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CANOPY-ASSOCIATED ARTHROPODS IN *ACACIA KOA* AND *METROSIDEROS* TREE COMMUNITIES ALONG AN ALTITUDINAL TRANSECT ON HAWAII ISLAND[1]

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Abstract. The spatial distribution and zonation of canopy-associated arthropods of *Acacia koa* and *Metrosideros* tree communities along an altitudinal transect on the SE flank of Mauna Loa and Kilauea volcanoes, Hawaii I was determined by insecticidal fogging of the canopy with pyrethrum. Eight sites were samples on the Mauna Loa Transect. Transect zones were determined on the basis of arthropod distribution. The influence of ecological factors, plant community structure and climate are interpreted according to distribution patterns. The distribution of arthropod groups coincided quite closely with vascular plant communities of the transect, as defined by other studies. The composition, spatial distribution, and environmental relationships of arthropod canopy-communities along the Mauna Loa Transect are compared with the situation pertaining along other lower elevational transects to sea level in Hawaii Volcanoes National Park as well as other ecosystems, in order to further characterize the arthropod canopy-community. Host specificity, vegetation structure, competition between ecological homologs, and climate appear to have the most important influence on population density and spatial distribution patterns of the arthropod taxa studied.

The Island Ecosystems Integrated Research Program was initiated in 1970 in Hawaii as part of the International Biological Program (IBP). This multidisciplinary team approach to ecosystem studies focused on integrated sampling along altitudinal transects on Mauna Loa and Kilauea volcanoes within Hawaii Volcanoes National Park. The 2 principal transects are diagrammed in Fig. 1. The Mauna Loa Transect (Transect 1) extends from the top of Mauna Loa Volcano to a point where its lava flows are covered by Kilauea Volcano lavas at about 1200 m elevation. A second transect extends from near this point southwards on Kilauea lavas to sea level (Transect 2). Most IBP participants concentrated sampling along the Mauna Loa Transect from the top of Mauna Loa to a site near the Thurston Lava Tube at 1195 m elevation. This was for the purpose of integrating the transect analyses to test Whittaker's (1970) hypotheses on species distribution patterns.

Hawaii Volcanoes National Park presents the greatest altitudinal range under one political jurisdiction in the Hawaiian Islands. As such, the Park afforded a unique opportunity for a team approach to ecosystem analyses to test Whittaker's hypotheses.

The 2 dominant or most prevalent native tree species or macrophanerophytes on the Mauna Loa Transect are 'ohi'a (*Metrosideros collina* subsp. *polymorpha*) and koa

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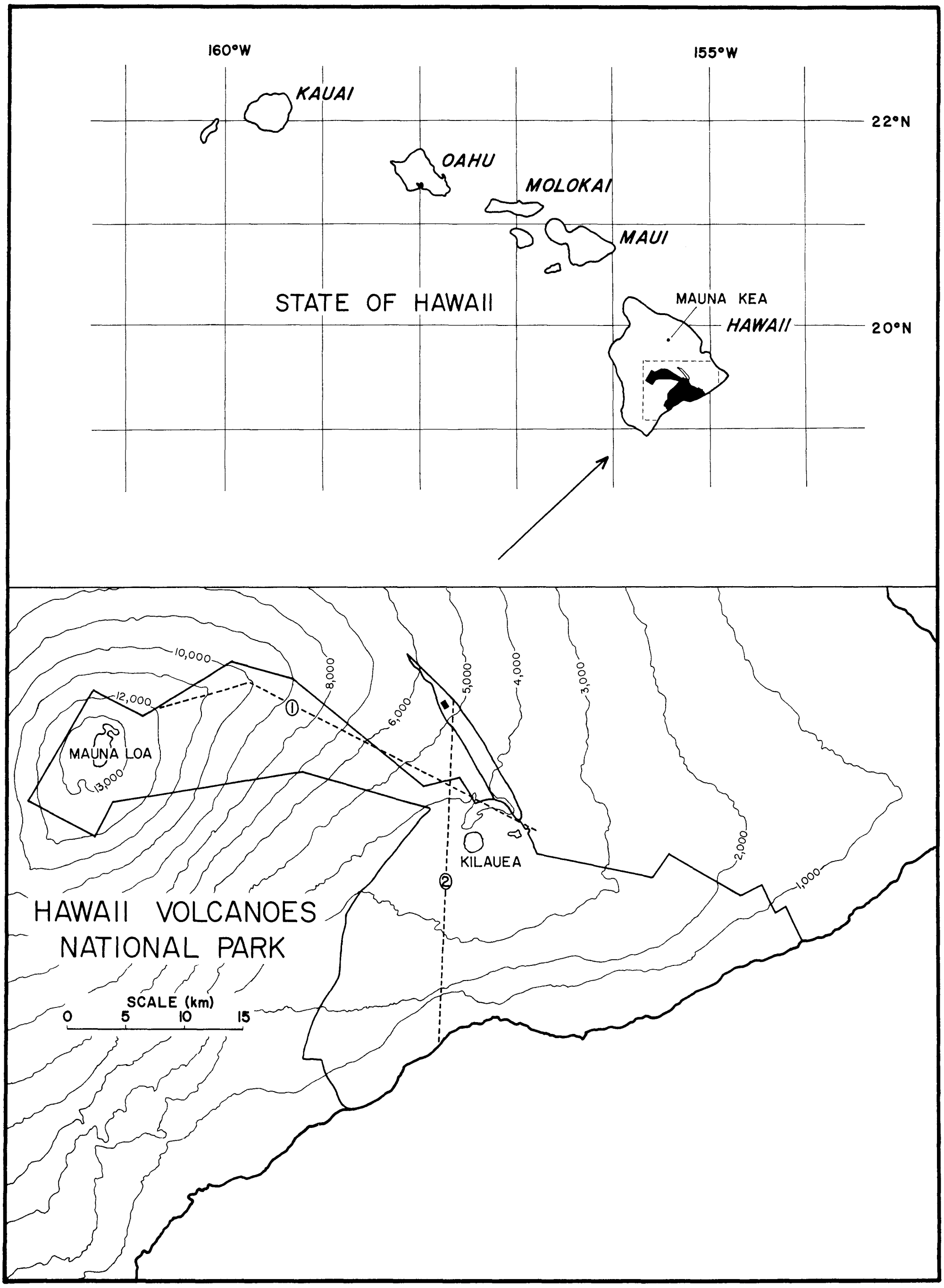

FIG. 1. Orientation map of the Hawaiian Is with Hawaii Volcanoes National Park. Transects are indicated by broken lines.

(*Acacia koa* var. *hawaiiensis*). Since these are such wide-ranging ecological dominants and are the major community structure-forming species of the tree communities, they were selected for a detailed analysis of their foliar arthropod communities. Trees were sampled at approximately 300 m intervals on transects from the open *Metrosideros* scrub forest near sea level to tree line of *Metrosideros* at about 2500 m elevation.

TABLE 1 provides details of 14 sampling sites on the Mauna Loa Transect. Bimonthly samples were taken for 2¾ years, beginning March 1971 and terminating December 1973, as detailed below. The sampling sites were specifically selected to provide a basis for direct comparison with data from other biotic groups sampled at these IBP focal sites.

This paper presents all of the data on foliar insects obtained during the IBP studies throughout Transects 1 and 2 described above. A part of these findings dealing with foliar insects of the Mauna Loa Transect is being presented elsewhere in an International Biological Program synthesis volume now in preparation (Mueller-Dombois & Bridges, in prep.).

We had several initial working hypotheses which involved special consideration of species distributions. One of these was that insects and other arthropods evolved primarily in adaptation to the community structure-forming dominant native plant species. To test the degree of spatial association of native biota, we sampled along the Mauna Loa Transect.

Another initial working hypothesis was that climatic factors have significant effects on ecosystem stability. We surmised from general observations that rain forest ecosystems would be more stable than seasonal ones. As an initial index of native ecosystem stability, we intended to use the proportions of native and exotic population sizes within organism or life-form groups of an ecosystem, realizing, however, that stability involves persistence over time in the presence of certain disrupting forces or perturbations. Since both rain forest and seasonal environments occur along the Mauna Loa Transect, data from our studies should allow us to test this general hypothesis of ecosystem stability.

Investigations of species distribution problems similar to ours had been conducted in continental ecosystems prior to our study. In order to compare our results with results of other studies, we adopted the hypotheses proposed by these investigators, with suitable modifications and elaborations.

According to Whittaker (1970), there are currently 4 hypotheses on species distribution patterns. For clarity, these are here quoted in full as he has presented them (Whittaker 1970: 35):

> 1. Competing species, including dominant plants, exclude one another along sharp boundaries. Other species evolve towards close association with the dominants and toward adaptation for living with one another. There thus develop distinct zones along the gradient, each zone having its own assemblage of species adapted to one another, and giving way at a sharp boundary to another assemblage of species adapted to one another.
> 2. Competing species exclude one another along sharp boundaries, but do not become organized into groups with parallel distributions.

