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CANOPY-ASSOCIATED ARTHROPODS IN *ACACIA KOA* AND *METROSIDEROS* TREE COMMUNITIES ALONG THE MAUNA LOA TRANSECT

Wayne C. Gagné

Entomology Department
B. P. Bishop Museum
P.O. Box 6037
Honolulu, Hawaii 96818

ISLAND ECOSYSTEMS IRP

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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 east flank of Mauna Loa was determined by insecticidal fogging of the canopy with pyrethrum. Eight sites were on the Mauna Loa Transect, which has been intensively sampled by IBP participants in the Island Ecosystems IRP. Two sets of transect zones were determined on the basis of arthropod distribution. The influence of environmental and biotic 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 with other ecosystems in order to further characterize the arthropod canopy community. Host specificity, vegetation structure, competition between ecological homologs, and climate appeared to have the most important influence on population density and spatial distribution patterns of the arthropod taxa studied.

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INTRODUCTION

The two dominant or prevalent native tree species or macrophanerophytes on the Mauna Loa Transect are 'ohi'a (Metrosideros collina subsp. polymorpha) and koa (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. A similar analysis for all plant species on the IBP transect would have been a staggering task since Metrosideros alone harbors hundreds of arthropod taxa. Trees were sampled at approximately 300 m intervals on Transect 1 from the closed Metrosideros rain forest at 1190 m to tree line at about 2500 m elevation.

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 three 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.

The arthropods were sampled by capturing them in cloth funnels suspended beneath the trees after fogging the foliar crowns with pyrethrum synergized with piperonyl butoxide. The sampling method was modified from that of Martin (1966) and Gagnê and Martin (1968), the major modification being the use of a Dynafog® insecticidal fogger (Fig. 1) rather than a hydraulic sprayer. The fogger had the advantage of lightness (approximately 11 kg when filled) and manueverability. It also dislodged less debris into the sample and thus contributed to less loss of arthropods with debris removal.

The shape and size of the funnels varied with the size and spacing of the trees sampled. For the subalpine relevés 13 and 14 with open canopies, a flat sheet 2.4 m square was used (Fig. 1). The sheet was usually placed about the trunk of the trees such that the tree was in the center of the sheet. The sample was then aspirated by hand from the sheet.

In young, well stocked stands such as the pole sized koas at IBP site 6 and for similar sized Metrosideros trees at IBP site 2, a cloth funnel 2.4 m square

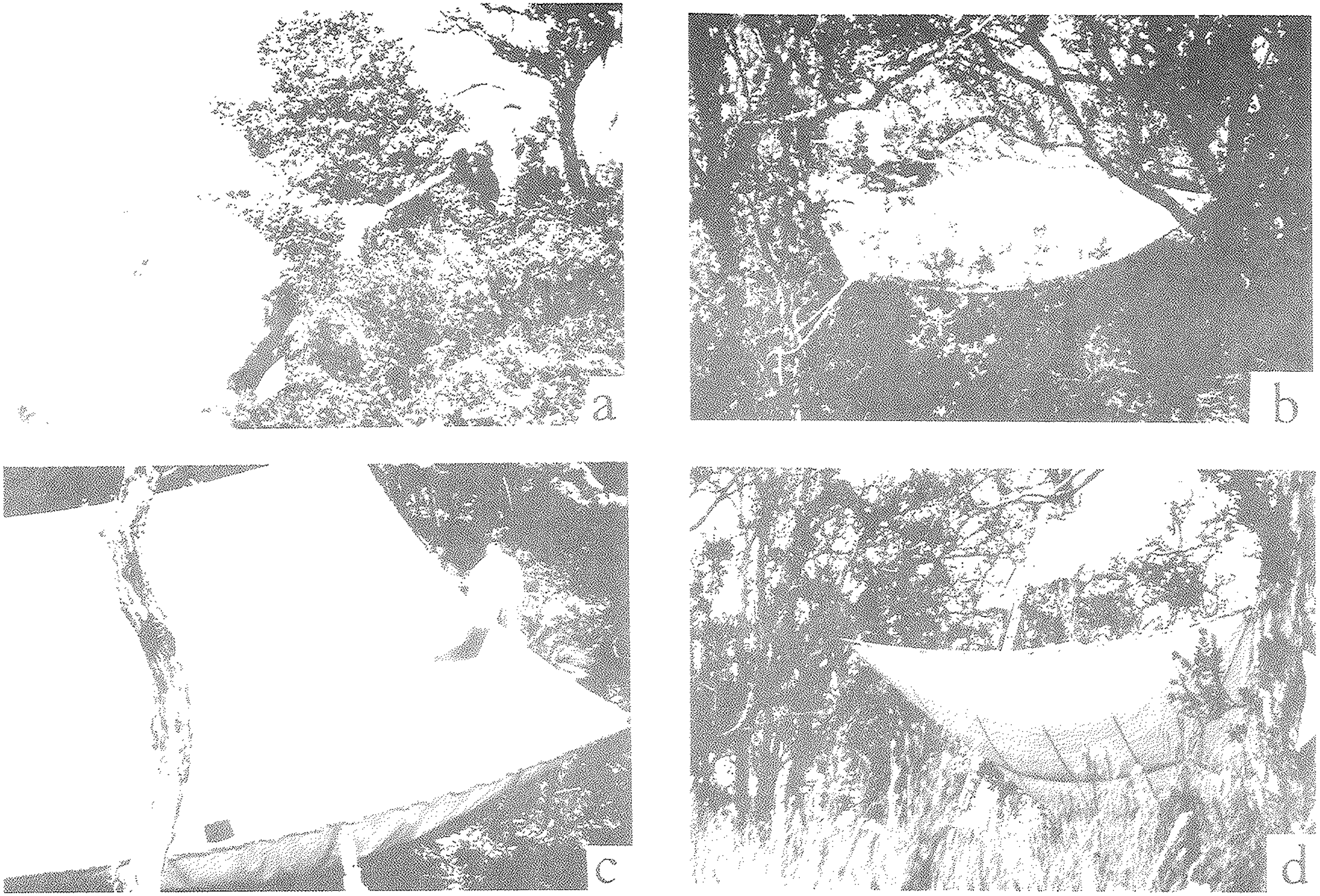

FIG. 1. Canopy arthropod sampling technique using pyrethrum fogger and canvas catchment sheets: a) application of pyrethrum, b) flat 2.4 m square canvas sheet for sites with open canopies, c) funnel shaped 2.4 m square by 1.2 m deep canvas sheet for sampling pole-sized trees, d) funnel-shaped 4.8 m square by 2.4 m deep canvas sheet for sampling large-sized trees.

and 1.2 m deep was fastened to the trunks of four trees as shown in Figure 1.

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 one-quarter of the crown of each tree extended over the funnel. Thus, each funnel sampled four quarters. Weather permitting, each sample was replicated at each IBP site for each tree species sampled. For taller closed-canopy stands the funnels used were larger, namely 4.8 m square and about 2.4 m deep.

Sampling at each of the eight IBP sites (as described in Table 6.2, TR 66) was carried out bimonthly beginning March 1971 and terminating in December 1973. As a rule, the insecticide was applied early in the morning before the trade winds began. The material falling into the sheets was shaken into the bottles several times during the day and the bottles were then collected about mid-afternoon. Bark fragments, twigs and leaves were removed from the funnels prior to each shaking. Seventy percent alcohol was added to the mason jars which were then capped and stored until sorted.

