculating the distance matrices, abundances were $\log_{10}(X + 1)$ transformed to reduce the influence of a few highly abundant species. Transformed abundances were then relativised by dividing by their sum for each sample, to reduce the effect of differences among samples in total abundance and therefore to emphasise differences in relative proportions of taxa. Euclidean distances ('distance between species profiles', Legendre & Gallagher, 2001) then were calculated; qualitatively similar results were obtained using several non-Euclidean measures (e.g. Bray–Curtis distance).

Hypotheses for change in community composition were tested with non-parametric multivariate analysis of variance (NPMANOVA; Anderson, 2001; McArdle & Anderson, 2001). In effect, NPMANOVA partitions the distance matrices 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, 4999 permutations of the raw data were used, in units defined by the 'error' term of the corresponding pseudo- F ratio. Data were analysed for all trophic levels, and both with and without *Salina celebensis* (Schaeffer) (Collembola), which alone accounted for almost 70% of individuals. Metric multidimensional scaling (principal coordinates analysis, PCO; Legendre & Legendre, 1998) was used to reduce the dimensionality of the species data to orthogonal axes and further explore relationships to treatments (this analysis using Euclidean distances is equivalent to principal components analysis, Legendre & Legendre, 1998).

Redundancy analysis (RDA; Legendre & Legendre, 1998) was used to constrain these ordinations by original experimental treatments, and to relate these axes back to individual species. RDA was conducted using the 'vegan' package, version 1.6-4 (<http://cc.oulu.fi/~jarioksa/>), in the R statistical language, version 1.9.1 (<http://www.r-project.org>). Partial redundancy analysis demonstrated that the fertilisation factor explained little variation beyond that explained by morphotype class alone; thus, canonical redundancy analysis proceeded on this single factor with three levels, ignoring blocks. RDA results were visualised in a two-dimensional biplot with the strongest species vectors, calculated as the sum of the absolute values of species loadings from both RDA axes, plotted in relation to sample scores and centroids for morphology classes. Sample scores in biplots were weighted sums of species scores, using RDA scaling 1 (site scores scaled proportional to axis eigenvalues and species unscaled), which preserves distances among samples.

Results

Foliar characteristics

Fertilisation strongly decreased LMA in unscraped leaf discs (Fig. 1; $F_{1,7} = 225.86$, $P < 0.0001$), and LMA also was greater in pubescent (P) leaves than intermediate (GP) forms ($F_{1,7} = 21.60$, $P = 0.002$). Leaf scraping allowed separation of these two effects into their components: mass of leaf hairs was responsible for the significant difference in LMA between P and GP ($F_{1,7} = 82.74$, $P < 0.0001$), and fertilisation decreased mass per area of leaf tissue exclusive of pubescence ($F_{1,7} = 164.01$, $P < 0.0001$). Fertilisation did not change pubescence, and none of 88 marked trees changed morphology class over 33 months.

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 unfertilised plots was slightly higher than from fertilised plots (fertilised 234.6 g ± 6.0 SE, unfertilised 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 standardised to foliage biomass of collections. To maintain consistency with other studies (Fretz, 2000; Gruner, 2004b), results based on loads are reported.

Abundance and biomass

A total of 8840 individuals in 99 species and morpho-species from 13 arthropod orders were collected from *M. polymorpha* clippings in this study (see Appendix).

The effects of fertilisation and leaf morphology on density and biomass differed among arthropod orders, but in

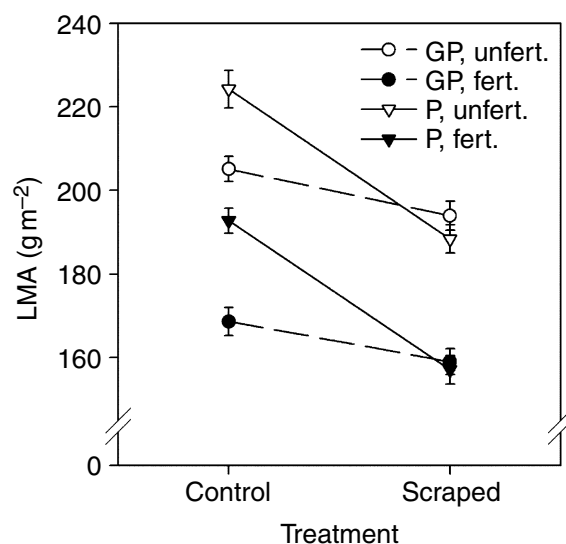


Fig. 1. Means (± 1 SE) of LMA (g m^{-2}) of leaf discs from pubescent (P) and intermediate (GP) foliar morphologies in fertilised (fert.) and unfertilised (unfert.) plots. Discs were either un-manipulated or scraped of all leaf hairs.

no case was there statistically significant interaction between them (Fig. 2; Table 1). Density and biomass of Acari were higher on intermediate morphologies (Fig. 2a,b) although these effects varied among blocks. Spiders were more abundant on fertilised plots, irrespective of leaf form (Fig. 2c), but did not differ in biomass (Fig. 2d). Collembola density and biomass, dominated by a single species (*S. celebensis* > 99% of all Collembola individuals), increased strongly with fertilisation, decreased with increasing leaf pubescence, and varied across blocks (Fig. 2e,f). Fertilisation increased the density but not biomass of both Heteroptera and Homoptera, and Heteroptera were more abundant on increasingly pubescent foliage (Fig. 2g,j); Heteroptera density also showed a significant fertilisation \times block interaction (Table 1). Psocoptera density and biomass did not respond to fertilisation, but both were significantly elevated on pubescent forms relative to the glabrous and intermediate morphologies (Fig. 2k,l). The aggregate grouping from less abundant orders did not change with treatments (Fig. 2m,n).

