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D. H. Janzen, Michele Ataroff, M. Farinas, S. Reyes ...+4 more authors

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Changes in the Arthropod Community along an Elevational Transect in the Venezuelan Andes

D. H. Janzen

Department of Ecology and Evolutionary Biology, Division of Biology, University of Michigan, Ann Arbor, Michigan 48109, U.S.A.[1]

and

M. Ataroff, M. Fariñas, S. Reyes, N. Rincon, A. Soler, P. Soriano, and **M. Vera**

Ecologia Vegetal, Departamento de Biologia, Universidad de los Andes, Mérida, Venezuela

ABSTRACT

Sweep samples of insects at 200, 1600, 3550, and 3600 m elevation in secondary vegetation in the Venezuelan Andes near Mérida show that the greatest number of insect species and dry weight occurs at the intermediate elevation, that the species richness of Diptera and parasitic Hymenoptera is not as proportionately reduced by elevation as is the species richness of other insect groups, that at higher elevations there are a reduced number of species and an increasingly unequal distribution of the individuals among the species, and that large insects are much less abundant at high than low elevations. These results confirm trends first indicated in an earlier elevational transect of Costa Rican insects.

WE REPORT the results of sweep sampling the insect community at 3600 m, 3550 m, 1600 m, and 200 m elevation in the Venezuelan Andes near Mérida, and at 3380 m in Costa Rica. The study is a continuation of the examination of large scale heterogeneity in tropical insect community structure that was initiated by Janzen (1973a,b). Here, we ask how sweep samples of low secondary vegetation differ at elevations characterized by paramo, mid-elevation evergreen forest which is generally converted to coffee and sugar cane plantations in Venezuela, and lowland ("tierra caliente") evergreen forest, which is generally converted to cattle pasture and sugar cane in Venezuela.

METHODS

The 800 sweeps at each site were taken with the technique as described in the previous sweep sample study (Janzen 1973a). Eight hundred sweeps were taken with a 15 inch diameter muslin beating net and for most orders the catch was sorted as eight 100-sweep subsamples. The sweeping at 3600 m was done by A. Soler, at 3550 m by S. Reyes, at 1600 m by M. Vera, and at 200 m by N. Rincon. The senior author did all the sorting to species and has no reason to believe that his error term is different from that for the samples described in Janzen 1973a,b.

SAMPLE SITES

The sample sites are described here in some detail to facilitate comparison with later studies. The general reader may wish to skip over them to the Results section.

"PARAMO" (3600 m, fig. 1a).—The general area is known as Mucubaji and is in the Parque Nacional Sierra Nevada about 1.5 km south of the field station of the Universidad de los Andes. This field station is about 70 km east of Mérida, Venezuela on the road from Mérida to Barinas. The vegetation was a dense 40 acre patch of 0.5 to 1.5 m tall shrubs on a fairly steep west-facing slope. At least 50 percent of the vegetation contacted by the net was the shrub *Senecio pachipus* Greenm. and the swept remainder was made up of *Valeriana triplinervis* Briq., *Hypericum laricoides* Gleas., *H. laricifolium* Juess., *Vaccinium meridionale* SW, *Arcytophyllum caracasanum* Standl., *Polylepis sericea* Wedd., and *Hesperomeles pernettyoides* Wedd. There was a very low ground cover below the bushes, consisting of such plants as *Castilleja fissifolia* L.F., *Luzula gigantea* Desv., and *Agrostis hanveana* Hichc., but these were not contacted by the sweep net. The sloping site is on the east side of the upper end of a north-south valley containing the Rio Mucubaji; the east-facing west slope was a fairly dense stand of 3 to 5 m tall *Polylepis sericea* trees. The lower end of the sweep site is contiguous with the many acres of *Espeletia schultzii* Wedd. and *Hypericum laricoides* which contained the sweep site at 3550 m.

There were flowers on the *Hypericum* but there

[1] Present address: Department of Biology, University of Pennsylvania, Philadelphia, Pa. 19174, U.S.A.


were almost no seeds, flowers, or fruits on any of the other vegetation contacted with the sweep net.