Sampling was integrated on eight sampling relevés on the Mauna Loa Transect (Table 1). This approximately covered the natural range of A. koa on Mauna Loa, i.e. sites 4, 6, and 9. Sampling of Metrosideros was integrated with bark and phenology sampling projects at a number of focal sites on Transects 1 and 2. The sampling relevés in common on Transect 1 were IBP sites 1 to 4, 6, and 9 to 11. There were four additional relevés on Transect 2 to carry on the sampling down to sea level. These were the Kilauea Forest Reserve (site 15), junction of Hilina Pali and Chain of Craters Roads (site 16), Kipuka Keana Bihopa (site 17) and near Kamoamoa (site 18). The data from these four additional sites were not incorporated into the dendrograph and two-way table treatments since they were applied only to the integrated analysis along the Mauna Loa Transect. However, the data from the additional sites provided for an assessment of still wider variations and helped to elucidate more clearly the conditions along the Mauna Loa Transect.

This sampling produced a tremendous body of information both in quantity and quality of taxa of canopy-associated arthropods. The taxa are listed alphabetically in Table 2 by order, family, genus and species. Also indicated are the altitudinal distribution, host association (M = Metrosideros, A = Acacia) and ecological role. From this body of data 68 taxa occurring on portions of the

TABLE 1. Grouping of relevés by IBP sites.

IBP Focal Site	Ecosystem Type	No. of Canopy Relevés (arthropod community samples) Acacia	Metrosideros
1	Closed rain forest	None	21
2	Open rain forest	None	13
3	Open dry forest	None	13
4	Savannah	19	[22]*
5	Mt. parkland	None	None
6	Mt. parkland	23	[19]*
7	Mt. parkland	None	None
8	Mt. parkland	None	None
9	Mt. parkland	19	None
10	Subalpine scrub forest	None	23
11	Subalpine scrub forest	None	None
12	Treeline ecosystem	None	11
13	Alpine scrub	Treeless area, not sampled	
14	Alpine scrub		
	Total Relevés	61	81 [122]

* Tree communities on recent lava flows occupying a minor surface area. These were eliminated from the integrated analysis as quantitatively insignificant variations in the respective ecosystem types.

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).[1]

Taxa	Elevation (m) IBP Focal Site	15 18	760 17	1190 1	1220 2 & 3	1280 4	1600 6	2030 9	2130 10	2440 12	Ecological Role*
ACARINA											
Mesostigmata spp.			M	M	M	A M		A			V
Oribatoidea spp.		M	M	M	M	A M	A M	A	M	M	Sd
Prostigmata spp.		M	M	M	M	A M	A M	A	M	M	V
ARANEIDA spp.		M	M	M	M	A M	A M	A	M	M	Pr
BLATTARIA											
X Blattidae											
Allacata similis			M	M	M	A M	A M				Sd
Other species		M	M								Sd
(X) CHILOPODA sp.		M									Pr
COLEOPTERA											
Anobiidae spp.			M								St
Carabidae spp.				M		A	A			M	Pr
Cerambycidae											
Plagithmysus spp.						A	A	A			Tw
X Exotic spp.		M	M								V
Chrysomelidae											
Diachus auratus			M			A M	A M	A			?
Ciidae											
Cis bicolor						A M	A				Sf
C. cognatissimus						A M	A	A			Sf
C. evanescens			M			A	A				Sf
C. porcatus		M	M	M	M	A M	A M	A		M	Sf
C. setarius			M	M	M	A		A	M		Sf
C. signatus						A			M		Sf
C. sp. #786			M	M		A M	A	A	M		Sf
C. sp. #787			M	M							Sf

TABLE 2 (Continued).

Taxa	Elevation (m)	15	760	1190	1220	1280	1600	2030	2130	2440	Ecological Role*
	IBP Focal Site	18	17	1	2 & 3	4	6	9	10	12	
COLEOPTERA (con't.)											
Clambidae											
Clambus spp.				M		M					Sd
Coccinellidae spp. (see TR 53)											Pr
Cryptophagidae											
Henoticus serratus				M							Sd
Cucujidae spp.			M			A M					Pr
Curculionidae											
Oodemas konanum				M							Tw
O. sp.			M								Tw
X *Pantomorus cervinus*			M	M	M	A M	A M				D
Dermestidae											
Labrocerus spp.			M			A M	M				Sd
X Elateridae spp.							A				?
Histeridae											
Acritus spp.						M					Pr
Lathridiidae											
Corticaria sp.			M								Sf
Lathridius nodifer				M							Sf
Nitidulidae spp.						A M	A	A	M		?
Proterhinidae											
Proterhinus affinis				M		M					Tw
P. blackburni				M				A			Tw
P. desquamatus								A			Tw
P. ferrugineus						A					Tw
P. similis						A M		A			Tw
P. tarsalis				M				M			Tw
Ptiliidae											
Ptiliodes insignis			M			A M	A	A			Sf
Scolytidae spp.						A M					Tw
Staphylinidae spp.			M	M	M	A M	A M	A	M		Pr

TABLE 2 (Continued).

Taxa	Elevation (m) IBP Focal Site	15 18	760 17	1190 1	1220 2 & 3	1280 4	1600 6	2030 9	2130 10	2440 12	Ecological Role*
(X?) COLLEMBOLA											
Brachystomellidae											
Brachystomella parvula							A				Sd
Entomobryidae											
Entomobrya atrocinata			M	M	M	A M	A M	A			Sd
E. clittellaria			M	M		A M		A	M		Sd
E. nivalis		M	M	M		A M	A M	A	M	M	Sd
Entomobryoides sp.						A					Sd
Homidia sauteri			M			A M	A	A			Sd
H. socia			M				A	A			Sd
Lepidocyrtus ruber			M			A					Sd
Salina maculata			M	M		A M					Sd
S. sp.				M		A M					Sd
Genus & sp. A			M		M	A M	A		M		Sd
Hypogastruridae											
Hypogastrura sp.						A M	M				Sd
Isotomidae											
Isotoma sensibilis							A				Sd
I. sp.						A					Sd
DIPTERA											
Agromyzidae spp.							A				Ph
Anthomyiidae spp.								A			?
Asteiidae											
Asteia apicalis							A	A			?
Calliphoridae spp.				M		M	A				?
Cecidomyiidae spp.			M	M	M	A M	A	A	M		?
Ceratopogonidae spp.		M	M	M	M	A M	A M	A			Sd
Chironomidae spp.			M	M	M	A M	A M	A	M		?
X Cryptochaetidae											
Cryptochaetum iceryae		M						A	M		Pr
X Drosophilidae spp.		M	M	M	M	A M	A M	A			p

TABLE 2 (Continued).