Fertilisation increased the density of all trophic levels on *M. polymorpha* (Table 2, Fig. 3). Detritivores, dominated by Collembola (Fig. 2e,f), were the most abundant trophic group (Fig. 3c). Highly significant effects of fertilisation, leaf morphology, and blocks on detritivore density drove the same suite of results for all arthropods in aggregate (Fig. 3a,b). Fertilisation effects on herbivore density varied significantly across blocks (Table 2). There were no significant effects of morphology or fertilisation on trophic-level biomass (Fig. 3), except for significant fertilisation \times block interactions for herbivore, detritivore, and total arthropod biomass (Table 2). Detritivore biomass varied across blocks, and the plot term was significant for carnivore

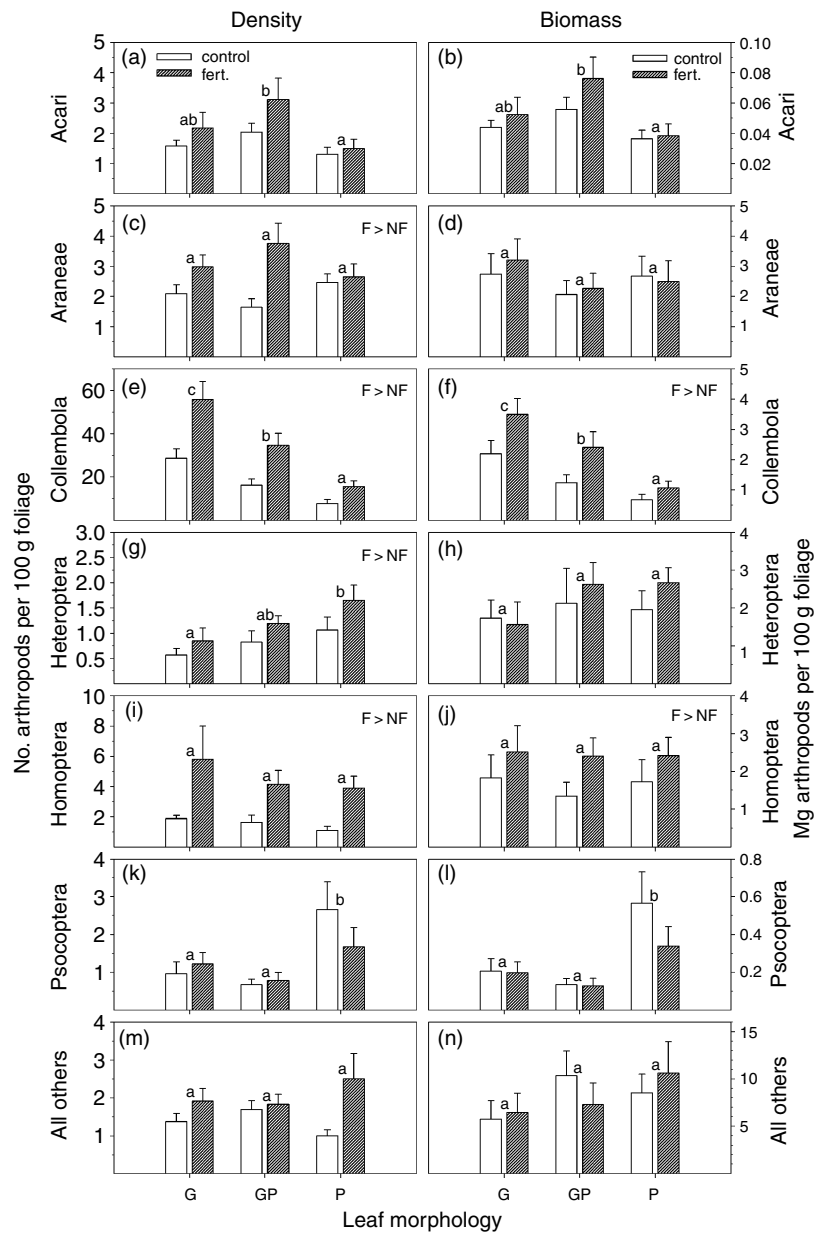


Fig. 2. Means (± 1 SE) of density and biomass of arthropod taxonomic orders, as a function of dry foliage biomass, on glabrous (G), intermediate (GP), and pubescent (P) foliar morphologies in fertilised (fert.; filled bars) and unfertilised (control; unfilled) plots. The 'all others' (m, n) category combines less abundant orders (Coleoptera, Diptera, Hymenoptera, Isopoda, Lepidoptera, Neuroptera, and Thysanoptera). Lowercase letters denote significant differences in the leaf morphology main effect tested by the Tukey–Kramer test (adjusted $\alpha = 0.05$); insets (F, NF, not fertilised) indicate the direction of significant F -ratios from GLMs.

biomass. Although the block factor was significant in tests with various arthropod variables, there were no discernible temporal trends. Fertilisation led to higher arthropod numbers relative to unfertilised plots on most sampling dates and across morphological classes. This result was more equivocal for arthropod biomass and for the pubescent morphology.

Species diversity

Fertilisation increased species density (number of species per unit foliage) for all trophic levels (Fig. 4, Table 3). This fertilisation effect also varied significantly

across blocks for all trophic levels except detritivores. There were no significant effects of leaf morphology on species density, other than the morphology \times block interaction for carnivores (Table 3). Behaviour of the Shannon H' diversity index was distinct from species density results (Fig. 4, Table 3). Relative diversity for herbivores was higher with fertilisation (Fig. 4f). However, the fertiliser effect varied across blocks for both carnivores and herbivores, and all arthropods in aggregate varied across blocks and plots (Table 3). Detritivore diversity increased with increasing pubescence level (Fig. 4d), a result paralleled by arthropod totals (Fig. 4b). Morphology effects also interacted with block effects for all arthropods in aggregate.

Table 1. *P*-values from GLMs of density and biomass of taxonomic orders. The 'all other' category combines less abundant orders: Coleoptera, Diptera, Hymenoptera, Isopoda, Lepidoptera, Neuroptera, and Thysanoptera. Response variables were \log_e transformed prior to analysis. Italicised sources represent random terms. Significant *F*-values are indicated with boldface.