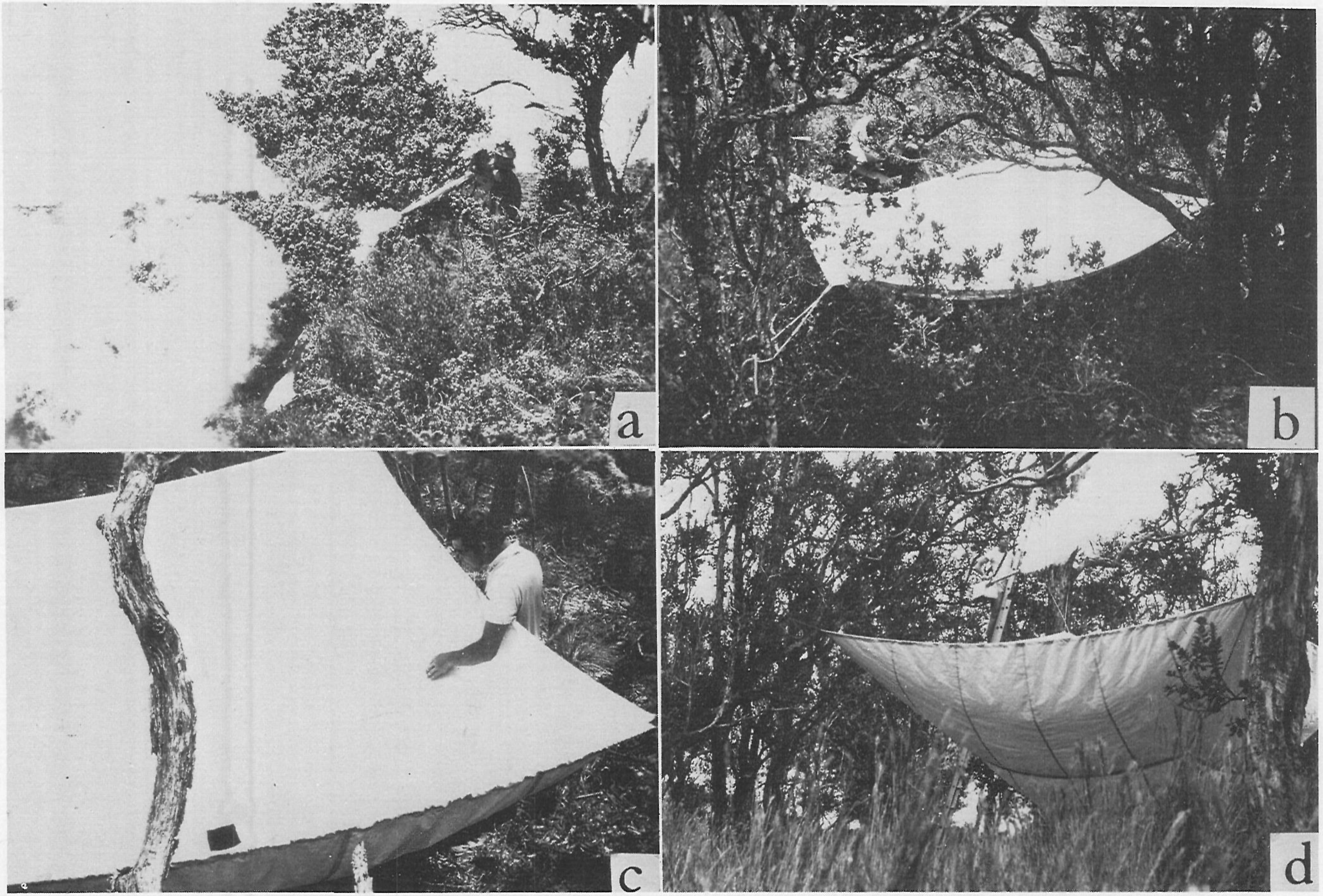

FIG. 2. Canopy arthropod sampling technique using pyrethrum fogger and canvas sheets: a, application of pyrethrum; b, flat 5.8 m^2 canvas sheet for sites with open canopies; c, funnel-shaped 5.8 m^2 by 1.2 m deep canvas sheet for sampling pole-sized trees; d, funnel-shaped 23 m^2 by 2.4 m deep canvas sheet for sampling large-sized trees.

3. Competition does not, for the most part, result in sharp boundaries between species populations. Evolution of species toward adaptation to one another will, however, result in the appearance of groups of species with similar distributions.

4. Competition does not usually produce sharp boundaries between species populations, and evolution of species in relation to one another does not produce well-defined groups of species with similar distributions. Centers and boundaries of species populations and evolution of species in relation to one another does not produce well-defined groups of species with similar distributions. Centers and boundaries of species populations are scattered along the environmental gradient.

All 4 spatial distribution patterns seem possible, although few tests have been made on the hypotheses. Whittaker's studies in continental temperate mountain ecosystems, for example, support the last hypothesis.

MATERIAL AND METHODS

Sampling layout

A uniform substrate was used throughout the transects in an effort to determine the altitudinal distribution of associated arthropods. The site sampled was the foliar canopy of apparently mature *Metrosideros collina* subsp. *polymorpha* var. *incana* and *Acacia koa* var. *hawaiiensis* trees approximately 10 m high. At 3 sampling sites (in the Subalpine, Tree Molds, and Sulphur Banks areas) the 'ohi'a host trees were about 5 m high with foliage extending to the ground. Here, the tree canopy was rather open. Since the trees were sampled year round, differences due to phenological phenomena (flower and seed production, foliar flushing, etc.) were minimized for this analysis.

Arthropods were sampled by fogging the foliar crowns with pyrethrum synergized with piperonyl butoxide and capturing the specimens in cloth funnels suspended beneath the trees. The sampling method was modified from that of Martin (1966) and Gagné & Martin (1968); the major modification was the use of a Dynafog® insecticidal fogger (FIG. 2a) rather than a hydraulic sprayer. The fogger had the advantage of lightness (approximately 11 kg when filled) and maneuverability. It also dislodged less debris into the sample and thus contributed to the loss of fewer arthropods with debris removal.

The shape and size of the funnels varied with the size and spacing of the tree sampled. For IBP sites 13, 14 and 18 with open canopies, a flat, square 5.8 m^2 sheet was used (FIG. 2b). The sheet was usually placed about the trunk of the trees such that the tree was in the center of the sheet. The arthropods were then aspirated by hand from the sheet.

In young, well stocked stands such as the pole-sized koas at site 6 and for similar-sized *Metrosideros* trees at site 2, a cloth funnel 5.8 m^2 and 1.2 m deep (FIG. 2c) was fastened to the trunks of 4 trees. A mason jar, the lid of which was soldered to a metal funnel, was fastened to the center point of the sheet. The weight of the bottle pulled the sheet down to form a shallow funnel. Roughly ¼ of the crown of each tree extended over the funnel. Thus, each funnel sampled 4 quarters. Weather permitting, each sample was replicated at each IBP site for each tree species sampled.

TABLE 1. Grouping of sampling sites by elevation, ecosystem type and host tree genus.

SAMPLING SITE	ELEVATION (m)	ECOSYSTEM TYPE	NO. OF CANOPY ARTHROPOD COMMUNITY SAMPLES	
			Acacia	*Metrosideros*
Mauna Loa Transect (transect 1)				
1	1195	Closed rain forest	None*	21
2	1220	Open rain forest	None	13
3	1220	Open dry forest	None	13
4	1280	Savannah	19	22
6	1600	Mountain parkland	23	19
9	2040	Mountain parkland	19	None
10	2130	Subalpine scrub forest	None	23
12	2440	Treeline ecosystem	None	11
Additional sites (transect 2)				
17	760	Open dry forest	None	23
18	15	Open dry forest	None	23
		Total samples	61	68

* Tree species absent when indicated "None."

For taller closed-canopy stands, the funnels used were larger, namely 23 m^2 and about 2.4 m deep (FIG. 2d).

As a rule, the insecticide was applied early in the morning before the trade winds and accompanying mist began. The material falling into the sheets was shaken into the bottles several times during the day and the bottles were collected about mid-afternoon. Bark fragments, twigs and leaves were removed manually from the funnels prior to each shaking. Seventy-percent ethyl alcohol was added to the mason jars, which were then capped and stored until sorted.

Sampling was done at 8 sites on Transect 1 and 2 sites on Transect 2 (TABLE 1). The data from the 2 sampling sites on Transect 2 were not incorporated into the dendrograph and 2-way table treatments, since these data manipulations were applied only to the integrated analysis along Transect 1, i.e., sampling sites 1–4, 6, 9, 10, and 12. The nonmanipulated data from sites 17 and 18 merely provided for an assessment of still wider variations and species distributions to help further elucidate conditions along the Mauna Loa Transect.

This sampling produced a large body of information both in number of species and number of individuals of canopy-associated arthropods. The taxa are listed alphabetically in TABLE 2 by order, family, genus and species. Also indicated are the altitudinal distributions, host associations and ecological roles. From this body of data, 68 taxa occurring on portions of the Mauna Loa Transect were selected for distributional analysis. This represents a cross section of nonubiquitous taxa in various ecological roles.

The few taxa that could be considered as transitory residents (implying chance occurrences at the sampling sites) were designated in TABLE 2 as "perching" (P) or "ecological role undetermined" (?).

TABLE 2. Distribution of arthropod taxa along the Mauna Loa and adjacent transects on *Acacia koa* var. *hawaiiensis* (A) and *Metrosideros collina* subsp. *polymorpha* var. *incana* (M).

	SAMPLING SITE (ELEVATION IN M)									
TAXA**	18 (15)	17 (760)	1 (1190)	2&3 (1220)	4 (1280)	6 (1600)	9 (2030)	10 (2130)	12 (2400)	Eco-logical role*
Acarina ++										
Mesostigmata		M	M	M	AM		A			V
Oribatoidea	M	M	M	M	AM	AM	A	M	M	Sd
Prostigmata	M	M	M	M	AM	AM	A	M	M	V
Araneida ++	M	M	M	M	AM	AM	A	M	M	Pr
Blattaria										
Blattidae +										
Allacta similis		M	M	M	AM	AM				Sd
Other species	M	M								Sd
Chilopoda sp. ++	M									Pr
Coleoptera										
Anobiidae		M								Sd
Carabidae			M		A	A			M	Pr
Cerambycidae										
Plagithmysus spp.					A	A	A			Tw
Exotic spp. +	M	M								V
Chrysomelidae +										
Diachus auratus		M			AM	AM	A		M	?
Ciidae										
Cis bicolor					AM	A				Sf
C. cognatissimus					AM	A	A			Sf
C. evanescens		M			A	A				Sf
C. porcatus	M	M	M	M	AM	AM	A		M	Sf
C. setarius		M	M	M	A		A	M		Sf
C. signatus					A			M		Sf
C. sp. #786		M	M		AM	A	A	M		Sf
C. sp. #787		M	M							Sf
Clambidae										
Clambus spp.		M		M						Sd
Coccinellidae + (see Leeper 1976)										Pr
Cryptophagidae										
Henoticus serratus		M								Sd
Cucujidae	M				AM					Pr
Curculionidae										
Oodemas konanum		M								Tw
Oodemas sp.	M									Tw
Pantomorus cervinus +	M	M	M		AM	AM				D
Dermestidae										
Labrocerus spp.	M				AM	M				Sd
Elateridae ++						A				?
Histeridae										
Acritus spp.					M					Pr
Lathridiidae										
Corticaria sp.	M									Sf
Lathridius nodifer +		M								Sf
Nitidulidae					AM	A	A	M		?
Proterhinidae										
Proterhinus affinis		M			A					Tw

TABLE 2. Continued.