Taxa	Elevation (m)	15	760	1190	1220	1280	1600	2030	2130	2440	Ecological Role*
	IBP Focal Site	18	17	1	2 & 3	4	6	9	10	12	
Dolichopodidae											
Campsicnemus modicus or *setiger*							M				Pr
C. macula						M			M		Pr
C. spinicoxa				M							Pr
C. sp.				M		M			M		Pr
Eurynogaster angustifascies				M							Pr
E. argentata			M	M		M					Pr
E. sp.				M							Pr
Lonchaeidae spp.						A					?
Milichiidae spp.							A	A		M	?
Mycetophilidae											
Orfelia (*Tylparua*) sp.				M							P
Phoridae spp.			M	M		A M		A			P
Pipunculidae											
Pipunculus spp.						M			M		Pa
Psychodidae											
mostly *Psychoda* spp.											Sd
(X)Sciaridae spp.											Sf
X Syrphidae spp.						A	A				Pr
X Tephritidae spp.						M					P
Tipulidae spp.			M	M		A M	A				Sd
HETEROPTERA											
X Anthocoridae											
Orius persequens								A			Pr
Lygaeidae											
Neseis o. ochriasis								A			P
Nysius blackburni				M	M	M		A			P
N. nemorivagus			M								P
N. nigriscutellatus					M						P
Oceanides pteridicola			M	M	M	M	M		M	M	Se
O. vulcan			M	M	M	M	M		M		Se
X *Pachybrachius vincta*							M		M		P

TABLE 2 (Continued).

Taxa Elevation (m) IBP Focal Site	15 18	760 17	1190 1	1220 2 & 3	1280 4	1600 6	2030 9	2130 10	2440 12	Ecological Role*
Miridae										
(X)*Hyalopeplus pellucidus*	M		M		M					An
Koanoa hawaiiensis		M	M	M	A M	A M	A	M	M	Pr
Orthotylus azalais		M	M	M	A M	A M	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
S. sp.					A M					P
Nabidae										
Nabis oscillans		M	M	M	A M	A	A			Pr
Pentatomidae										
Oechalia sp. nr. *acuta*			M	M		A				Pr
X Plataspidae										
Coptosoma xanthogamma	M									P
Reduviidae										
X? *Empicoris rubromaculatus*					M	A M				Pr
Scutelleridae										
Coleotichus blackburniae						A				Sa
X Tingidae										
Teleonemia scrupulosa	M									P
HOMOPTERA										
X Aphidae spp.	M	M		M	A M	A M	A	M	M	Sa
Cicadellidae										
Nesophrosyne spp.			M	M		M	A	M	M	Sa
Cixiidae										
Iolania perkinsi			M							Sa
Oliarus inconstans						M				Sa
(X)Coccidae spp.		M	M	M	A M	A M	A	M		Sa

TABLE 2 (Continued).

Taxa	Elevation (m)	15	760	1190	1220	1280	1600	2030	2130	2440	Ecological Role*
	IBP Focal Site	18	17	1	2 & 3	4	6	9	10	12	
Delphacidae											
Leialoha naniicola				M		A M					Sa
Nesosydne koae						A					Sa
N. koaephyllodi						A	A				Sa
Nesothoe gulicki			M								Sa
X Flatidae											
Siphanta acuta		M	M	M		M	M	A	M	M	Sa
Psyllidae											
X *Psylla striola*						A	A	A			Sa
mostly *Trioza* spp.		M	M	M	M	M	M		M	M	Sa
HYMENOPTERA											
X Ampulicidae											
Ampulex compressa		M									Pa
Bethylidae											
mostly *Seriola* spp.			M	M	M	A M	A M	A	M	M	Pa
X Braconidae spp.		M	M			A					Pa
Ceraphronidae spp.								A		M	Pa
Chalcidoidea spp.		M	M	M	M	A M	A M	A	M	M	Pa
Colletidae											
Nesoprosopis spp.				M		M				M	An
Cynipidae spp.								A	M	M	Pa
Diapriidae spp.							A				Pa
X Formicidae											
Iridomyrmex humilis				M	M	A M	A M	A	M	M	O
Pheidole megacephala		M	M								O
Plagiolepis alluaudi		M	M								?
(X) Ichneumonidae spp.		M	M	M	M	A M	M	A	M	M	Pa
Proctotrupidae spp.							A				Pa
Scelionidae spp.			M	M	M	A M	A		M		Pa
X ISOPODA spp.			M	M	M	A M	M	A			Sd

TABLE 2 (Continued).

Taxa	Elevation (m)	15	760	1190	1220	1280	1600	2030	2130	2440	Ecological Role*
	IBP Focal Site	18	17	1	2 & 3	4	6	9	10	12	
LEPIDOPTERA (larvae)											
Lycaenidae											
Vaga blackburni							A	A			D
(X)Other families		M	M	M	M	A M	A M	A	M	M	D
NEUROPTERA											
(X)Chrysopidae spp.		M	M	M	M	A M	A M	A			Pr
(X)Hemerobiidae spp.		M	M	M	M	A M		A			Pr
ORTHOPTERA											
Gryllidae											
Paratrigonidium spp.				M	M	M					Sd
Tettigoniidae											
Banza nitida				M							Pr
X *Conocephalus saltator*		M									Pr
X *Elimaea punctifera*		M									D
(X?) PSEUDOSCORPIONIDA spp.			M			A					Pr
(X) PSOCOPTERA spp.		M	M	M	M	A M	A M	A	M	M	Sd
STREPSIPTERA											
Elenchidae											
Elenchus sp.						A					Pa
THYSANOPTERA											
Phaeothripidae											
X *Aleurodothrips fasciapennis*		M									Pr
Dermothrips hawaiiensis								A			Sf
Haplothrips davisi				M	M	A M	A M	A	M	M	Sf
H. rosai			M	M	M	A M					Sf
X *Hoplothrips flavitibia*						A					Sf
H. laticornis				M		A M					Sf
H. mauiensis						M					Sf
H. swezeyi				M	M	M	M	A			Sf

TABLE 2 (Continued).

Taxa	Elevation (m)	15	760	1190	1220	1280	1600	2030	2130	2440	Ecological
	IBP Focal Site	18	17	1	2 & 3	4	6	9	10	12	Role*
Phaeothripidae (con't.)											
X *Karnyothrips flavipes*			M			A M			M		Pr
X *K. longiceps*						A M					Pr
X *Macrophthalmothrips argus*			M	M		A M	A				Sf
X *Nesothrips brevicollis*		M									Sf
Phlaeothrips mauiensis									M		Sf
X *Rhaebothrips lativentris*		M							M		Sf
Thripidae											
X *Aptinothrips rufus*				M	M	A M	A	A			Gr
X *Baliothrips minutus*				M							Gr
X *Chirothrips patruelis*			M			A M	A M	A			Gr
X *Dorcadothrips cyperaceae*						M					Gr
X *Heliothrips haemorrhoidalis*		M	M	M			A				Sa
Neurisothrips antennatus			M	M	M	A M	A		M		An
N. carteri				M		A M	A				Sf
N. multispinus			M	M		A M	A M	A	M		An
N. williamsi			M	M		M	A				An
N. sp. #24			M	M		A M	A	A	M		?
N. sp. #39								A			An
X *Thrips hawaiiensis*			M								An
X THYSANURA sp.		M									Sd

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[1] Data for site 15 in the Kilauea Forest Reserve and site 16 at the Junction of Hilina Pali and Chain of Craters Roads are omitted.

* 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

X = Exotic or probably exotic taxa

(X) = Includes some exotic species

Mauna Loa Transect were selected. This represents a cross section of non-ubiquitous taxa in various ecological roles including those that could be positively identified throughout the sampling period.