Source	d.f. ^a	Density load						Biomass load							
		Acari	Araneae	Collembola	Heteroptera	Homoptera	Psocoptera	Others	Acari	Araneae	Collembola	Heteroptera	Homoptera	Psocoptera	Others
Fertilisation (F)	1,7	0.472	0.008	< 0.001	0.049	0.007	0.426	0.090	0.424	0.813	< 0.0001	0.295	0.036	0.279	0.387
Block (B)	7, ^b	0.507	0.285	0.001	0.363	0.060	0.077	0.029	0.396	0.216	< 0.0001	0.203	0.284	0.109	0.007
F × B	7,16	0.039	0.579	0.498	0.608	0.006	0.829	0.246	0.022	0.800	0.955	0.708	0.395	0.323	0.227
Pit/(F/B)	16,46	0.224	0.651	0.058	0.028	0.619	0.360	0.271	0.226	0.032	0.001	0.015	0.625	0.422	0.729
Morphology (M)	2,14	0.048	0.972	< 0.0001	0.047	0.171	0.007	0.623	0.028	0.424	< 0.0001	0.191	0.993	0.012	0.334
M × F	2,46	0.702	0.076	0.795	0.614	0.375	0.090	0.156	0.423	0.714	0.134	0.136	0.886	0.246	0.504
M × B	14,46	0.049	0.641	0.396	0.063	0.238	0.292	0.096	0.043	0.581	0.044	0.070	0.516	0.045	0.164

^aNumerator, denominator d.f.

^bDenominator d.f. variable; estimated by Satterthwaite approximation.

Species composition

NP MANOVA showed no effect of fertilisation, nor any interaction involving fertilisation on the total community or any of the trophic level assemblages. However, leaf morphology strongly influenced the composition of the entire community (pseudo- $F_{2,14} = 3.808$, $P = 0.0002$), the detritivorous assemblage (pseudo- $F_{2,14} = 7.950$, $P = 0.0002$), and there was a suggestion of an effect on herbivores (pseudo- $F_{2,14} = 2.426$, $P = 0.060$). When the most abundant collembolan species (*S. celebensis*) was removed from the detritivorous and aggregate assemblages, leaf morphology effects remained significant, although less strongly so (total: pseudo- $F_{2,14} = 2.753$, $P = 0.007$; detritivores: pseudo- $F_{2,14} = 3.770$, $P = 0.044$). The block term was strongly significant for all trophic levels (all P -values < 0.001). Blocks also interacted significantly with leaf morphology in the community overall, but not within trophic levels [significant morphology × block interaction, total: pseudo- $F_{14,46} = 1.194$, $P = 0.038$; total (no *Salina*): pseudo- $F_{14,46} = 1.169$, $P = 0.042$]. Visual inspection of scatterplots of blocks against time or spatial proximity did not reveal clear seasonality or directional temporal trends (i.e. increasing fertilisation effect) in arthropod response variables or PCO axes.

Constrained ordination (RDA) showed little overlap between communities from pubescent and glabrous trees; samples from GP trees mostly fell between the two extreme morphologies, fairly distinct from the cluster of P samples but overlapping substantially with the G samples (Fig. 5a). Samples from pubescent trees were characterised by the high abundances of the detritivorous psocid *Kilauella* sp. 3, the herbivorous mirid *Sarona adonias* Kirkaldy, and the pit gall-forming *Kuwayama* sp. 1, and by low abundances of the cicadellid *Nesophrosyne giffardi* Kirkaldy and the collembolan *S. celebensis* (Fig. 5b; Appendix). Conversely, high abundances of *S. celebensis*, *N. giffardi*, and the psocid *Valenzuela badiostigma* (Okamoto), along with low abundances of *Kuwayama* sp. 1, *S. adonias*, and the isopod *Porcellio scaber* Latreille typified communities on glabrous trees. Intermediate pubescence (GP morphology) was correlated with low abundance of *Kilauella* sp. 3 and high abundances of three predatory arachnids: the spiders *Tetragnatha acuta* Gillespie and *Misumenops anguliventris* (Simon), and the mite Anystidae g. sp. 1.

Discussion

Is foliar pubescence ecologically labile?

In this highly nutrient-limited environment, LMA decreased but trichome mass did not change in response to the experimental fertilisations (Fig. 1). Previous studies of *M. polymorpha* showed that morphological traits, such as trichome structure and density, have a genetic basis, whereas ecophysiological behaviour and anatomical

Table 2. *P*-values from GLMs of density and biomass of arthropod trophic groups. Response variables were log_e transformed prior to analysis. Italicised sources represent random terms. Significant *F*-values are indicated with boldface.

Source	d.f. ^a	Density load				Biomass load			
		All	Carnivores	Herbivores	Detritivores	All	Carnivores	Herbivores	Detritivores
Fertilisation (F)	1,7	< 0.001	0.010	0.008	0.002	0.116	0.462	0.143	0.333
Block (B)	7, ^b	< 0.001	0.330	0.110	0.005	0.083	0.191	0.722	0.011
F × B	7,16	0.384	0.208	0.004	0.158	0.048	0.928	0.005	0.013
Plot(F B)	16,46	0.113	0.807	0.855	0.265	0.727	0.034	0.984	0.883
Morphology (M)	2,14	< 0.001	0.982	0.833	< 0.001	0.981	0.679	0.470	0.864
M × F	2,46	0.313	0.141	0.302	0.488	0.859	0.756	0.709	0.298
M × B	14,46	0.235	0.277	0.255	0.580	0.570	0.088	0.403	0.248

^aNumerator, denominator d.f.^bDenominator d.f. variable; estimated by Satterthwaite approximation.

features, such as LMA, were inducible by environmental factors in a common garden setting (Cordell *et al.*, 1998). This independence of morphological and physiological features has been documented in other plant species (Roy *et al.*, 1999; Forkner & Hare, 2000). However, increased trichome density may be induced by heavy herbivore defoliation or by intense disturbance events, such as hurricanes (Pullin & Gilbert, 1989; Dalin & Björkman, 2003; Spiller & Agrawal, 2003) – this alternative has not been tested in the present system.