	SAMPLING SITE (ELEVATION IN M)									
TAXA**	18 (15)	17 (760)	1 (1190)	2&3 (1220)	4 (1280)	6 (1600)	9 (2030)	10 (2130)	12 (2400)	Eco-logical role*
P. blackburni		M				A				Tw
P. desquamatus						A				Tw
P. ferrugineus					A					Tw
P. similis					AM		A			Tw
P. tarsalis							M			Tw
Ptiliidae										
Ptiliodes insignis	M				AM	A	A			Sf
Scolytidae ++					AM					Tw
Staphylinidae ++	M	M	M		AM	AM	A	M		Pr
Collembola ++										
Brachystomellidae										
Brachystomella parvula						A				Sd
Entomobryidae										
Entomobrya atrocincta +		M	M	M	AM	AM	A			Sd
E. clittellaria +		M	M		AM		A	M		Sd
E. nivalis +	M	M	M		AM	AM	A	M	M	Sd
Entomobryoides sp. +					A					Sd
Homidia sauteri +		M			AM	A	A			Sd
H. socia +		M				A	A			Sd
Lepidocyrtus cf. *ruber* +			M		A					Sd
Salina maculata		M	M		AM					Sd
Salina sp.			M		AM					Sd
Genus & sp. A.		M		M	AM	A		M		Sd
Hypogastruridae										
Hypogastrura sp.					AM	M		M		Sd
Isotomidae										
Isotoma sensibilis +						A				Sd
Isotoma sp.					A					Sd
Diptera (origin of spp. after Hardy 1960, 1964)										
Agromyzidae +						A				Ph
Anthomyidae							A			?
Asteiidae										
Asteia apicalis						A	A			?
Calliphoridae ++			M		M	A				?
Cecidomyidae ++		M	M	M	AM	A	A	M		?
Ceratopogonidae	M	M	M	M	AM	AM	A			Sd
Chironomidae ++		M	M	M	AM	AM	A	M		?
Cryptochaetidae +										
Cryptochaetum iceryae	M						A	M		Pr
Drosophilidae ++	M	M	M	M	AM	AM	A			P
Dolichopodidae										
Campsicnemus modicus or *setiger*						M				Pr
C. macula					M			M		Pr
C. spinicoxa			M							Pr
Campsicnemus sp.			M		M			M		Pr
Eurynogaster angustifascies			M							Pr
E. argentata		M	M		M					Pr
Eurynogaster sp.			M							Pr

TABLE 2. Continued.

	SAMPLING SITE (ELEVATION IN M)									
TAXA**	18 (15)	17 (760)	1 (1190)	2&3 (1220)	4 (1280)	6 (1600)	9 (2030)	10 (2130)	12 (2400)	Eco-logical role*
Lonchaeidae +					A					?
Milichiidae +						A	A		M	?
Mycetophilidae										
Orfelia (*Tylparua*) sp.			M							P
Phoridae ++		M	M		AM		A			P
Pipunculidae										
Pipunculus spp.					M			M		Pa
Psychodidae										
mostly *Psychoda* spp.			M							Sd
Sciaridae ++	M	M	M	M	AM	AM	A	M	M	Sf
Syrphidae +					A	A				Pr
Tephritidae +					M					P
Tipulidae ++		M	M		AM	A				Sd
Heteroptera										
Anthocoridae										
Orius persequens +							A			Pr
Lygaeidae										
Neseis o. ochriasis							A			P
Nysius blackburni			M	M	M		A			P
N. nemorivagus		M								P
Oceanides pteridicola		M	M	M	M	M		M	M	Se
O. vulcan		M	M	M	M	M		M		Se
Pachybrachius vincta +						M		M		P
Miridae										
Hyalopeplus pellucidus ++	M		M		M					An
Koanoa hawaiiensis		M	M	M	AM	AM	A	M	M	Pr
Orthotylus azalais		M	M	M	AM	AM	A	M	M	Pr
O. iolani		M								P
O. kanakanus				M				M		P
Psallus luteus		M	M	M	M	M	A	M		Pr
P. sharpianus					A	A	A			Pr
Sarona adonias		M	M	M	M	M	A	M	M	Sa
Sarona sp.					AM					P
Nabidae										
Nabis oscillans		M	M	M	AM	A	A			Pr
Pentatomidae										
Oechalia sp. nr. *acuta*			M	M		A				Pr
Plataspidae +										
Coptosoma xanthogamma	M									P
Reduviidae										
Empicoris rubromaculatus +?					M	AM				Pr
Scutelleridae										
Coleotichus blackburniae						A				Sa
Tingidae +										
Teleonemia scrupulosa	M									P
Homoptera										
Aphidae +	M	M		M	AM	AM	A	M	M	Sa
Cicadellidae										
Nesophrosyne spp.			M	M		M	A	M	M	Sa

TABLE 2. Continued.

	SAMPLING SITE (ELEVATION IN M)									
TAXA**	18 (15)	17 (760)	1 (1190)	2&3 (1220)	4 (1280)	6 (1600)	9 (2030)	10 (2130)	12 (2400)	Ecological role*
Cixiidae										
Iolania perkinsi			M							Sa
Oliarus inconstans						M				Sa
Coccidae +		M	M	M	AM	AM	A	M		Sa
Delphacidae										
Leialoha hawaiiensis			M		AM					Sa
Nesosydne koae					A					Sa
N. koaephyllodi					A	A				Sa
Nesothoe gulicki		M								Sa
Flatidae +										
Siphanta acuta	M	M	M		M	M	A	M	M	Sa
Psyllidae										
Psylla uncatoides +					A	A	A			Sa
mostly *Trioza* spp.	M	M	M	M	M	M		M	M	Sa
Hymenoptera										
Ampulicidae +										
Ampulex compressa	M									Pa
Bethylidae										
mostly *Seriola* spp.		M	M	M	AM	AM	A	M	M	Pa
Braconidae ++	M	M			A					Pa
Ceraphronidae ++							A		M	Pa
Chalcidoidea ++	M	M	M	M	AM	AM	A	M	M	Pa
Colletidae										
Nesoprosopis spp.			M		M				M	An
Cynipidae							A	M	M	Pa
Diapriidae ++						A				Pa
Formicidae +										
Iridomyrmex humilis			M	M	AM	AM	A	M	M	O
Pheidole megacephala	M	M								O
Plagiolepis alluaudi	M	M								?
Ichneumonidae +	M	M	M	M	AM	M	A	M	M	Pa
Proctotrupidae ++						A				Pa
Scelionidae ++		M	M	M	AM	A		M		Pa
Isopoda +		M	M	M	AM	M	A			Sd
Lepidoptera (larvae only)										
Lycaenidae										
Vaga blackburni						A	A			D
Other families ++	M	M	M	M	AM	AM	A	M	M	D
Neuroptera										
Chrysopidae ++	M	M	M	M	AM	AM	A			Pr
Hemerobiidae ++	M	M	M	M	AM		A			Pr
Orthoptera										
Gryllidae										
Paratrigonidium spp.			M	M	M					Sd
Tettigoniidae										
Banza nitida			M							Pr
Conocephalus saltator +	M									Pr
Elimaea punctifera +	M									D

TABLE 2. Continued.

	SAMPLING SITE (ELEVATION IN M)									
TAXA**	18 (15)	17 (760)	1 (1190)	2&3 (1220)	4 (1280)	6 (1600)	9 (2030)	10 (2130)	12 (2400)	Ecological role*
Pseudoscorpionida ++		M			A					Pr
Psocoptera ++	M	M	M	M	AM	AM	A	M	M	Sd
Strepsiptera										
Elenchidae										
Elenchus sp.					A					Pa
Thysanoptera										
Phlaeothripidae										
Aleurodothrips fasciapennis +	M									Pr
Dermothrips hawaiiensis							A			Sf
Haplothrips davisi			M	M	AM	AM	A	M	M	Sf
H. rosai		M	M	M	AM					Sf
Hoplothrips flavitibia +					A					Sf
H. laticornis			M		AM					Sf
H. mauiensis					M					Sf
H. swezeyi			M	M	M	M	A			Sf
Karnyothrips flavipes +		M			AM			M		Pr
K. longiceps +					AM					Pr
Macrophthalmothrips argus +		M	M		AM	A				Sf
Nesothrips brevicollis +	M									Sf
Phlaeothrips mauiensis								M		Sf
Rhaebothrips lativentris +	M							M		Sf
Thripidae										
Aptinothrips rufus +			M	M	AM	A	A			Gr
Baliothrips minutus +			M							Gr
Chirothrips patruelis +		M			AM	AM	A			Gr
Dorcadothrips cyperaceae +					M					Gr
Heliothrips haemorrhoidalis +	M	M	M		A					Sa
Neurisothrips antennatus		M	M	M	AM	A		M		An
N. carteri			M		AM	A	A			Sf
N. multispinus +		M	M		AM	AM	A	M		An
N. williamsi		M	M		M	A				An
N. sp. #24		M	M		AM		A	M		?
N. sp. #39							A			An
Thrips hawaiiensis +		M								An
Thysanura (unknown sp.) +	M									Sd

* Symbols: An = anthophagous, D = defoliators, Gr = graminivorous, O = omnivorous, P = perching, Pa = parasitic, Ph = leafminers, Pr = predaceous, Sa = sap suckers, Sd = detritivorous, Se = seed predators, Sf = fungivorous, Tw = twig borers, V = various ecological roles, ? = ecological role unknown.