Most of the arthropods sampled from the foliar environment in this study can be considered as confined to the distribution ranges in which they were found. 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" (?).

ZONATION PATTERNS

The data sets were prepared for computer analysis to produce a two-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 = 1, 3-4 specimens = 2, 5-8 specimens = 3, etc.) of its mean abundance in each sample set (two samples). Species groups could then be identified that had similar distributional trends across the altitudinal transect.

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 two elevational extremes. At sea level, large roaches (Blattaria) 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.

Computerized data analysis

Two methods were used to determine the zonation patterns of selected groups of arthropods, the dendrograph method and the two-way table method (see TR 66). The arthropod taxa selected from Table 2 were based on the reliability with which they could be identified throughout the sampling period, and on their quantitative importance. The two-way synthesis table technique (see Section 6.8-2, TR 66) attempts to identify groups of taxa with similar distribution ranges, which in turn are used to identify transect zones.

Application of the 66/10 rule generated eight species groups along the Mauna Loa Transect. These were formed by 48 taxa in 26 relevés (Fig. 2). The data are comprised of 183 samples of foliar canopies (122 canopy relevés from Metrosideros collina and 61 canopy relevés from Acacia koa) taken along the Mauna Loa Transect (see Table 1). The outcome of the dendrograph cluster analysis is also shown on Figure 2. This affords a direct comparison of the clustering patterns and transect zones that were derived from the same data set by the two previously mentioned analysis methods. As can be seen, the dendrograph method resulted in less zonal or community differentiation than the two-way table method. The three zones indicated by the dendrograph method are I = the subalpine zone, II = the mountain parkland and savanna zone, and III = the mid-elevation Metrosideros forest zone. The two-way table method resulted in finer differentiations, i.e. in a separation of the mountain parkland and savanna zone and in a separation of the closed forest (zone V) from the open forest (zone IV) in the mid-elevation Metrosideros zone.

Table 2 gives an indication of taxonomic richness from sea level to tree line. The richest arthropod communities occurred at mid-elevations where they were three times 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 (Ananeida), 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) and a spring tail (Entomobrya nivalis, Collembola). Most of these groups were comprised of exotic species in the lower elevations, the notable exception being the psyllids. Conversely, 14% of the taxa found only between 750 m and 2150 m appear to be comprised mostly of native taxa. 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. The 5% of the taxa found only at sea level sampling sites appeared to be wholly exotic in origin.

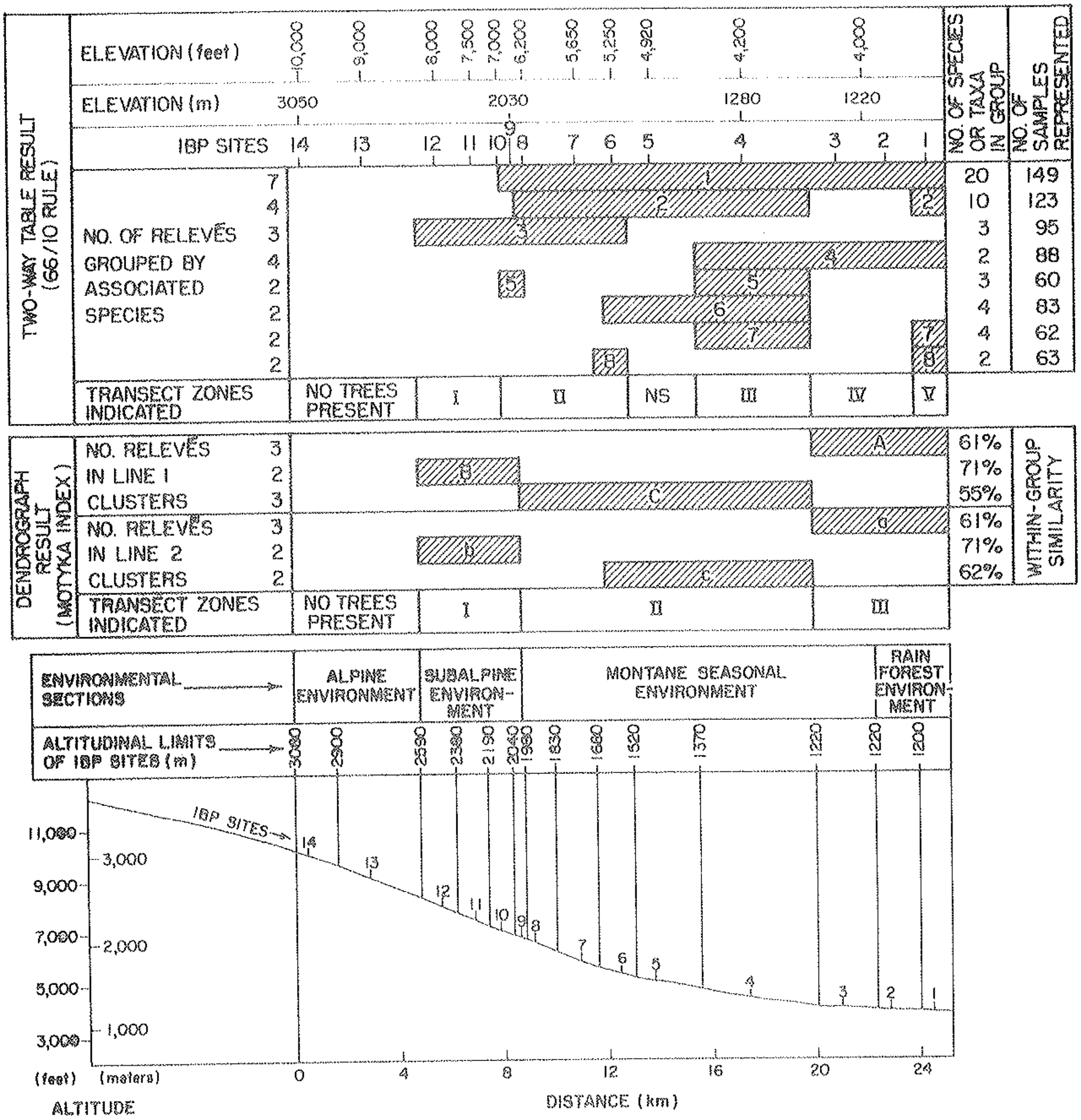

FIG. 2. Altitudinal transect zones derived from two-way (66/10 rule) and dendrograph (with Motyka's index) techniques of 183 canopy samples (i.e. 122 Metrosideros and 61 Acacia relevés at eight sample sites from beginning of transect to tree line of Metrosideros at 2590 m). Transect zones resulting from two-way table analysis are: I Subalpine Metrosideros scrub forest, II Mountain parkland, Acacia koa tree colonies, III Savannah, IV Mixed kipuka forest, V Open Metrosideros dry and wet forest, VI Closed Metrosideros rain forest, NS = not sampled.

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 striola) and spring tails (Collembola), the latter during the wetter, winter months.

SPECIES DISTRIBUTION TRENDS

To interpret the individual clusters derived from the two-way table technique, referral to the results derived from the floristic analysis is necessary. 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.