Community responses to fertilisation

Increased densities in response to fertilisation were observed in four arthropod orders and all trophic levels

(Figs 2 and 3; Tables 1 and 2). Reviews of population and community responses to fertilisation have shown positive effects on herbivorous arthropod abundance in many studies (Waring & 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 defence (Mattson, 1980; Strong *et al.*, 1984; Keinanen *et al.*, 1999; Ritchie, 2000). In this study, fertilisation decreased LMA (Fig. 1), which is positively related to leaf toughness (Wright & Cannon, 2001), an important deterrent to leaf herbivory (Coley & 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

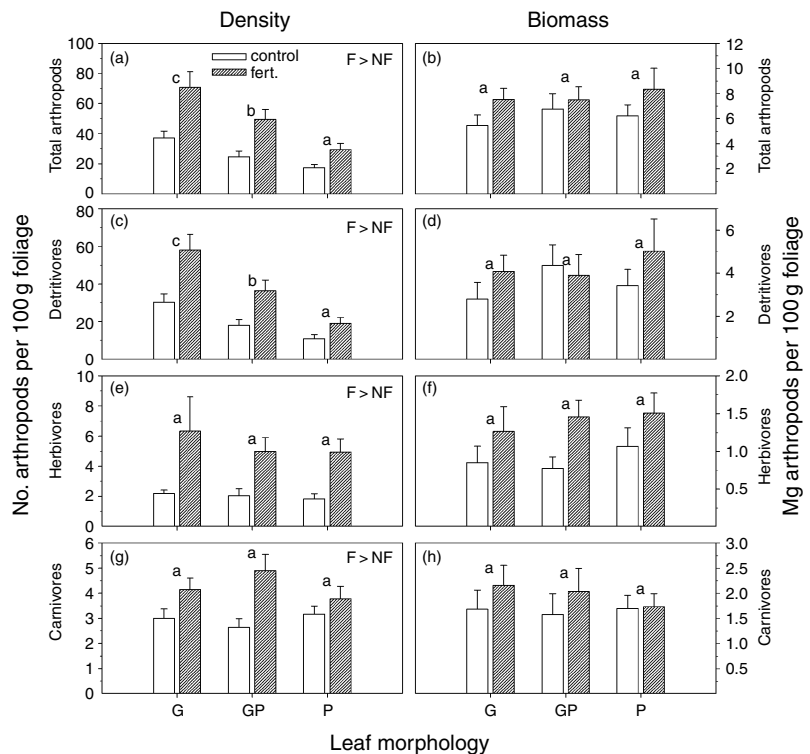


Fig. 3. Means (± 1 SE) of arthropod trophic level density and biomass, as a function of dry foliage biomass, on glabrous (G), intermediate (GP), and pubescent (P) foliar morphologies in fertilised (fert.; filled bars) and unfertilised (control; unfilled) plots. Lowercase letters denote significant differences in the leaf morphology main effect tested by the Tukey–Kramer test (adjusted $\alpha = 0.05$); insets (F, fertilised; NF, not fertilised) indicate the direction of significant *F*-ratios from GLMs.

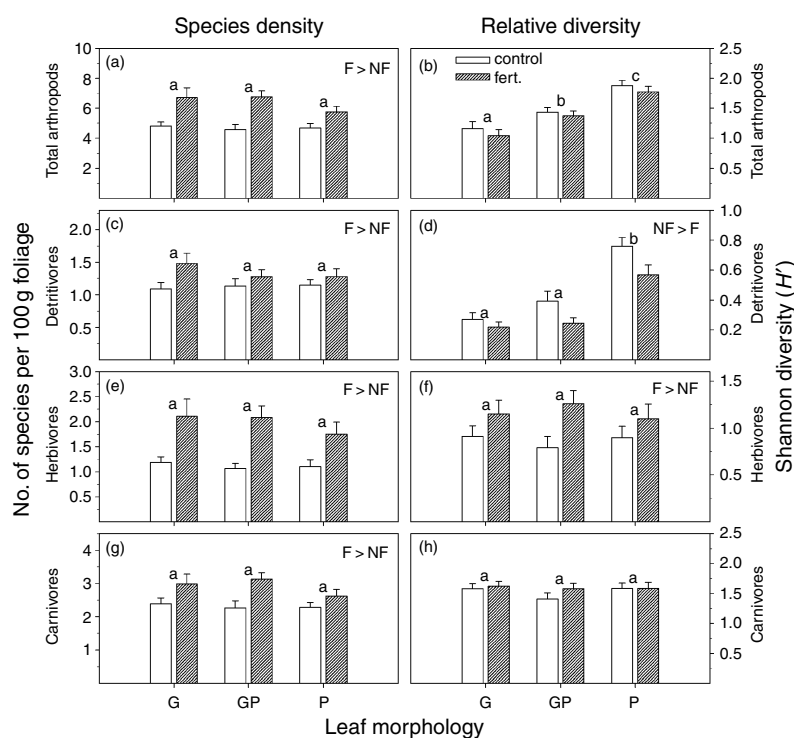


Fig. 4. Means (± 1 SE) of arthropod trophic level species density (richness per 100 g foliage) and relative diversity (Shannon H') on glabrous (G), pubescent (P), and intermediate (GP) foliar morphologies in fertilised (fert.; filled bars) and unfertilised (control; unfilled) plots. Results for Fisher's α were similar to Shannon H' , and are not shown. Lowercase letters denote significant differences in the leaf morphology main effect tested by the Tukey–Kramer test (adjusted $\alpha = 0.05$); insets (F, fertilised; NF, not fertilised) indicate the direction of significant F -ratios from GLMs.

can cascade up to natural enemies (Forkner & 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 fertilised plots (Langellotto & Denno, 2004). Herbivore and detritivore biomass also increased in some fertilised blocks, but this effect was weak and variable (Table 2), consistent with a related study that showed smaller individuals dominate the response to nutrient enrichment (Gruner, 2004b).