** + = exotic or probably exotic taxa. ++ = includes some exotic species. Remainder of taxa are endemic.

Zonation patterns

The data sets were prepared for computer analysis to produce a 2-way table in altitudinal sequence. After the differently-sized samples were standardized, a quantitative value was assigned to each taxon based on a log base 2 index (e.g., 1–2 specimens = 2, 5–8 specimens = 3, etc.) of its mean abundance in each sample set (2 samples). Groups of species that had similar distributional trends across the altitudinal transect could then be identified.

Computerized data analysis

Two methods were used to determine the zonation patterns of selected groups of arthropods: the dendrograph method using Motyka's quantitative modification of Sørensen's index; and the 2-way table method, adapting the Ceska-Roemer (1971) program (see Mueller-Dombois & Bridges, in prep.). Selections of taxa from TABLE 2 were based on the reliability with which the arthropods could be identified throughout the sampling period and on their quantitative importance. These taxa are listed on FIG. 4–7. The 2-way synthesis table technique (see Mueller-Dombois & Bridges, in prep., Section 6. 8-2) attempts to identify groups of taxa with similar distribution ranges, which in turn are used to identify transect zones.

RESULTS

Biomass distribution of samples

The standardized, mean arthropod biomass was uniform between 1150 m and 2150 m elevation. It was lower at 760 m and subject to great fluctuations at the 2 elevational extremes. At sea level, large roaches (Blatteria) and their parasites (Hymenoptera) raised the otherwise low biomass, which was composed mostly of ants (Formicidae). At elevations above 760 m, spiders (Araneida) and true bugs (Heteroptera), both of which were largely comprised of native taxa, contributed to most of the biomass. In absolute numbers though, bark lice (Psocoptera) outranked all other taxa at most sites above 750 m. There were sporadically large populations of springtails (Collembola) at and above 1190 m along the Mauna Loa Transect.

Data analysis

Application of the most discriminating 66/10 option of the Ceska-Roemer (1971) program generated 8 species groups along the Mauna Loa Transect. These were formed by 46 taxa at 8 sampling sites (FIG. 3). The data comprised 182 samples of foliar communities (122 from *Metrosideros collina* and 61 from *Acacia koa*) taken along the Mauna Loa Transect (see TABLE 1). The outcome of the dendrograph cluster analysis is also shown in FIG. 3. This affords a direct comparison of the clustering patterns and transect zones that were derived from the same data set by the 2 previously mentioned analysis methods. As can be seen, the dendrograph method resulted in less zonal or community differentiation than the 2-way table method. The

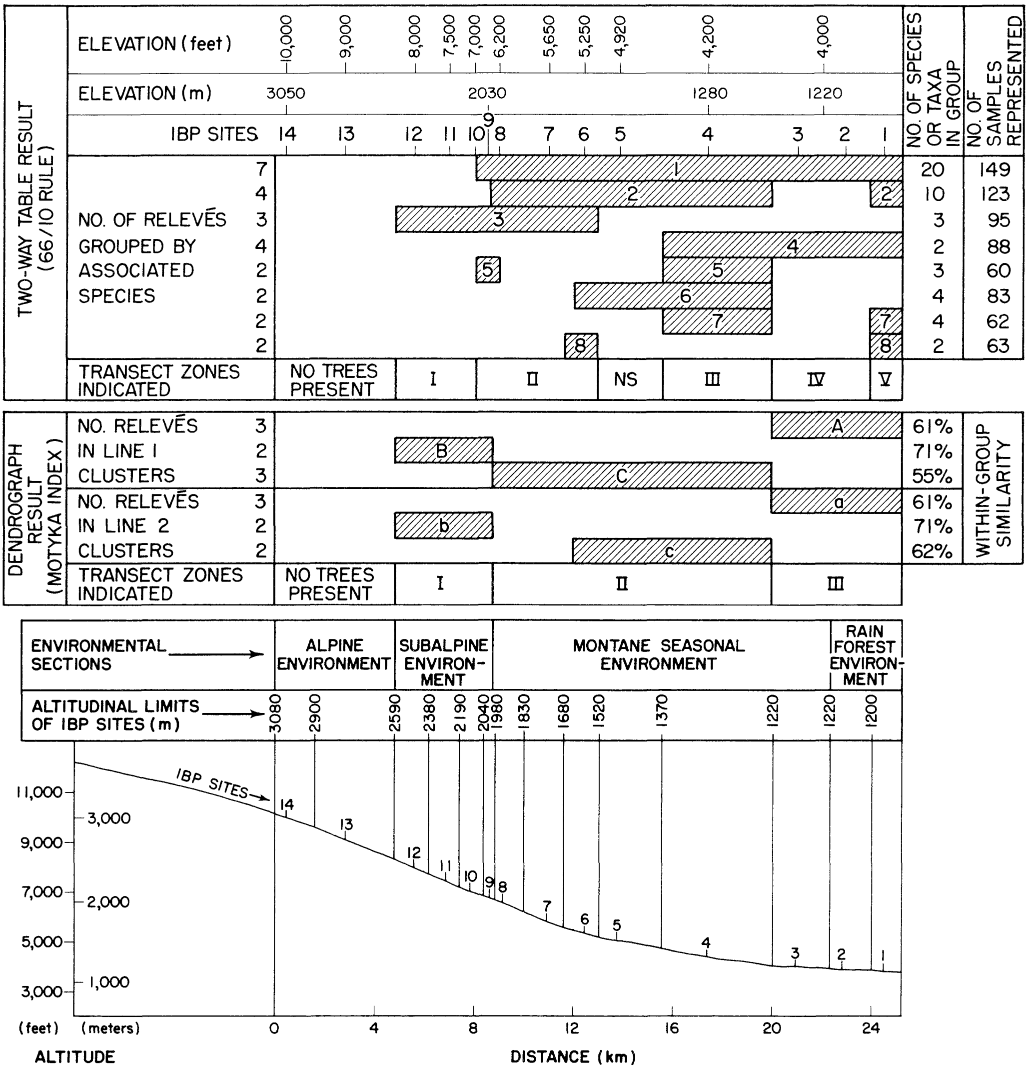

Fig. 3. Altitudinal transect zones derived from Ceska-Roemer 2-way (66/10 table option) and dendrograph (with Motyka's index) techniques of 183 canopy samples. The word "releve" is the equivalent of community samples, i.e., a sample containing usually more than 1 species.

5 zones resulting from the 2-way table analysis are as follows: I, subalpine *Metrosideros* scrub forest; II, mountain parkland *Acacia koa* tree colonies; III, savannah; IV, mixed kipuka forest and open *Metrosideros* dry and wet forest; and V, closed *Metrosideros* rain forest. The 2-way table method resulted in finer differentiations, i.e., in a separation of the mountain parkland and savannah zones and in a separation of the closed forest from the open forest in the mid-elevation *Metrosideros* zone.

TABLE 2 gives an indication of arthropod diversity from sea level to tree line. The arthropod communities richest in species occurred at mid-elevations where they were 3× richer than at sea level or at 2440 m. The number of taxa was relatively uniform between 750 m and 1200 m. About 16% of the taxa occurred at all elevations. These were of the following groups: parasitic wasps (Chalcidoidea), caterpillars (Microlepidoptera), spiders (Araneida), bark lice (Psocoptera), jumping plant lice (Psyllidae), predaceous mites (Anystidae), ants (Formicidae), lace wings (Neuroptera), fungus gnats (Sciaridae), thrips (Thysanoptera), lady beetles (Coccinellidae), biting midges (Ceratopogonidae), torpedo bugs (*Siphanta acuta*), Homoptera, and a springtail (*Entomobrya nivalis,* Collembola). Most of these groups were comprised of exotic species in the lower elevations, the notable exception being the psyllids. Conversely, the taxa found only between 750 m and 2150 m (14%) appear to be comprised mostly of native species. Most of the endemic true bug species (Heteroptera) occurred at 2440 m. At least 6% of the taxa were restricted to mid-elevations and the endemic beetles (Coleoptera) accounted for most of these. Taxa found only at sea level sampling sites (5%) appeared to be wholly exotic in origin.

In terms of the absolute numbers of individuals per sample, at mid- to higher elevations, the bark lice (Psocoptera) usually outnumbered all other taxa combined. Sporadically, there were large populations of the koa psyllid (*Psylla uncatoides*) and springtails (Collembola), the latter occurring during the wetter winter months.

Species distribution trends

To interpret the individual clusters derived from the 2-way table technique, it is necessary to refer to the results derived from the floristic analysis. The clustering in the dendrograph analysis is obvious. A and a, as well as B and b, clusters relate to the transect area occupied by *Metrosideros* tree communities, while C and c clusters relate to the transect area largely occupied by *Acacia koa* tree communities (FIG. 3).

The 2-way table offers the advantages of specifying the taxa responsible for the clusters in the printout. TABLE 3 lists the 46 species and taxa that were clustered into 8 associated groups on FIG. 3. Taxa from separate ecological functional groups that define the same transect section, such as taxa within groups 5, 1, 2, and 7, can be considered as spatially associated also. The reasons for extracting these spatially associated species and taxa into separate groups are related to a number of possible ecological factors which will be analyzed below.