The two-way table technique offers the advantage of specifying the taxa responsible for the clusters in the printout. Table 3 lists the 48 species and taxa that were clustered into eight associated groups on Figure 2. The order of listing follows groups on Table 3, from subalpine Metrosideros scrub forest to closed Metrosideros rain forest. Taxa from separate ecological functional groups that define exactly the same transect section, such as groups 5, 1, 2 and 7 can be considered as spatially associated also. The reasons why these spatially associated species and taxa were extracted into separate groups is 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*, they were diagrammed separately (Fig. 3) from the endemic arthropods (Fig.'s 4 to 6). The endemic arthropods were further broken into three ecological functional groups-- 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 two-way table analysis) with those of

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

TABLE 3. List of 48 taxa of arthropods found in eight spatially associated groups along the Mauna Loa Transect. [Generated with two-way table 66/10 rule. Computer-derived number sequence from top to bottom as are species distribution diagrams, Figures 3 to 6.]

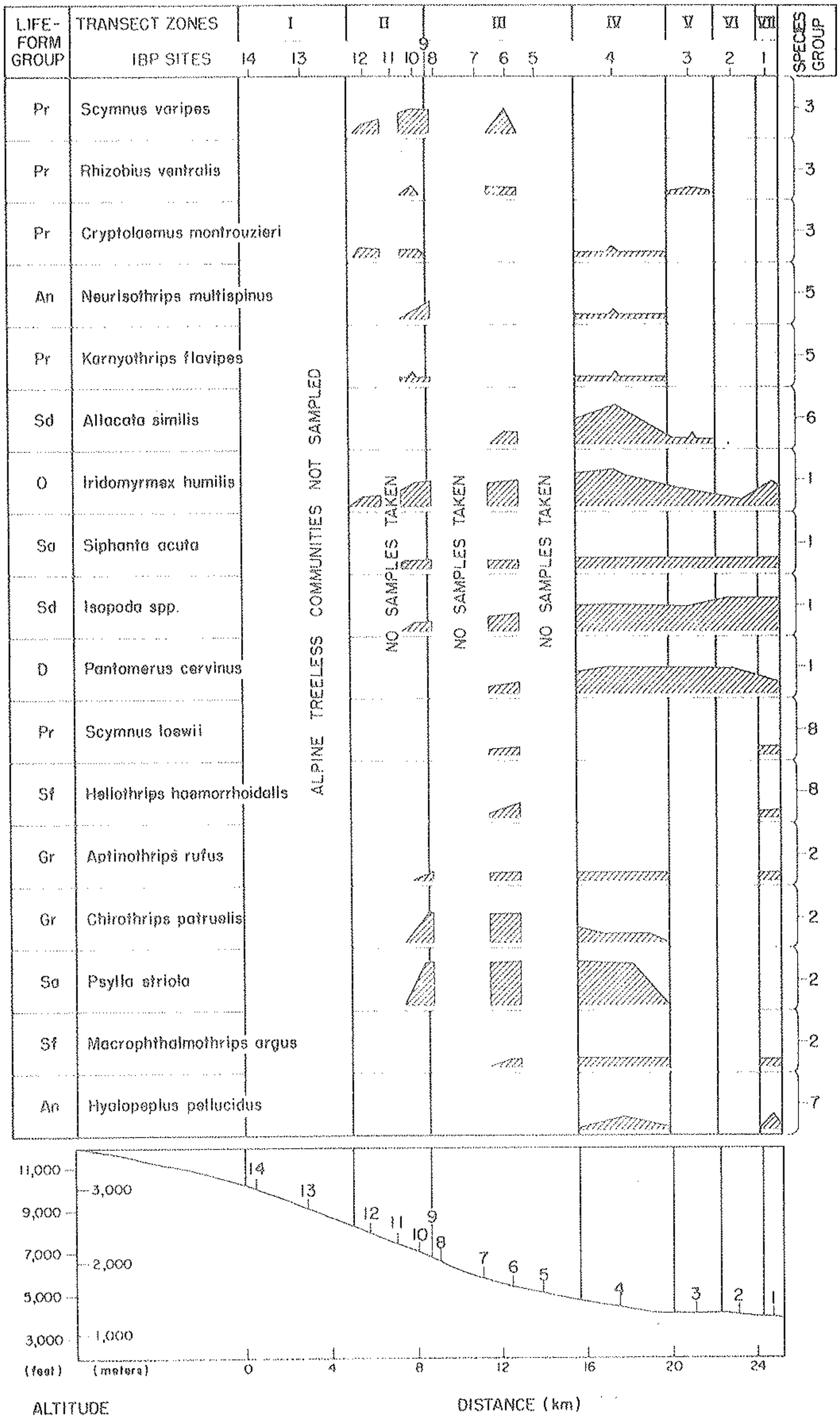
Group No.	Species and Taxa	Life form
3	X *Scymnus varipes*	Predaceous lady beetles of temperate origin, exotic
	X *Rhizobius ventralis*	
	X *Cryptolaemus montrouzieri*	
5	X *Neurisothrips multispinus*	Flower-feeding thrips of temperate origin, exotic
	X *Karnyothrips flavipes*	Predaceous flower-feeding thrips of temperate origin, exotic
	Cis signatus	Fungivorous beetle, endemic
6	X *Allacata similis*	Detritivorous roach, possibly 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	
	X *Iridomyrmex humilis*	Omnivorous ant of temperate origin, exotic
	(X) Lepidoptera spp.	Phytophagous defoliators of various origin
	(X) Araneida spp.	Predaceous, (?) mostly endemic
	mostly Trioza spp.	Phytophagous gall formers on *Metrosideros*, endemic

TABLE 3 (Continued).

Group No.	Species and Taxa	Life form
1 con't.	*Haplothrips davisi*	Fungus hyphae feeders in dead wood, endemic
	Hoplothrips swezeyi	
	Neurisothrips antennatus	Flower-feeding thrips, endemic
	Neurisothrips spp.	
	Sarona adonias	Host-specific sap-sucker of *Metrosideros*, endemic
	X *Siphanta acuta*	Polyphagous sap-sucker, exotic
	Oceanides pteridicola	Host-specific seed predators of *Metrosideros*, endemic
	Oceanides vulcan	
	Cis porcatus	Fungivorous beetles, endemic
	Cis setarius	
	X Isopoda spp.	Detritivorous pillbugs, exotic
	X *Pantomorus cervinus*	Phytophagous, polyphagous, exotic
8	X *Scymnus loewii*	Predaceous lady beetle of tropical origin, exotic
	X *Heliothrips haemorrhoidalis*	Polyphagous, phytophagous thrips, exotic
2	*Neurisothrips carteri*	Rust fungus feeder of *Acacia koa*, endemic
	X *Aptinothrips rufus*	Graminivorous thrips hibernating on trees, exotic
	X *Chirothrips patruelis*	
	X *Macrophthalmothrips argus*	Fungus hyphae feeder, temperate exotic origin
	Psallus sharpianus	Primarily predaceous bug associated with *Acacia koa*, endemic
	Proterhinus similis	Twig-feeding beetle, endemic
	X *Psylla striola*	Phytophagous on phyllodes of *Acacia koa*, exotic
	Neurisothrips williamsi	Polyphagous flower feeder, endemic

TABLE 3 (Continued).