Responses of community species richness or diversity in other studies have been more variable and equivocal than abundances (Hurd & 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 & Heegaard, 2003), trophic or taxonomic focus (Haddad *et al.*, 2000), diversity metric or standardisations employed (McCabe & Gotelli, 2000), or experimental time frame (Haddad *et al.*, 2000). For example, long-term fertilisations frequently decrease plant richness or otherwise alter species composition concomitant with increasing productivity (Siemann, 1998; Waide *et al.*, 1999; Haddad *et al.*, 2000). Potential confounding from plant community compositional changes with fertilisation was avoided by isolating the single host, the dominant tree species *M. polymorpha*. Concerns about scale were addressed by sampling periodically over a 1-year time frame, and by reference to a study examining arthropod responses to a productivity gradient across the Hawaiian archipelago (Gruner, 2004c). Moreover, all trophic levels and taxonomic orders were

Table 3. P -values from GLMs for species density and Shannon H' of arthropod trophic levels. Italicised sources represent random terms. Significant F -values are indicated with boldface.

Source	d.f. ^a	Species density				Shannon H'			
		All	Carnivores	Herbivores	Detritivores	All	Carnivores	Herbivores	Detritivores
Fertilisation (F)	1,7	0.009	0.038	0.024	0.002	0.264	0.445	0.044	0.042
Block (B)	7, ^b	0.321	0.543	0.461	0.437	0.046	0.185	0.262	0.361
$F \times B$	7,16	0.013	0.027	0.001	0.953	0.309	0.007	0.048	0.325
Plot(FB)	16,46	0.627	0.636	0.694	0.497	0.026	0.960	0.864	0.063
Morphology (M)	2,14	0.407	0.574	0.490	0.705	<0.0001	0.439	0.973	<0.0001
$M \times F$	2,46	0.230	0.342	0.486	0.418	0.847	0.519	0.494	0.247
$M \times B$	14,46	0.116	0.027	0.210	0.541	0.004	0.258	0.175	0.169

^aNumerator, denominator d.f.

^bDenominator d.f. variable; estimated by Satterthwaite approximation.

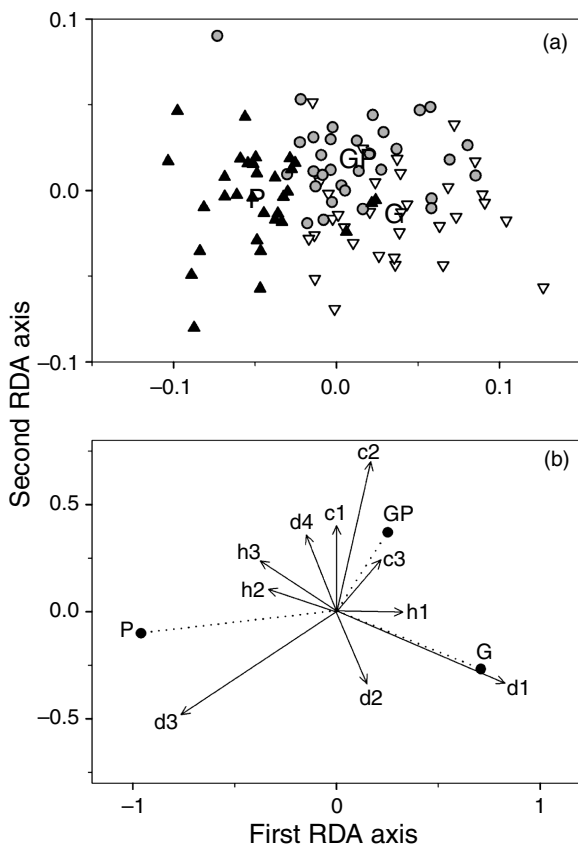


Fig. 5. Redundancy analysis of species abundances in relation to leaf pubescence type. The two RDA axes represent the principal components of the multivariate (all 99 species) means for the three leaf morphologies. (a) Constrained ordination of the 96 samples, coded by leaf morphology. Empty triangles, glabrous (G); grey circles, intermediate (GP); filled triangles, pubescent (P); letters indicate centroids. (b) Biplot representing correlations of leaf morphologies (labelled dashed lines) and species (arrows); 10 most important only: *Salina celebensis*, *Valenzuela badiostigma*, *Kilauella* sp. 3, *Porcellio scaber* (detritivores, d1–d4); *Nesophrosyne giffardi*, *Kuwayama* sp. 1, *Sarona adonias* (herbivores, h1–h3); *Tetragnatha acuta*, *Misumenops anguliventris*, *Anystidae* g. sp. 1 (carnivores c1–c3; see Appendix for species information). Note the differing scales of axes among plots.

examined to provide a broad understanding of community-wide responses, and multiple diversity metrics were compared within these groups.

Species density of all trophic levels increased with fertilisation (Fig. 4), but this result may be attributable to increased abundances. Using the Shannon index to account for relative abundance, herbivore diversity alone was elevated with fertilisation (Fig. 4d, Table 3), whereas the diversity of detritivores actually decreased (Fig. 4f, Table 3). Because fertilisation increased herbivore abundance but did not change equitability (Pielou's J' overall mean \pm SE: 0.89 ± 0.01 , all F -tests NS), higher herbivore diversity may be an indirect result of rare species becoming abundant enough to persist locally ('consumer rarity hypothesis' *sensu*

Siemann, 1998; 'more individuals hypothesis' *sensu* Srivastava & Lawton, 1998). In contrast, detritivore diversity declined with fertilisation due to increasing dominance of a single species, *S. celebensis*, which was by far the most abundant animal on trees (>99% of Collembola individuals in Fig. 2e). Somewhat surprisingly, despite these differing effects on abundance and diversity of different trophic groups, analysis of overall community composition (NPMANOVA) revealed no consistent effect of fertilisation. It may be that temporal or spatial variation among blocks, or the relatively short duration of the fertilisation manipulation (<2 years), obscured a modest fertilisation effect.