For the various groups in TABLE 3, the quantitatively more important species were selected for diagrammatic representation of their individual species distributions. The *Metrosideros* trees in Zone I (subalpine transect zone), are occupied by a number of endemic as well as exotic taxa, but none of the endemic taxa appear restricted to this portion of the transect. Because of the rather recent appearance of the exotic arthropods on the transect,[3] they were diagrammed separately (FIG. 4) from the

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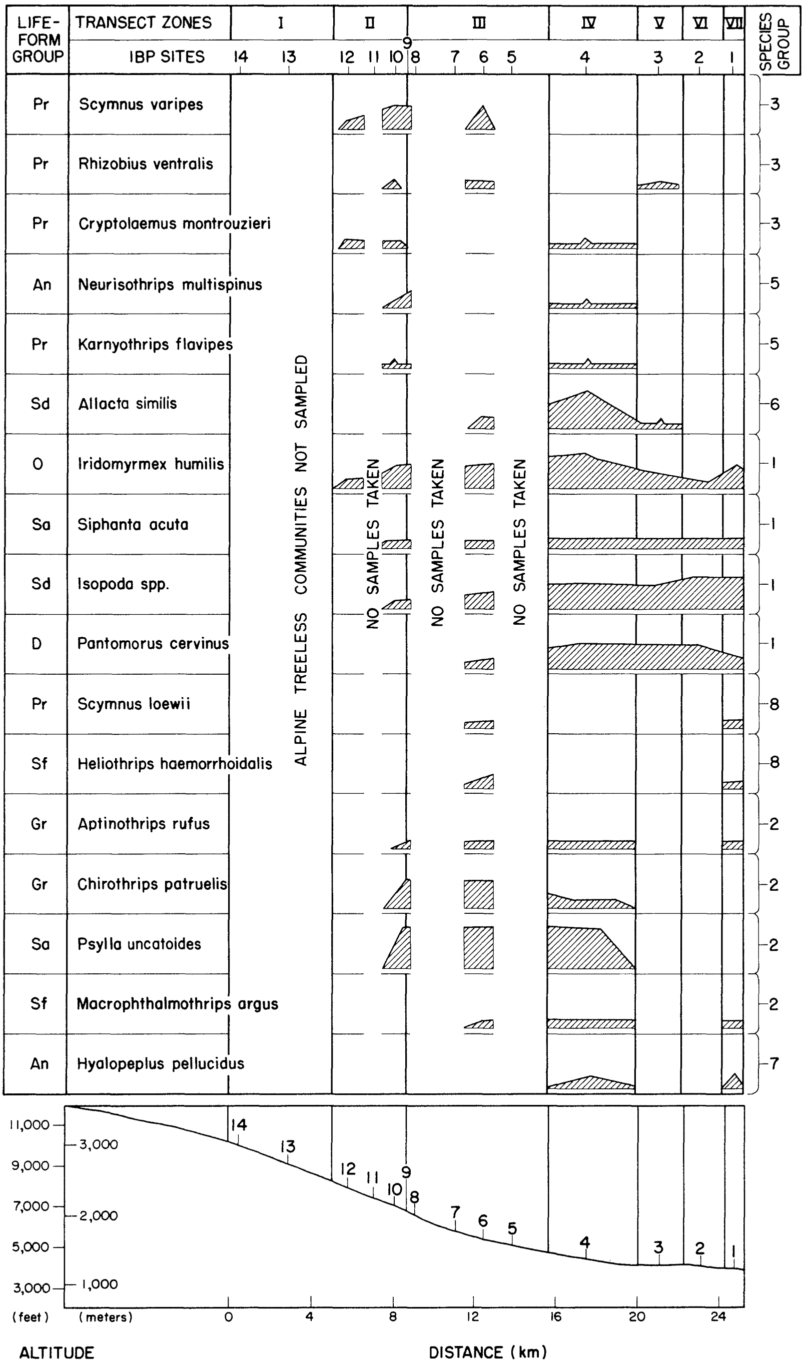
[3] Most exotic arthropods arrived only within the last century, according to records in the *Proceedings of the Hawaiian Entomological Society.*


LIFE-FORM GROUP
TRANSECT ZONES
I
II
III
IV
V
VI
VII
IBP SITES
14 13 12 11 10 9 8 7 6 5 4 3 2 1
SPECIES GROUP
Pr Scymnus varipes 3
Pr Rhizobius ventralis 3
Pr Cryptolaemus montrouzieri 3
An Neurisothrips multispinus 5
Pr Karnyothrips flavipes 5
Sd Allacta similis 6
O Iridomyrmex humilis 1
Sa Siphanta acuta 1
Sd Isopoda spp. 1
D Pantomorus cervinus 1
Pr Scymnus loewii 8
Sf Heliothrips haemorrhoidalis 8
Gr Aptinothrips rufus 2
Gr Chirothrips patruelis 2
Sa Psylla uncatoides 2
Sf Macrophthalmothrips argus 2
An Hyalopeplus pellucidus 7
ALPINE TREELESS COMMUNITIES NOT SAMPLED
NO SAMPLES TAKEN
NO SAMPLES TAKEN
NO SAMPLES TAKEN
11,000
9,000
7,000
5,000
3,000
(feet)
3,000
2,000
1,000
(meters)
0 4 8 12 16 20 24
ALTITUDE
DISTANCE (km)

endemic arthropods (FIG. 5–7). The endemic arthropods were further divided into 3 ecological functional groups or life forms: (1) phytophagous, (2) fungivorous and detritivorous, and (3) predaceous. A separate discussion of each group follows. Because of the similarity of the arthropod zonation patterns (that resulted from the 2-way table analysis) with those of the flora (see Mueller-Dombois & Bridges, in prep.), the arthropods can well be discussed in the context of the vegetation patterns. Consequently, FIG. 4–7 show the various arthropod distribution patterns under the 7 zones resulting from the 2-way table vegetational analysis. These zones are: I, sparse alpine heath scrub; II, subalpine *Metrosideros* scrub forest; III, mountain parkland, *Acacia koa* tree colonies; IV, *Sapindus-Acacia koa* savannah; V, open *Metrosideros* rain forest; and VII, closed *Metrosideros* rain forest. Arthropod sampling was carried out in all but the treeless Zone I.

Exotic arthropod distribution trends

Of the species and taxa found in the spatially associated groups along the Mauna Loa Transect (FIG. 3 and TABLE 3), 17 were of exotic origin. Their distributions are diagrammed in FIG. 4. Exotics were found in all spatial groups except group 4; therefore, this group does not appear on FIG. 4. Species group 3 (on FIG. 4) is comprised wholly of predaceous lady beetles (Coccinellidae) of temperate origin which are most prevalent in the subalpine *Metrosideros* scrub forest (Zone I). Although there would appear to be abundant prey at still lower elevations, these temperate species do not appear to have been able to exploit those warmer habitats. Another ungrouped coccinellid (not diagrammed) is the nearctic *Hippodamia convergens,* which was encountered only at site 12. Leeper (1976) has paid special attention to this and other coccinellids found on Hawaii I transects from all plant communities, and the interested reader should refer to him for additional information. The temperate-derived species are able to maintain themselves in the tropical montane environment because there are also a number of introduced prey elements such as plant lice (Aphidae). These in turn are able to exploit both native and introduced plant species. Gagné & Martin (1968) have shown that temperate Coccinellidae show differential capabilities as larvae to find prey in seral red pine (*Pinus resinosa*) plantations. As the trees get older and larger, the coccinellid community changes from one of high prey density–low predator searching capacity to one of low prey density–high predator searching capacity. Two of the genera (*Scymnus* and *Hippodamia*) on our transect also occurred in the red pine plantation.

←

FIG 4. Distribution of 17 selected exotic arthropod taxa along the Mauna Loa Transect. Group numbers from 66/10 rule. Life form code: Pr = predaceous; An = anthophagous; Sd = detritivore on dead plant matter; O = omnivorous; Sa = sap sucker; D = leaf chewer; Gr = graminivorous, hibernating in tree canopy; Sf = fungivorous. Abundance scale: 1 unit = mean of 1–2 specimens per sample; 2 units = mean of 3–4 specimens per sample; . . . 10 units = mean greater than 513 specimens per sample. Transect zones from 2-way table vegetational analysis (see text).

TABLE 3. List of 46 taxa of arthropods found in 9 spatially associated groups along the Mauna Loa Transect. (Generated with 2-way table 66/10 rule. Computer-derived number sequence from top to bottom as are species distribution diagrams. FIG. 4–7).

GROUP NO.	SPECIES	LIFE FORM
3	*Scymnus varipes*	Predaceous lady beetles of temperate origin, exotic
	Rhizobius ventralis	
	Cryptolaemus montrouzieri	
5	*Neurisothrips multispinus*	Flower-feeding thrips of temperate origin, exotic
	Karnyothrips flavipes	Predaceous flower-feeding thrips of temperate origin, exotic
	Cis signatus	Fungivorous beetle, endemic
6	*Allacta similis*	Detritivorous roach, exotic
	Labrocerus spp.	Detritivorous beetle, endemic
	Cis bicolor	Fungivorous beetles associated primarily with *Acacia koa,* endemic
	Cis evanescens	
1	*Koanoa hawaiiensis*	Predaceous bugs, endemic
	Orthotylus azalais	
	Psallus luteus	
	Nabis oscillans	
	Iridomyrmex humilis	Omnivorous ant of temperate origin, exotic
	mostly *Trioza* spp. (incl. *Kuwayama* spp.)	Phytophagous gall-forming jumping plant lice on *Metrosideros,* endemic
	Haplothrips davisi	Fungus hyphae feeding thrips in dead wood, endemic
	Hoplothrips swezeyi	
	Neurisothrips antennatus	Flower-feeding thrips, endemic
	Neurisothrips sp.	
	Sarona adonias	Host-specific sap-sucking bug on *Metrosideros,* endemic
	Siphanta acuta	Polyphagous sap-sucking planthopper, exotic
	Oceanides pteridicola	Host-specific seed bug predators of *Metrosideros,* endemic
	Oceanides vulcan	
	Cis porcatus	Fungivorous beetles, endemic
	Cis setarius	
	Isopoda spp.	Detritivorous pillbugs, exotic
	Pantomorus cervinus	Phytophagous, polyphagous weevil, exotic
8	*Scymnus loewii*	Predaceous lady beetle of tropical origin, exotic
	Heliothrips haemorrhoidalis	Polyphagous, phytophagous thrips, exotic
2	*Neurisothrips carteri*	Rust fungus feeder of *Acacia koa,* endemic
	Aptinothrips rufus	Graminivorous thrips hibernating on trees, exotic
	Chirothrips patruelis	
	Macrophthalmothrips argus	Fungus hyphae feeder, temperate exotic origin
	Psallus sharpianus	Primarily predaceous bug associated with *Acacia koa,* endemic
	Proterhinus similis	Twig-feeding beetle, endemic
	Psylla uncatoides	Phytophagous jumping plant louse on phyllodes of *Acacia koa,* exotic
	Neurisothrips williamsi	Polyphagous flower feeder, endemic
	Cis sp. #786	Fungivorous beetles primarily of *Metrosideros,* endemic
	Cis cognatissimus	Fungivorous beetle of *Acacia koa,* endemic

TABLE 3. Continued.