Group No.	Species and Taxa	Life form
2 con't.	*Cis* sp. #786	Fungivorous beetle primarily of *Metrosideros*, endemic
	Cis cognatissimus	Fungivorous beetle of *Acacia koa*, endemic
7	X *Hyalopeplus pellucidus*	Polyphagous flower feeder, possibly exotic
	Proterhinus affinus	Twig-feeding beetle, endemic
	Hoplothrips laticornis	Fungus hyphae feeder, endemic
	Clambus sp.	Associated with decaying plant matter, (?) endemic


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 Allacota similis 6
O Iridomyrmex humilis 1
Sa Siphanta acuta 1
Sd Isopoda spp. 1
D Pantomerus cervinus 1
Pr Scymnus loewii 8
Sf Heliothrips haemorrhoidalis 8
Gr Aptinothrips rufus 2
Gr Chirothrips patruelis 2
Sa Psylla striola 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)

the floristic analysis (in TR 66), the arthropods can well be discussed in the context of the vegetation patterns.

Exotic arthropod distribution trends

Of the 48 species and taxa found in the eight spatially associated groups along the Mauna Loa Transect (Fig. 2 and Table 3), 17 were of exotic origin. Their distributions are diagrammed in Figure 3. Exotics were found in all spatial groups except in Group 4. Therefore, this group does not appear on Figure 3. Species Group 3 (on Fig. 3) 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 supply at still lower elevations, these temperate species do not appear to have been able to exploit these warmer habitats. Another ungrouped coccinellid, not diagrammed, is the nearctic Hippodamia convergens which was encountered only at IBP site 12. Leeper has paid special attention to these and other coccinellids found on Hawaii Island transects from all plant communities in TR 53, to which the interested reader should refer 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 and 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 plantations.

Two of the three species comprising Group 3 are thrips of temperate origin. Little is known of the ecological functions of these other than that one is predaceous while the other is anthophagous (Sakimura, pers. comm.).

In Group 6, only the detritivorous roach Allacata similis is of presumably exotic origin. Although this roach 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 appears to be excluded from higher montane environments by cooler temperature 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 spp.) which have moisture dependent external gills, would be expected to be more abundant in the rainforest portions of the transect. The phytophagous Fuller rose weevil (Pantomorus cervinus), another Group 1 element, showed less penetration than those above.

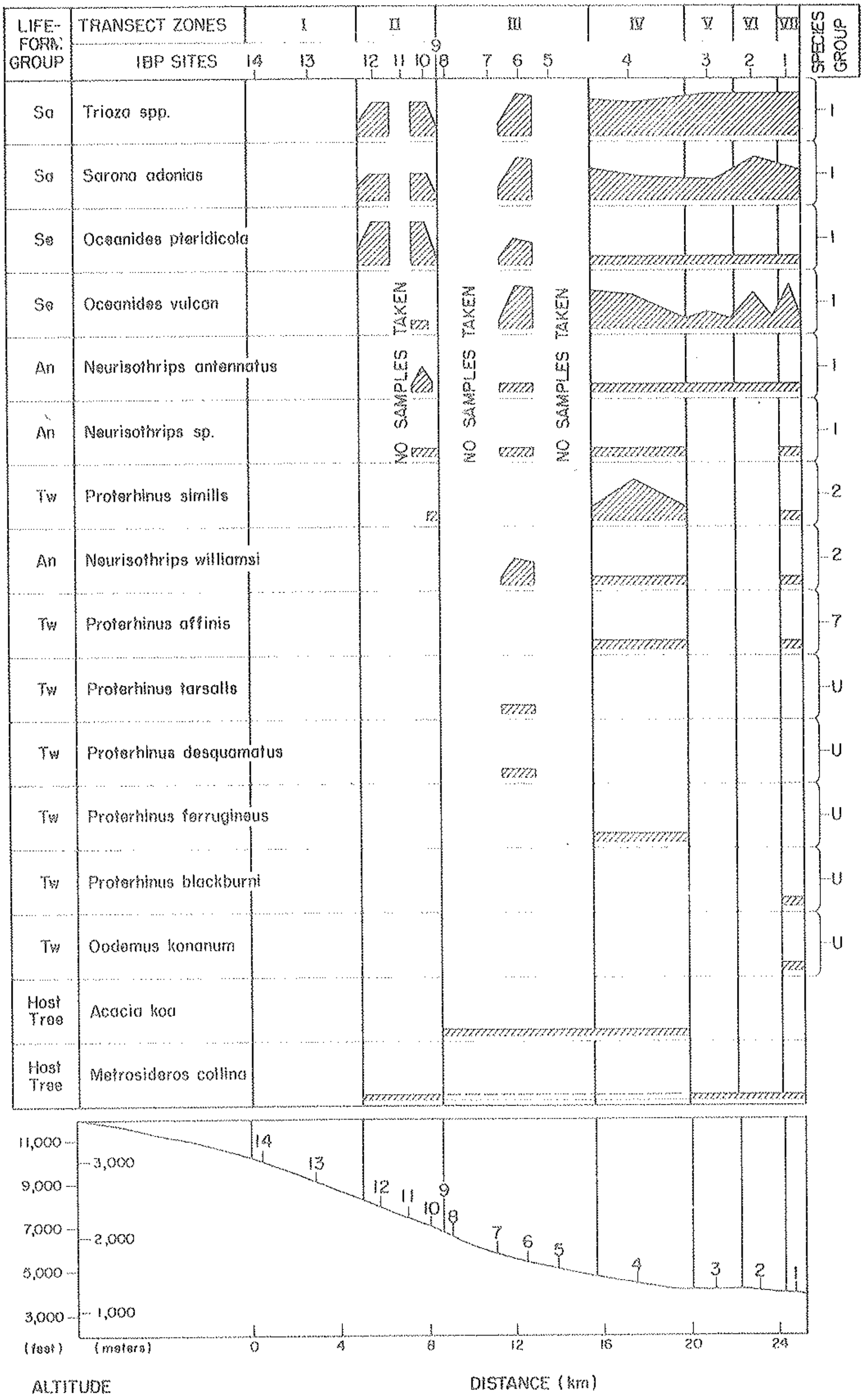
Two species with unexplained bimodal occurrence, a predaceous lady beetle (Scymnus loewii) and a polyphagous, phytophagous thrips (Heliothrips haemorrhoidalis) (fide Sakimura, pers. comm.) make up species Group 8. This group occurred only at IBP site 6 (on Acacia koa) and IBP site 1 (on Metrosideros). This may be an artifact of insufficient sampling; S. loewii, at least, occurs over a wide elevational range on other islands (Leeper TR 53).

Two of three species of Group 2 restricted to the Acacia koa tree communities (Aptinothrips rufus and Chirothrips patruelis) are known to be graminivorous (grass feeding) 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 striola) is a recently introduced species which is restricted to and abundant on koa on the transect. (This species was studied in detail by Beardsley and Leeper for this project and so is not further dealt with here.)