Community responses to foliar pubescence

Arthropod responses to *M. polymorpha* pubescence classes varied with, and within, taxonomic orders and trophic levels (Figs 2, 3 and 4). Although previous studies have shown that trichomes can interfere with the foraging behaviour of insect predators or parasitoids (Van Lenteren *et al.*, 1995; Eisner *et al.*, 1998), natural enemies did not vary with leaf pubescence on *M. polymorpha* (Figs 3 and 4). Herbivore variables also were unchanged overall across leaf pubescence levels, despite evidence for associations of individual species (Fig. 5b) and observations that oviposition or damage by several species were more frequent on glabrous morphologies at this and nearby sites (Lee, 1981; Alyokhin *et al.*, 2004; D. S. Gruner, unpublished data). Many of the herbivorous lineages that utilise *Metrosideros* in this community are internal feeders, predominantly bud-mining Lepidoptera and gall-forming psyllids. Cornell (1989) hypothesised that gall-formers, leaf-miners, and other endophagous insects can avoid leaf defences, and empirical studies have shown that some gall-formers can manipulate the mechanical or chemical defences of their host plants (Hartley, 1998; Nyman & Julkunen-Tiitto, 2000). The abundance of internal-feeding species on manzanita (*Arctostaphylos* spp. Ericaceae) was not influenced by length, density or glandularity of trichomes (Andres & Connor, 2003). Demographic studies on developing *Metrosideros* leaf cohorts may more effectively evaluate this prediction for herbivore species in their most actively feeding juvenile stages (D. S. Gruner, unpublished data).

Detritivores as a group increased in abundance (Fig. 3c) but decreased in diversity (Fig. 4d) on more glabrous morphologies. Much of the increase in density again can be attributed to *S. celebensis*; nevertheless, deletion of *S. celebensis* did not erase the significant influence of leaf morphology on detritivore community composition (NPMANOVA pseudo- $F_{2,14} = 3.770$, $P = 0.044$). Higher abundance of detritivores on glabrous forms could arise from several mechanisms. Although nitrogen concentrations did not differ among morphologies (one-way ANOVA from unfertilised trees, $F_{2,30} = 1.42$, $P = 0.257$, see Methods in Gruner, 2004b), pubescent leaf litter may be less palatable because of higher levels of cellulose, lignins, or condensed tannins. Alternatively, detritivores may

respond indirectly to herbivory by phytophagous insects. In particular, stem galls (*Trioza hawaiiensis* Crawford) occurred in higher frequency among glabrous morphotypes, less so on intermediate forms, and never on pubescent morphologies at this site (D. S. Gruner, unpublished data). These galls often 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 (D. Gruner, pers. obs.). On *Salix*, insect stem galls increased the growth of lateral shoots, 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 observed foraging or residing within excavated gall tissues on leaves or stems.

Arthropod response was heterogeneous among orders, with species of Psocoptera (*Kilauella* sp. 3), Heteroptera (*Sarona adonias*), and Homoptera (*Kuwayama* sp. 1) in highest numbers on the most pubescent leaves, and a predatory anystid mite most abundant on intermediate forms (Figs 2 and 5b). Some small arthropods also may benefit from habitat heterogeneity offered by trichomes. On bean plants, predatory mites preferentially selected artificial pubescence as habitat structure and were more abundant on leaves with trichomes (Roda *et al.*, 2001). Diametrically opposed responses of different phytophagous taxa have been reported in response to glandular trichomes of *Datura wrightii* (van Dam & Hare, 1998), and across guilds on *Arbutus xalapensis* (Ezcurra *et al.*, 1987). Psocoptera distributions could reflect negative competitive outcomes with abundant Collembola, as species from both groups scavenge dead organic matter and graze lichens, fungi, and algae (Thornton, 1985; Christiansen & Bellinger, 1992). Alternatively, there may be differences in bark structure, tree architecture, or distribution and abundance of microepiphytes or endophytic fungi correlated with foliar pubescence. Pubescent leaves may have a longer leaf lifespan (Cordell *et al.*, 2001; D. S. Gruner, unpublished data), which would favour the development of psyllids that induce galls later in leaf ontogeny (i.e. leaf pit galls, *Kuwayama* sp. 1; Fig. 5b), and may favour inquiline arthropods that utilise these evacuated shelters.

Conclusions

This study demonstrates the bottom-up influence of *M. polymorpha* foliar pubescence on arthropod communities. Although the functional significance of trichomes in *M. polymorpha* is unclear, distributional gradients of morphological forms suggest that pubescence is linked to resources or abiotic factors (Corn & Hiesey, 1973; Geeske *et al.*, 1994; Cordell *et al.*, 1998; Melcher *et al.*, 2000). However, responses of aggregate arthropod variables to pubescence generally acted independently of resource

availability, and effects were more pronounced on the relative diversity and species composition of the community than observed with fertilisation. Fertilisation increased the numbers and species densities of most arthropod groups; in contrast, leaf morphology had contrasting positive and negative effects on restricted taxonomic groups within trophic levels. Thus, qualitative differences in trichome density and leaf structure appeared to be more important than resource quantity for *Metrosideros* arthropod community composition. Moreover, the effects of such leaf traits vary greatly among species, depending on details of their natural history, and may be difficult to predict with much specificity. Given the diversity of effects, and the abundance of detritivores in this forest ecosystem (Gruner, 2004b), leaf morphology may have implications equal or greater in importance for decomposers and litter processors 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.

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Appendix

Arthropod species sampled from *Metrosideros polymorpha* clipping samples in 1999 and 2000. Also listed are residency status (I, historically introduced; N, native; U, undetermined); trophic level assignments (d, detritivore; h, herbivore;

c, carnivore; t, tourist or undetermined); total abundance (Abund.); and loadings with axis 1 and 2 of the redundancy analysis (see Fig. 5). Boldface and numbered trophic assignments refer to labels of species vectors in Fig. 5b. Taxa are listed in alphabetical order within each decreasing taxonomic rank without regard to phylogenetic relationships.