GROUP NO.	SPECIES	LIFE FORM
7	*Hyalopeplus pellucidus*	Polyphagous flower feeding bug, possibly exotic
	Proterhinus affinus	Twig-feeding beetle, endemic
	Hoplothrips laticornis	Fungus hyphae feeder, endemic
	Clambus sp.	Fringe-winged beetle associated with decaying plant matter, (?) endemic
4	*Haplothrips rosai*	Fungivorous thrips, endemic
	Paratrigonidium spp.	Omnivorous crickets, endemic

Two of the 3 species comprising group 5 are thrips of temperate origin. Little is known of the ecological functions of these, other than that one is predaceous and the other is anthophagous (Sakimura, pers. commun.).

In group 6, only the detritivorous cockroach *Allacta similis* is of presumably exotic origin. Although this cockroach is primarily associated with native plant communities, it is considered exotic since all other roaches in Hawaii are known to be exotic and because it shows no tendency to speciate on all of the main islands where it occurs. It is also known from Australia and elsewhere. It appears to be excluded from higher montane environments by cooler temperatures and by the greater moisture in the rainforest along the transect.

Next are several arthropods of comparatively high ecological "penetration," that is, they were found almost throughout the Mauna Loa Transect although at decreasing abundance as altitude increased. The pillbugs (Isopoda), since they have moisture-dependent external gills, would be expected to be more abundant in the rainforest portions of the transect. The phytophagous Fuller's rose weevil (*Pantomorus cervinus*), another group 1 element, showed less penetration than those above.

Two species with unexplained biomodal occurrence, a predaceous lady beetle (*Scymnus loewii*) and a polyphagous, phytophagous thrips (*Heliothrips haemorrhoidalis*) (fide Sakimura, pers. commun.), make up species group 8. This group occurred only at site 6 (on *Acacia koa*) and site 1 (on *Metrosideros*). This may be an artifact of insufficient sampling: *S. loewii*, at least, occurs over a wide elevational range on other islands (Leeper 1976).

Two of 3 species of group 2 restricted to the *Acacia koa* tree communities (*Aptinothrips rufus* and *Chirothrips patruelis*) are known to be graminivorous thrips which hibernate on koa trees. Their occurrence on koa appears to be a reflection of the abundance of their grass hosts that grow in association with koa. The koa psyllid (*Psylla uncatoides*) is a recently introduced species which is restricted to and is abundant on koa on the transect. This species was studied in detail by Leeper & Beardsley (1976) and is not further dealt with here.

The remaining 2 species diagrammed in FIG. 4 are a fungivorous thrip of temperate origin (*Macrophthalmothrips argus*) in group 2 and a suspectedly exotic antho-

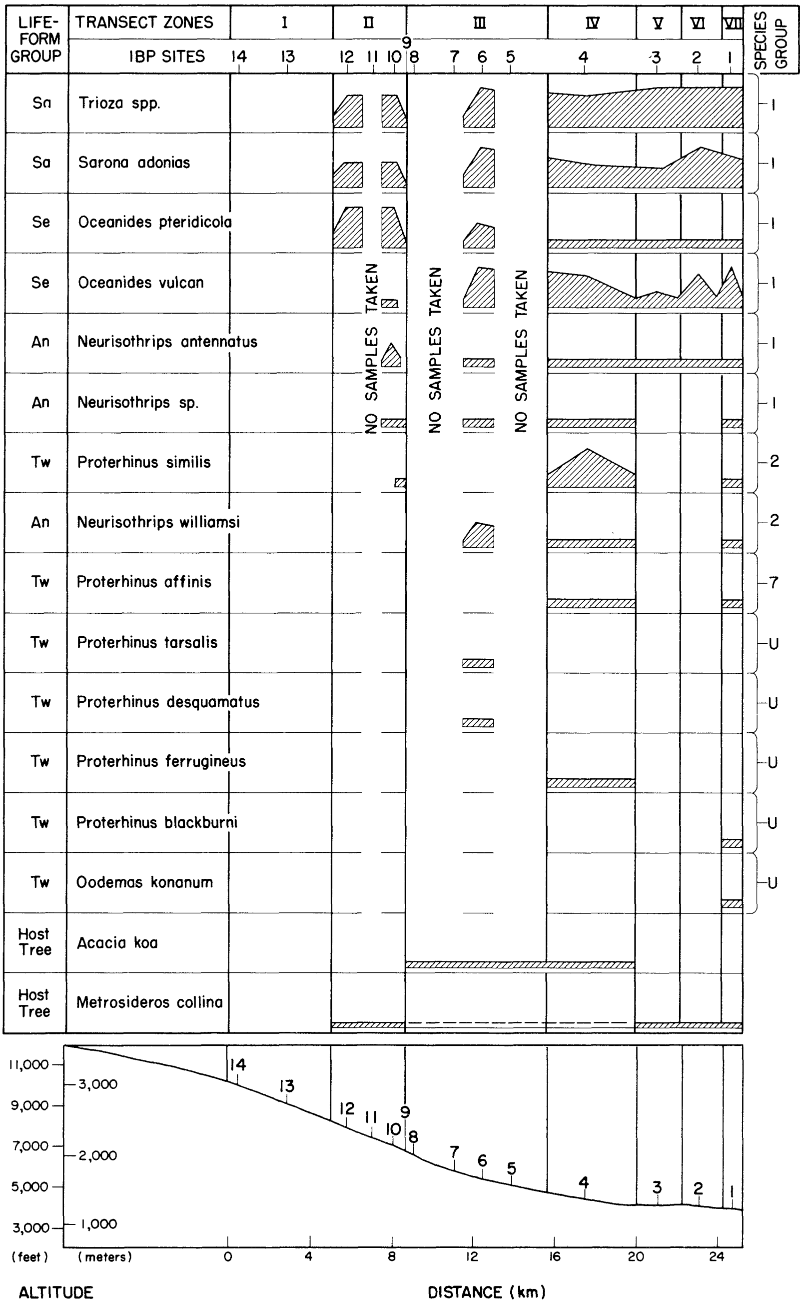


FIG. 5. Distribution of 14 selected endemic, phytophagous arthropod species along the Mauna Loa Transect. Group numbers from 66/10 rule. Life form code: Sc = seed predator; Tw = twig borer; others as in FIG. 4. Abundance scale and transect zones as in FIG. 4.

phagous plant bug (*Hyalopeplus pellucidus*) in group 7. Their slight biomodality is probably related to insufficient collecting. The latter species becomes increasingly common at lower elevation (see TABLE 2) where it feeds on nectar of a great variety of plant species in addition to 'ohi'a. Its upper limits on the transect, however, would appear to be real and to be temperature limited.

Endemic phytophagous arthropod distribution trends

Of the 14 endemic phytophagous taxa found along the transect, 9 are groupable and are diagrammed in FIG. 5. Additionally, 5 weevil species forming an ungrouped, twig-boring ecological functional group or "guild" (see Opler 1974 for an elaboration of the ecological "guild" concept) are diagrammed. The grouped taxa were found in only 3 spatial groups (1, 2 and 7) with ¾ of these in group 1.

It is of interest to note that the quantitatively most important taxa (*Trioza* spp., *Sarona adonias* and *Oceanides pteridicola*) are particularly ubiquitous over the Mauna Loa Transect. Each attacks 'ohi'a. *Trioza* spp. are gall makers on petioles and leaves, *S. adonias* is a sap-sucker, and *O. pteridicola* attacks seeds. All are true bugs, and their lack of significant discontinuities over the transect would indicate that they are well adapted to the prevailing ecological conditions there. *O. pteridicola* is less common than the congener *Oceanides vulcan* in the moister section of the transect at the lower end. *O. vulcan* was also of wide occurrence but, significantly, was not taken at site 12, the highest and driest part of the transect. Two taxa of anthophagous thrips, *Neurisothrips* sp. and *N. antennatus,* showed the same distribution as *O. vulcan* presumably for the same reason, since flowering 'ohi'a are not readily available at cooler and drier site 12.

The greater abundance of the twig borer *Proterhinus similis* in the kipuka forest (savannah) Zone III, coupled with the presence of 2 other twig borers there (*P. affinis* and *P. ferrugineus*) may indicate the propensity of these taxa to attack the more susceptible, mature koa and 'ohi'a which were prevalent there. This is supported by the occurrence again of *P. affinis,* plus 2 other twig borers of 'ohi'a, *P. blackburni* and *Oodemas konanum,* in the apparently mature closed 'ohi'a rain forest at site 1 near Thurston Lava Tube. The ungrouped borers *P. tarsalis* and *P. desquamatus* were restricted to site 6, a mid-elevation mesic site.

By comparing the feeding sites of all these phytophagous species, it can be seen that the more widespread grouped species feed during all of their stages in or on photosynthetic petioles and/or leaves or flowers, while all of the species in the more restricted groups on the transect feed during their larval stages internally on non-photosynthetic twigs. The more widespread species also are volant hemimetabolous insects, whereas the more restricted ones are almost all flightless and holometabolous.

Factors contributing to the distribution of the more restricted arthropods appear to be related to climate and, for the twig borers additionally, to interspecific competition. The *Proterhinus* weevils are among the more highly specialized endemic insects, with over 180 species listed for the Hawaiian Islands (Zimmerman 1948).