The remaining two species on the diagram (Fig. 3) are a fungivorous thrips of temperate origin (Macrophthalmothrips argus) in Group 2 and a suspectedly exotic anthophagous 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 48 taxa found along the transect, nine are groupable and are diagrammed in Figure 4. Additionally, five weevil species forming an ungrouped,


LIFE-FORM GROUP
TRANSECT ZONES
I
II
III
IV
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VI
VII
IBP SITES
14
13
12
11
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9
8
7
6
5
4
3
2
1
SPECIES GROUP
Sa
Trioza spp.
Sa
Sarona adonias
Se
Oceanides pteridicola
Se
Oceanides vulcan
An
Neurisothrips antennatus
An
Neurisothrips sp.
Tw
Proterhinus similis
An
Neurisothrips williamsi
Tw
Proterhinus affinis
Tw
Proterhinus tarsalis
Tw
Proterhinus desquamatus
Tw
Proterhinus ferrugineus
Tw
Proterhinus blackburni
Tw
Oodemus konanum
Host Tree
Acacia koa
Host Tree
Metrosideros collina
NO SAMPLES TAKEN
NO SAMPLES TAKEN
NO SAMPLES TAKEN
1
1
1
1
1
1
2
2
7
U
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11,000
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7,000
5,000
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(feet)
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2,000
1,000
(meters)
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12
16
20
24
ALTITUDE
DISTANCE (km)

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 three spatial groups (1, 2, and 7), with three-fourths 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 *O. 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 IBP 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 site 12.

The greater abundance of the twig borer *Proterhinus similis* in the Kipuka Forest (savannah zone IV) coupled with the presence of two 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 two other twig borers of 'ohi'a, *P. blackburni* and *Oodemas konanum* in the apparently mature closed 'ohi'a rain forest at IBP 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 more restricted grouped species on the transect feed during their more fragile 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.

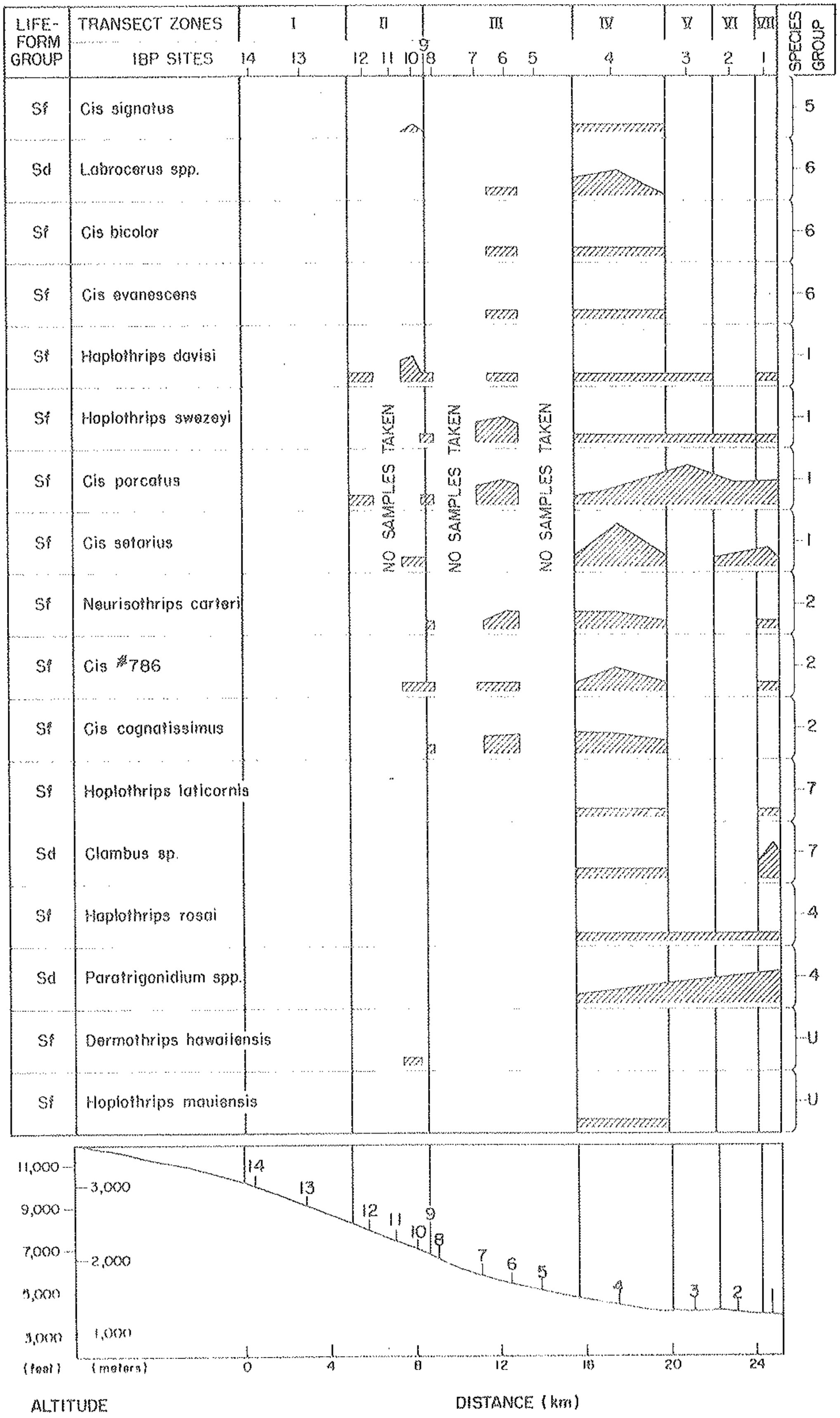
Factors contributing to the distribution of the more restricted arthropods would appear to be related to climate, and for the twig borers additionally to interspecific competition. The *Proterhinus* weevils are one of the most highly specialized components of the endemic insects with over 180 species listed for the Hawaiian Islands (Zimmerman 1948). It may therefore be expected that these would fall into comparatively narrow niches for which host-specificity and adaptation to narrow climatic ranges are responsible. Zimmerman (*loc. cit.*) also indicated further specialization in this group, 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" (p. 142).

Endemic, fungivorous, and detritivorous arthropod distribution trends

Steffan has paid particular attention to the fungus gnat (Sciaridae) component in Section 7.8 of the forthcoming 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 Figure 5. Additionally, two ungrouped thrips species, *Dermothrips hawaiiensis* and *Hoplothrips mauiensis*, which also feed on fungal hyphae, are diagrammed. The species belong to all spatial groups except to Groups 3 and 8.

The species on Figure 5 can be further separated functionally into the fungus beetles of the genus *Cis* (with seven species) and into the fungal hyphae-feeding species of thrips (also with seven species). The remainder were taxonomically unrelated detritivores--dermestid beetles (*Labrocerus* spp.) which feed as larvae on arthropod remains, and the other 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 predominate in yet moister, warmer sites at the lower portions of the transect.

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 applies also to these. Some show host-specificity (i.e. *C. cognatissimus*, *C. signatus*, and *C. serius* on koa; *C. evanescens* and *C. sordidus* and *C.* sp. #787 on 'ohi'a), others show altitudinal


LIFE-FORM GROUP
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SPECIES GROUP
Sf Cis signatus 5
Sd Labrocerus spp. 6
Sf Cis bicolor 6
Sf Cis evanescens 6
Sf Haplothrips davisi 1
Sf Haplothrips swezeyi 1
Sf Cis porcatus 1
Sf Cis setarius 1
Sf Neurisothrips carteri 2
Sf Cis #786 2
Sf Cis cognatissimus 2
Sf Haplothrips laticornis 7
Sd Clambus sp. 7
Sf Haplothrips rosai 4
Sd Paratrigonidium spp. 4
Sf Dermothrips hawaiiensis U
Sf Haplothrips mauiensis U
NO SAMPLES TAKEN
NO SAMPLES TAKEN
NO SAMPLES TAKEN
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9,000
7,000
5,000
3,000
(feet)
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ALTITUDE
DISTANCE (km)

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 savanna; 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 which would have been of much value for the analysis, but unfortunately, predaceous 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. Yet they have not been treated by specialists.