Order	Family	Genus species (author)	Origin	Trophic	Abund.	RDA1	RDA2
Subphylum Chelicerata: class Arachnida							
Acari	Acari f.	Acari g. sp. 2	U	t	8	0.021	0.145
Acari	Acari f.	Acari g. sp. 4	U	t	3	-0.006	-0.045
Acari	Acari f.	Acari g. sp. 5	U	t	4	0.019	-0.029
Acari	Acari f.	Acari g. sp. 7	U	t	10	-0.075	0.050
Acari	Acari f.	Acari g. sp. 9	U	t	1	0.003	0.029
Acari	Acari f.	Acari g. sp. 10	U	t	5	-0.008	0.005
Acari	Acari f.	Acari g. sp. 12	U	t	4	0.034	-0.087
Acari	Acari f.	Acari g. sp. 13	U	t	1	-0.019	-0.014
Acari	Acari f.	Acari g. sp. 14	U	t	1	-0.019	-0.013
Acari	Anystidae	Anystidae g. sp. 1	I	c3	397	0.167	0.696
Araneae	Araneidae	<i>Araneus emmae</i> Simon, 1900	N	c	1	0.009	-0.023
Araneae	Linyphiidae	<i>Erigone autumnalis</i> Emerton, 1882	I	c	96	-0.115	0.071
Araneae	Linyphiidae	Linyphiidae g. sp. 1	I	c	9	-0.062	0.028
Araneae	Linyphiidae	Linyphiidae g. sp. 2	I	c	13	-0.150	-0.108
Araneae	Miturgidae	<i>Cheiracanthium mordax</i> L. Koch, 1866	I	c	37	-0.070	-0.022
Araneae	Philodromidae	<i>Pagiopalus atomarius</i> Simon, 1900	N	c	44	0.011	-0.178
Araneae	Salticidae	<i>Havaika</i> sp. 3	N	c	21	0.005	-0.067
Araneae	Tetragnathidae	<i>Tetragnatha acuta</i> Gillespie, 1992	N	c1	108	0.000	0.401
Araneae	Tetragnathidae	<i>Tetragnatha anuene</i> Gillespie, 2002	N	c	1	0.006	0.058
Araneae	Tetragnathidae	<i>Tetragnatha quasimodo</i> Gillespie, 1991	N	c	19	-0.024	-0.075
Araneae	Theridiidae	<i>Achaearanea</i> cf. <i>riparia</i> (Blackwall, 1834)	I	c	63	-0.093	-0.050
Araneae	Theridiidae	<i>Theridion melinum</i> Simon, 1900	N	c	5	-0.031	0.006
Araneae	Theridiidae	<i>Theridion praetextum</i> Simon, 1900	N	c	1	0.011	-0.029
Araneae	Thomisidae	<i>Misumenops anguliventris</i> (Simon, 1900)	N	c2	96	0.219	0.242
Araneae	Thomisidae	<i>Misumenops facundus</i> (Suman, 1970)	N	c	93	-0.019	-0.246
Subphylum Atelocerata: class Insecta							
Coleoptera	Carabidae	<i>Mecyclothorax deverilli</i> (Blackburn, 1879)	N	c	4	-0.021	-0.076
Coleoptera	Elateridae	<i>Eopenthes tinctus</i> Sharp, 1908	N	c	2	-0.014	0.027
Coleoptera	Nitidulidae	<i>Eupetinus striatus</i> (Sharp), 1881	N	d	5	0.035	0.000
Coleoptera	Staphylinidae	<i>Anotylus</i> sp. 2	I	c	1	0.003	0.029
Coleoptera	Staphylinidae	<i>Oligota glabra</i> Sharp, 1880	N	c	4	-0.016	0.018
Coleoptera	Staphylinidae	<i>Oligota</i> sp. 4	N	c	17	-0.066	0.256
Collembola	Entomobryidae	<i>Entomobrya laha</i> Christiansen & Bellinger, 1992	N	d	6	0.018	0.034
Collembola	Entomobryidae	<i>Entomobrya socia</i> (Denis, 1929)	I	d	25	-0.068	-0.099
Collembola	Entomobryidae	<i>Salina celebensis</i> (Schaeffer, 1898)	I	d1	6105	0.828	-0.335
Collembola	Entomobryidae	<i>Tomocerus minor</i> (Lubbock, 1862)	I	d	1	0.007	0.070
Collembola	Isotomidae	<i>Isotoma sensibilis</i> Tullberg, 1876	I	d	4	0.042	-0.064
Diptera	Ceratopogonidae	<i>Forcipomyia hardyi</i> Wirth & Howarth, 1982	N	d	7	0.025	-0.069
Diptera	Chironomidae	<i>Orthocladus williamsi</i> Hardy, 1960	N	d	4	-0.025	0.078
Diptera	Dolichopodidae	<i>Eurynogaster variabilis</i> Hardy & Kohn, 1964	N	c	6	0.066	0.107
Diptera	Drosophilidae	<i>Drosophila simulans</i> Sturtevant, 1919	I	d	1	0.011	-0.028
Diptera	Drosophilidae	<i>Scaptomyza infurcula</i> Hardy, 1965	N	d	5	0.034	0.021
Diptera	Limoniidae	<i>Dicranomyia variabilis</i> (Grimshaw, 1901)	N	d	4	-0.089	-0.064
Diptera	Sciaridae	<i>Ctenosciara hawaiiensis</i> (Hardy, 1956)	N	d	2	0.015	0.029
Diptera	Sciaridae	<i>Hyperlasion magnisensoria</i> (Hardy, 1965)	N	d	1	0.011	-0.027
Diptera	Sciaridae	Sciaridae g. sp. 4	U	d	1	0.007	-0.018
Heteroptera	Lygaeidae	<i>Nysius blackburni</i> White, 1881	N	h	2	0.003	-0.046
Heteroptera	Lygaeidae	<i>Oceanides vulcan</i> (White, 1881)	N	h	36	-0.041	0.098
Heteroptera	Miridae	<i>Hyalopeplus pellucida</i> (Stal, 1859)	N	h	7	-0.088	0.021
Heteroptera	Miridae	<i>Koanoa hawaiiensis</i> Kirkaldy, 1902	N	h	1	-0.012	-0.009