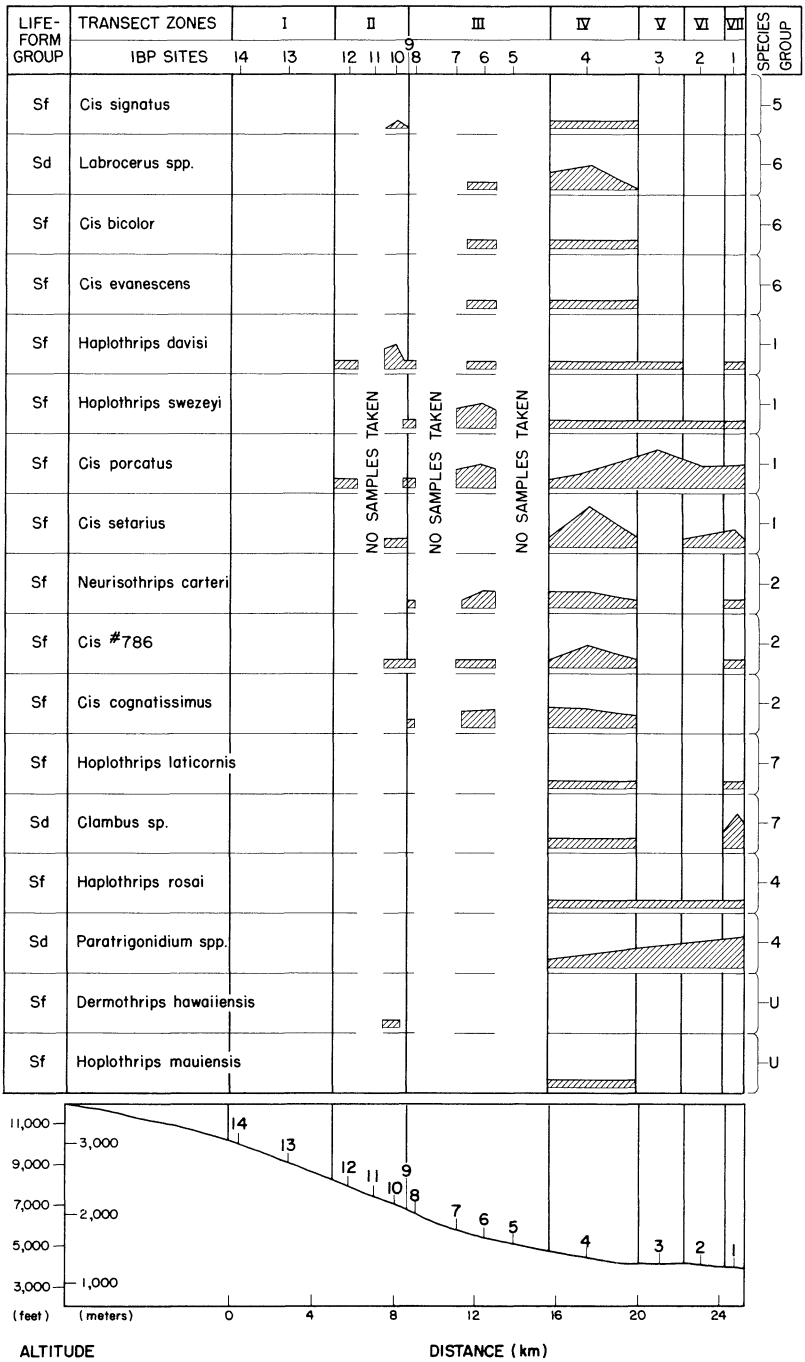


FIG. 6. Distribution of 17 selected endemic fungivorous and detritivorous arthropod species along the Mauna Loa Transect. Group numbers, transect zones, life form code and abundance scales as in FIG. 4.

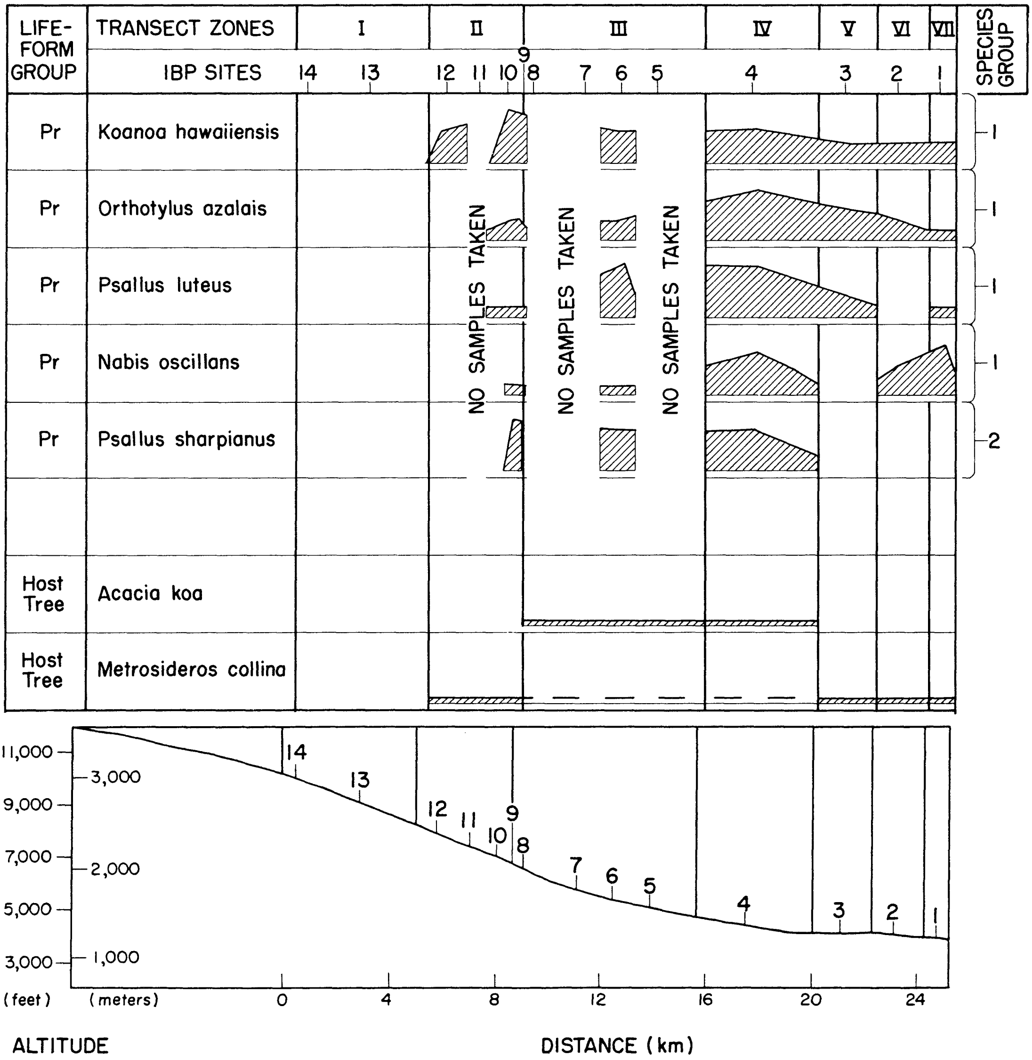


Fig. 7. Distribution of 5 selected endemic, predaceous entomophagous arthropod species along the Mauna Loa Transect. Group numbers from 66/10 rule. Life form code and transect zones as in Fig. 4.

Therefore, it may be expected that these would fall into comparatively narrow niches for which host-specificity and adaptation to narrow climatic ranges are responsible. Zimmerman (1948: 142) also indicated further specialization in these weevils, which relates to their ability to escape predators such as birds: "Our *Proterhinus* beetles closely match the colors of their hosts (as adults). Reddish species are found boring in red fern-frond stalks; dark species are found on dark-barked plants, and pale species on pale bark."

Endemic, fungivorous, and detritivorous arthropod distribution trends

Steffan (1974) has paid particular attention to the fungus gnat (Sciaridae) component (see also Section 7.8 of the forthcoming IBP synthesis volume). These fungus gnats are a detritiphagous group. Since part of his data set is derived from our pyrethrum samples, they will not be dealt with further here. Fifteen of the fungivorous and detritivorous arthropods were members of spatial groups along the Mauna Loa Transect. These are diagrammed in FIG 6. Additionally, 2 ungrouped thrips species, *Dermothrips hawaiiensis* and *Hoplothrips mauiensis*, which also feed on fungal hyphae, are diagrammed. The species belong to all spatial groups except groups 3 and 8.

The species in FIG. 6 can be further separated functionally into the fungus beetles of the genus *Cis* (with 7 species) and into the fungal hyphae-feeding species of thrips (also with 7 species). The remainder were taxonomically unrelated detritivorous dermestid beetles (*Labrocerus* spp.), which feed as larvae on arthropod remains, and an assemblage of primarily plant detritivorous tree crickets (*Paratrigonidium* spp.). The dermestids were restricted mostly to mid-elevational transect sites, where a mesic climate prevails, while the crickets predominated in yet moister, warmer sites at the lower portions of the transect, at 1200 m elevation.

Cis is another highly speciated endemic complex of over 35 species (Zimmerman 1948). The same distributional phenomena discussed above for the phytophagous twig-boring *Proterhinus* weevils apply also to these. Some show host-specificity (i.e., *C. cognatissimus, C. signatus,* and *C. serius* on koa; *C. evanescens, C. sordidus* and *C.* sp. #787 on 'ohi'a); others show altitudinal specificity (i.e., *C. sordidus* and *C. evanescens* at lower elevations, *C. cognatissimus* and *C. bicolor* at middle elevations); and still others show plant community specificity (i.e., *C. cognatissimus* in the koa tree savannah; *C. evanescens* and *C. sordidus* in somewhat xeric 'ohi'a tree communities).