Five species which showed grouping tendencies under the two-way table 66/10 rule are diagrammed in Figure 6. All but one belong to the somewhat ubiquitous Group 1. Psallus sharpianus, a Group 2 species, shows the common phenomenon among endemic predaceous insects in being host-plant specific but not prey specific. P. sharpianus is koa specific, while P. luteus and Nabis oscillans are 'ohi'a specific. These three predators are cryptically colored. Their coloration appears to be an adaptive adjustment to avoid predation by birds.

Of the four Group 1 species, only Koanoa hawaiiensis was able to maintain a population at IBP site 12, the upper tree line. 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.

The lower part of Figure 6 shows the total number of arthropod species plotted over the IBP sampling sites. This curve demonstrates that species diversity is relatively low (from 15 to 25 foliar arthropod species) in the open Metrosideros forests (IBP sites 2 and 3 and in the subalpine scrub forest sites 10 to 12). In contrast, arthropod species diversity is relatively high (over 30 species) in the closed-canopy Metrosideros rain forest (IBP site 1) and in Acacia koa tree canopies at low and mid-elevations along the Transect (sites 4 and 6).

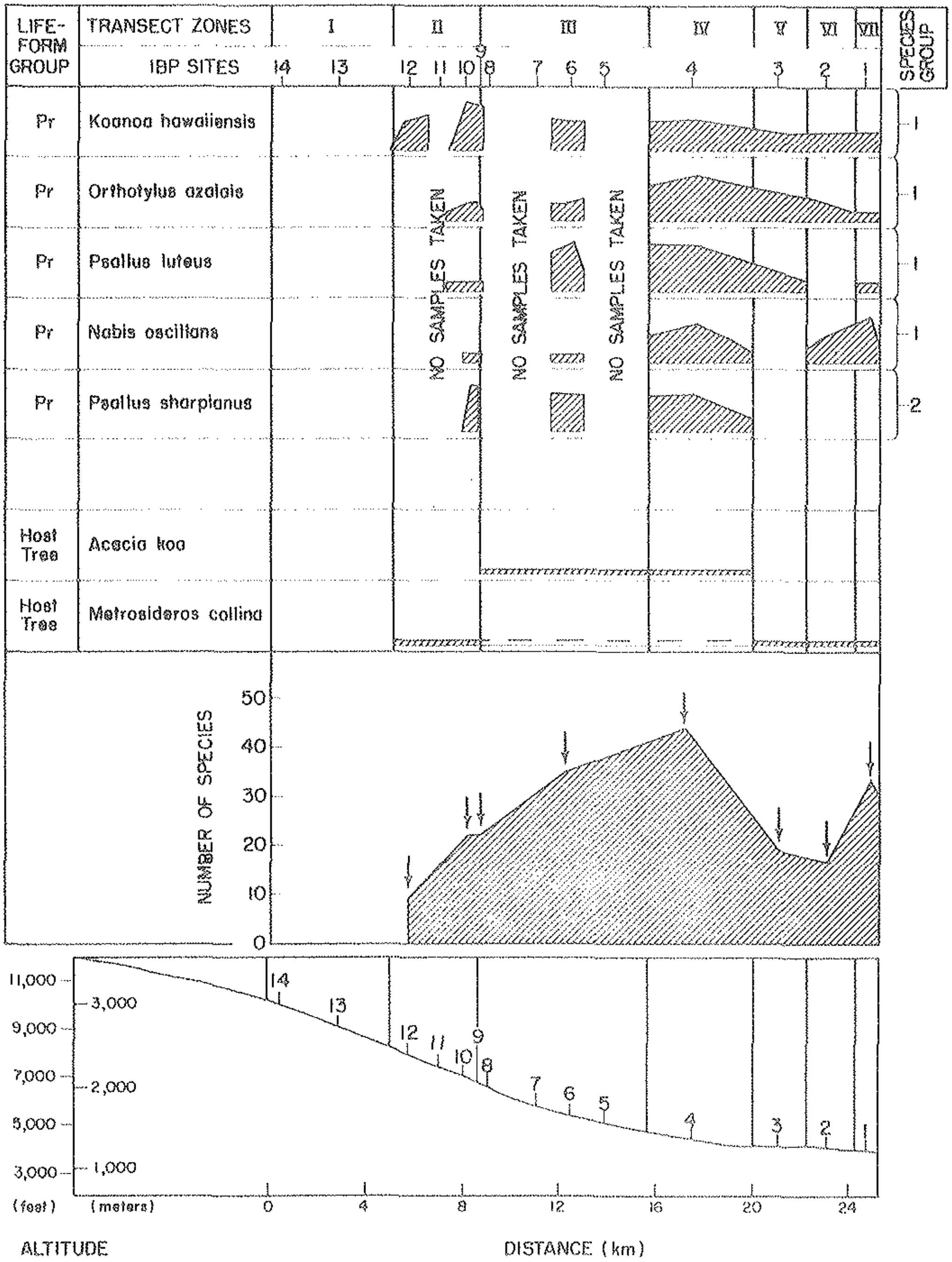

FIG. 6. Distribution of endemic, predaceous entomophagous arthropod species along the Mauna Loa Transect [Group numbers from 66/10 rule]. Lower diagram: number of grouped and ungrouped arthropod species on the Mauna Loa Transect [Arrows indicate sampling sites]. Abundance scale: 1 unit = mean of 1-2 specimens per sample, 2 units = mean of 3-4 specimens per sample, ... 10 units = mean greater than 513 specimens per sample.

However, on the latter host trees species diversity decreases markedly with altitude (from site 4 to 9) suggesting a climatic cause.

DISCUSSION AND CONCLUSIONS

The four arthropod distribution diagrams permit an evaluation of our data with species distribution hypotheses outlined in Synthesis Chapter 6 (TR 66), particularly with those of Whittaker (1970), which are stated in Section 6.6, p. 21 of TR 66.

Our data demonstrate two underlying themes with respect to Whittaker's hypotheses. Firstly, taxonomically closely related functional groups of endemic species, such as the fungus beetle of the genus *Cis* and the twig boring beetles of the genus *Proterhinus*, support Whittaker's *second* 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 two genera of native shrubs, *Styphelia* and *Vaccinium*. Each has two species (*S. tameiameiae* and *S. douglasii*, *V. peleanum* and *V. reticulatum*) which appear to exclude one another along fairly sharp boundaries.

Secondly, 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 *first* 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 three high-altitude species which make up Group 3 (or four species if the ungrouped lady beetle, *Hippodamia convergens*, is included), have closely parallel distributions. Group 1, comprised of native predators (see Fig. 5), 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. In other words, these associated species show their best quantitative development over their common distributional range.

There was more uniformity in the biomass between samples of *Acacia koa* than 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 three basic functional groups (phytophagous, fungivorous, and entomophagous) did discernable 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 forthcoming Synthesis Volume. 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 underlying 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 (2500 ft), i.e. below the Mauna Loa Transect, correlates with an increasing prevalence of ants, particularly the voracious big-headed ant (*Pheiole 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.

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