Heteroptera	Miridae	<i>Sarona adonias</i> Kirkaldy, 1902	N	h3	80	-0.379	0.238
Heteroptera	Nabidae	<i>Nabis curtipennis</i> Blackburn, 1888	N	c	1	0.019	-0.048
Heteroptera	Nabidae	<i>Nabis 'kilauea'</i>	N	c	1	-0.012	-0.009
Heteroptera	Nabidae	<i>Nabis oscillans</i> Blackburn, 1888	N	c	100	-0.117	0.113
Homoptera	Aphididae	<i>Greenidea formosana</i> (Maki, 1917)	I	h	10	0.066	-0.170
Homoptera	Cicadellidae	<i>Nesophrosyne giffardi</i> Kirkaldy, 1910	N	h1	84	0.330	-0.002
Homoptera	Cixiidae	<i>Iolania perkinsi</i> Kirkaldy, 1902	N	h	5	-0.006	-0.019
Homoptera	Cixiidae	<i>Oliarus inaequalis</i> Giffard, 1925	N	h	1	0.006	0.058
Homoptera	Cixiidae	<i>Oliarus inconstans</i> Giffard, 1925	N	h	3	-0.007	-0.012
Homoptera	Delphacidae	<i>Leialoha hawaiiensis</i> Muir, 1916	N	h	123	0.187	-0.110
Homoptera	Flatidae	<i>Siphanta acuta</i> (Walker, 1851)	I	h	48	-0.046	-0.151
Homoptera	Pseudococcidae	mealybug sp. 1	U	h	15	-0.021	-0.015
Homoptera	Triozidae	<i>Kuwayama</i> cf. <i>minuta</i> Crawford, 1918	N	h	1	0.009	-0.023
Homoptera	Triozidae	<i>Kuwayama</i> sp. 1	N	h2	52	-0.333	0.102
Homoptera	Triozidae	<i>Kuwayama nigricapita</i> Crawford, 1918	N	h	2	0.005	0.046
Homoptera	Triozidae	<i>Trioza hawaiiensis</i> Crawford, 1918	N	h	30	0.180	0.145
Homoptera	Triozidae	<i>Trioza ohiacola</i> Crawford, 1918	N	h	204	0.014	-0.064
Homoptera	Triozidae	<i>Trioza</i> sp. 2	N	h	131	-0.016	-0.116
Homoptera	Triozidae	<i>Trioza</i> sp. 5	N	h	4	0.021	-0.054
Hymenoptera	Bethylidae	<i>Sierola</i> sp. N	N	c	4	0.024	0.016
Hymenoptera	Bethylidae	<i>Sierola</i> sp. U	N	c	19	0.100	-0.259
Hymenoptera	Bethylidae	<i>Sierola</i> sp. V	N	c	3	0.036	-0.015
Hymenoptera	Colletidae	<i>Hylaeus pubescens</i> (Perkins, 1899)	N	t	1	0.011	-0.029
Hymenoptera	Diapriidae	<i>Trichopria</i> nr. <i>subtilis</i> (Perkins, 1910)	N	c	1	0.003	0.029
Hymenoptera	Dryinidae	<i>Dicondylus perkinsi</i> (Ashmead), 1901	N	c	1	0.003	0.028
Hymenoptera	Encyrtidae	<i>Anagyrus?nigricans</i> Perkins, 1910	N	c	5	0.010	0.089
Hymenoptera	Encyrtidae	<i>Metaphycus?alberti</i> (Howard, 1898)	I	c	1	0.006	-0.016
Hymenoptera	Encyrtidae	<i>Plagiomeris hospes</i> Timberlake, 1920	I	c	2	0.018	-0.045
Hymenoptera	Eulophidae	<i>Euderus metallicus</i> (Ashmead, 1901)	I	c	1	0.008	-0.022
Hymenoptera	Eulophidae	<i>Pauahiana swezeyi</i> Yoshimoto, 1965	N	c	14	0.033	0.249
Hymenoptera	Eupelmidae	<i>Eupelmus leptophyas</i> Perkins, 1910	N	c	1	0.016	-0.042
Hymenoptera	Ichneumonidae	<i>Pristomerus hawaiiensis</i> Perkins, 1910	N	c	1	0.009	-0.023
Hymenoptera	Ichneumonidae	<i>Spolas</i> sp. 2	N	c	1	0.025	-0.064
Hymenoptera	Mymaridae	<i>Polynema</i> sp. 1	N	c	23	0.064	-0.037
Hymenoptera	Scelionidae	<i>Telenomus vulcanus</i> Perkins, 1910	U	c	4	-0.024	0.060
Lepidoptera	Carposinidae	<i>Carposina</i> sp. 1	N	h	14	0.034	0.021
Lepidoptera	Geometridae	<i>Eupithecia monticolens</i> Butler, 1881	N	h	7	0.013	-0.136
Lepidoptera	Geometridae	Larentiinae g. sp. 4	U	t	2	-0.024	-0.017
Neuroptera	Chrysopidae	<i>Anomalochrysa hepatica</i> McLachlan, 1883	N	c	2	-0.009	0.022
Neuroptera	Chrysopidae	<i>Anomalochrysa maclachlani</i> Blackburn, 1889	N	c	1	0.003	0.030
Neuroptera	Hemerobiidae	<i>Hemerobius pacificus</i> Banks, 1897	I	c	2	-0.035	-0.025
Psocoptera	Caeciliidae	<i>Valenzuela badiostigma</i> (Okamoto, 1910)	I	d2	18	0.151	-0.339
Psocoptera	Elipsocidae	<i>Kilauella</i> sp. 3	N	d3	278	-0.763	-0.479
Psocoptera	Elipsocidae	<i>Kilauella</i> sp. 4	N	d	9	0.017	0.099
Psocoptera	Pseudocaeciliidae	<i>Lobocaecilius monicus</i> Lee & Thornton, 1967	I	d	4	0.008	-0.014
Psocoptera	Psocidae	<i>Ptycta</i> spp.	N	d	3	-0.009	-0.002
Thysanoptera	Phlaeothripidae	<i>Haplothrips davisii</i> Bianchi, 1946	N	d	1	0.011	-0.028
Thysanoptera	Thripidae	<i>Frankliniella</i> sp. 1	I	t	4	0.022	0.005
Thysanoptera	Thripidae	<i>Heliethrips haemorrhoidalis</i> (Bouche, 1833)	I	h	1	0.008	-0.022
Subphylum Crustacea: class Malacostraca							
Isopoda	Porcellionidae	<i>Porcellio scaber</i> Latreille, 1804	I	d4	225	-0.145	0.356