Endemic, entomophagous arthropod distribution trends

The analysis was restricted to a small number of predaceous heteropteran species. There were many other parasitic taxa in the material that would have been of much value for the analysis, but, unfortunately, parasitic arthropods are taxonomically among the most poorly known of the insects in Hawaii. These poorly known ones are primarily wasps (Hymenoptera) that belong to a large number of taxa. Many of these are endemic. They have not yet been adequately treated by systematists.

Five species which showed grouping tendencies under the 2-way table 66/10 rule are diagrammed in FIG. 7. All but 1 belong to the somewhat ubiquitous group 1. *Psallus sharpianus,* a group 2 species, shows a phenomenon common among endemic predaceous insects being host-plant specific but not prey specific. *P. sharpianus* is koa specific, while *P. luteus* and *Nabis oscillans* are 'ohi'a specific. These 3 predators are cryptically colored. Their coloration appears to be an adaptation to avoid predation by birds.

Of the 4 group-1 species, only *Koanoa hawaiiensis* was able to maintain a population

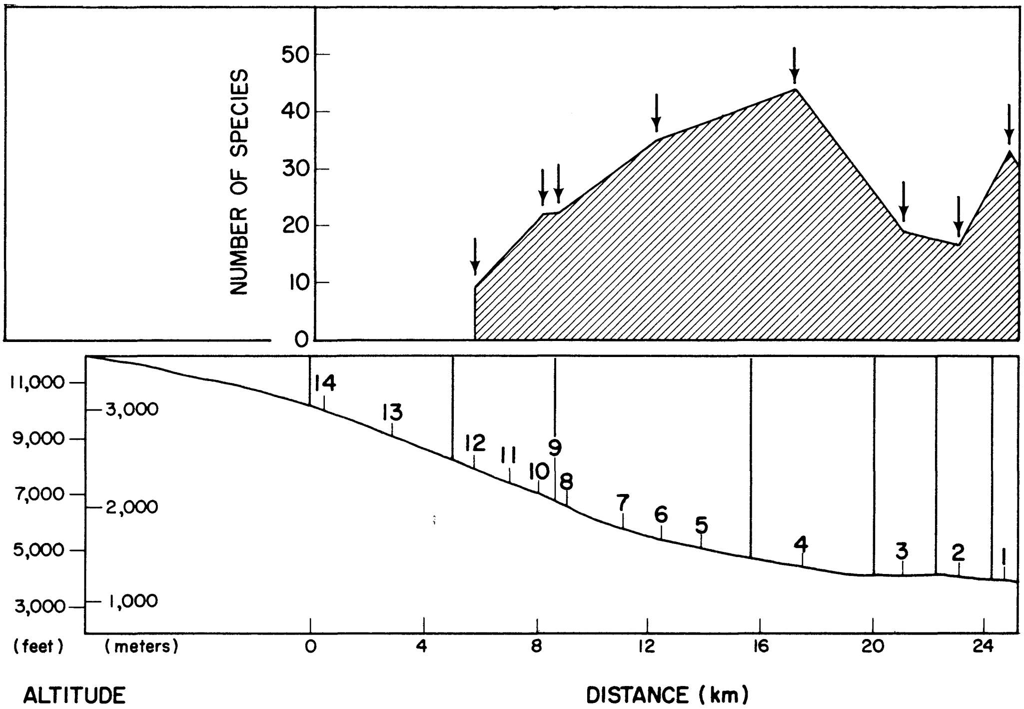


FIG. 8. Number of grouped and ungrouped arthropod species on the Mauna Loa Transect (arrows indicate sampling sites). Abundance scale as in FIG. 4.

at sampling site 12, the treeline site. But all other group-1 species occurred throughout the remainder of the transect on 'ohi'a. *K. hawaiiensis* and *Orthotylus azalais* also occur on koa where this host is present on the transect. Except for *N. oscillans,* which predominates in the lower and particularly moister portions of the transect, the group-1 species are most prevalent at mid-elevation along the Mauna Loa Transect. Their distribution suggests a normal, bell-shaped curve for the transect as a whole.

FIG. 8 shows the distribution of the 46 arthropod species studied over the IBP sampling sites. This curve demonstrates that species diversity is relatively low (from 15–25 foliar arthropod species) in the open *Metrosideros* forests (sites 2 and 3 and in the subalpine scrub forest sites 10–12). In contrast, arthropod species diversity is relatively high (over 30 species) in the closed-canopy *Metrosideros* rain forest (site 1) and in *Acacia koa* tree canopies at low and mid-elevations along the transect (sampling sites 4 and 6). However, on the latter host trees, species diversity decreases markedly with altitude (from sites 4–9), suggesting a climatic cause.

DISCUSSION AND CONCLUSIONS

The 4 arthropod distribution diagrams permit an evaluation of our data with Whittaker's (1970) distribution hypotheses outlined in the introduction to this paper. The data demonstrate 2 underlying themes with respect to those hypotheses. First, taxonomically closely related functional groups of endemic species, such as the fungus beetles of the genus *Cis* and the twig-boring beetles of the genus *Proterhinus,* support Whittaker's 2nd hypothesis in that the species do not appear to have evolved into associated groups, but rather to have excluded one another by competition along the gradient, thus resulting in sharp boundaries with little or no overlap between these competing species. Additionally, the few that did overlap altitudinally did not generally do so spatially, in that they were restricted to different plant hosts. This phenomenon finds some parallels in the nonoverlap of the distributions of species of 2 genera of native shrubs, *Styphelia* and *Vaccinium.* Each has 2 species (*S. tameiameiae* and *S. douglasii, V. peleanum* and *V. reticulatum,* respectively) which appear to exclude one another along fairly sharp boundaries.

Second, the distribution patterns of taxonomically unrelated but ecologically similar functional groups, such as the exotic predaceous lady beetles of temperate origin and the endemic predaceous bugs, support the 1st hypothesis of Whittaker. These species appear to have evolved into spatially associated groups that give way to other associated groups at relatively sharp boundaries along an environmental gradient. For example, the first 3 high-altitude species which make up group 3 (or 4 species if the ungrouped lady beetle, *Hippodamia convergens,* is included) have closely parallel distributions. Group 1, comprised of native predators (see Fig. 7), is less similar but its species do occupy virtually the same segment along the transect. In addition, they have similar abundance peaks at the various sampling sites.

There was more uniformity in the biomass between samples of *Acacia koa* than between samples of *Metrosideros.* Spiders (Araneida) and caterpillars (Lepidoptera) contributed to most of this biomass on koa. Although a more stable community could be implied from the uniform biomass on koa, the Lepidoptera are known to undergo spectacular outbreaks which virtually defoliate *A. koa.* This defoliation has been ascribed to *Scotorythra idolias* Meyrick on Hawaii and to other *Scotorythra* species on Maui and Oahu (Swezey 1954: 1–2). No outbreaks of these caterpillars were observed during the course of this study.

Distribution patterns were not so clear when all of the groupable species were examined en masse. Rather, only after they were ordered into the 3 basic functional groups (phytophagous, fungivorous, and entomophagous) did discernible patterns appear. Knowledge of evolutionary adaptations obtained from intensive comparative genetic studies of insect populations in localities of a much wider area than the transect itself will be presented in the Hawaii IBP's forthcoming synthesis volume (Mueller-Dombois & Bridges, in prep.). Since sampling of foliar arthropods of 'ohi'a was carried out at altitudinal intervals to sea level (see Table 2), the following explanatory statements of probable causes of certain peculiar distribution trends can be made with more confidence.

In many cases, limits to distribution or gaps in distribution appear more closely related to other environmental factors than to substrate differences. The absence of most endemic groups at and below 757 m elevation, i.e., below the Mauna Loa Transect, correlates with an increasing prevalence of ants, particularly the voracious big-headed ant (*Pheidole megacephala*), as well as with a number of other ant species. Thus, predation by ants is suggested as a major cause for the absence of endemics here. The upper limits of arthropods on the Mauna Loa Transect are probably determined by a combination of factors including low temperature, low relative humidity, and for detritivorous and fungivorous species, a decrease in the availability of decomposing or dead organic substrate being attacked by fungi which characterizes the subalpine environment (Stoner et al. 1975). For some species present only in the middle section of the Mauna Loa Transect, the physical effect of frequent rain showers seems to prevent their presence in the rain forest at the lower end of the transect.

The degree of penetration of exotic arthropod species correlates with their origins and feeding habits. Those species of temperate origin, e.g., some lady beetles, appear preadapted to higher and cooler portions of the transects. Omnivores (e.g., the Argentine ant, *Iridomyrmex humilis*) and polyphagous phytophagous species (e.g., the torpedo bug, *Siphanta acuta,* and Fuller's rose weevil, *Pantomorus cervinus*) also demonstrated higher penetrance, as did a species of koa psyllid (*Psylla uncatoides*) originating from phyllode-bearing *Acacia* species in Australia. Ecological specialists (e.g., a flower feeding plant bug, *Hyalopeplus pellucidus*) and species of tropical or subtropical origin (e.g., a cockroach, *Allacta similis*) show weaker penetration.

The bimodal distribution of the arthropods along the Mauna Loa Transect as a whole (FIG. 8), with a peak of diversity in the mixed kipuka forest and another in the closed 'ohi'a rain forest, would in turn appear to relate to the closed canopy structure. At other sites the environment has not yet been ameliorated through canopy closure. This appears to be an important factor influencing the arthropod community diversity, since the detrimental impact of persistent rain-bearing trade winds would be more severe at the comparatively exposed sampling sites pertaining at other than sites 4 and 1. Here, the presence of more amenable sheltered microsites appears to foster a greater diversity of arthropods.

The zonation pattern of the canopy-associated arthropod community as a whole coincided with the major tree species distribution. Motyka's similarity index produced 3 general canopy arthropod zones, while the 2-way table technique using the 66/10 rule results in a refinement to 5 community zones. This contrasted with 7 community zones for the vegetation, using the same analyses and 6 zones over the forested portion of the transect.

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