At the beginning of the sweep (10:30 to 11:30 am, 24 October 1973), the air temperature was 10.5° C and at the end it was 11.0° C. There was a light breeze, the sky was clear with scudding clouds, and the vegetation was totally dry. There was light fog and rain at the site the day before and the day after. This site almost never has snow, and when it does, it melts within a day. The monthly maximum and minimum temperatures are about 10.4° C and -0.3° C for the coldest month (December) and 10.1° C and 3.4° C for the warmest month (June). The average rainfall (1967 to 1972) is 1200 mm per year.

There were no cattle in the area, but there was evidence of light grazing by horses in the flats below the sweep area. Owing to the very low rate of plant regeneration at these elevations (Janzen 1973c), even this small amount of grazing may have an effect on the vegetation, but there is no way at presenr to determine how much. The vegetation is indigenous and has not been disturbed by fire or cattle for at least ten years and probably much longer. This vegetation is called "paramo shrub" throughout much of the higher elevations of South America.

"PARAMO" (3550 m, fig. 1b).—The site is flat and bordered by meanders of the Rio Mucubaji. It is at the mouth of the broad valley whose head contains the 3600 m sweep site. It is about 200 m south and 200 m west of the field station building. The vegegation swept was a dense 40 to 60 acre stand of 0.4 to 1.5 m tall *Espeletia schultzii* with *Poa trachyphylla* Pilg., *Calamagrostis effusa* Steud., *Senecio formosus* H.B.K., *Hypericum laricoides* occasionally contacted by the sweep net. At least 80 percent of the vegetation hit by the net was the flower stalks and leaves of *E. schultzii.* Below the level of the sweep net and only rarely contacted by it, if at all, were *Arenaria venezuelana* Briq., *Halenia viridis* Gilg., *Bidens humilis* H.B.K., *Hypericum brathys* SM, *Rumex acetocella* L., *Apium leptophyllum* F. Muell., *Geranium chamaense* Pitt., *Aciachne pulvinata* Benth., *Hinterhubera lanuginosa* Cuatr. et Arist., *Sisyrinchium bogotense* H.B.K., *Gnaphallium paramorum* Blak., *Bartsia laniflora* Benth., *Hypochoeris setosus* Rusb., *Gentiana nevadensis* Gilg., *Lobelia tenera* H.B.K., *Eryngium humile* Cav., *Bromus pitensis* H.B.K., *Castilleja fissifolia* L.F., and *Lupinus* sp. The site was chosen for the dominance by *E. schultzii* which was in full flower, for October-November is the main flowering season. However, from the standpoint of the insect community this is probably not significant, since the flowers seem to produce no nectar and their pollen does not appear to be collected by the very few bumblebees (*Bombus* spp.) present. The absence of a regular pollen collector on the immense number of flowers is a hint that the dense stands of *E. schultzii* are of recent occurrence and we predict that the plant is usually self-pollinated. *Hypericum laricoides, Senecio formosus*, and most of the other plants described as being in this site were also in flower.

At the time of the sweep (9:45 to 11:20 am, 17 October 1973) the weather conditions were identical to those described for the 3600 m site. The relative humidity was 76 percent. The vegetation swept was completely dry, though at ground level there was beaded moisture on some foliage.

There are no cattle allowed in the area, but there was evidence of light grazing by horses in the vegetation adjacent to the *E. schultzii* patch. This vegetation is regarded as "climax" vegetation by most local biologists, and it certainly is not the product of disturbance during the past 25 years and probably much longer. This vegetation is commonly called "paramo" in high elevation South America.

"PARAMO" (3380 m, Cerro Asuncion, Costa Rica).—This site is across the Pan-American highway from the Cerro 3340 m sweep site described by Janzen (1973a). The main difference between the two sites is that the Cerro 3340 m site has a lower proportion of *Chusquea.* The 800 sweeps were taken as a class project (Fundamentals of Tropical Biology, Organization for Tropical Studies) by R. Root, D. Weigmann, R. Lande, D. Moriarty, M. Friedman, and C. Jones on 20 July 1973, which is well into the rainy season. This timing contrasts with the dry season sweep sample for Cerro 3340 m previously described by Janzen (1973a). The sample was taken between 9:00 and 10:00 am, at a time when the mist/fog had lifted enough such that the vegetation was dry, but as is usual during the rainy season at this site, it rained all the previous day, the afternoon of the sweep day, and most of the next day. The air temperature was 11° C at the time of the sweep. The site is subject to very light cattle and horse

FIGURE 1. Upper.—The sweep site at 3600 m elevation. The area swept is the shrubby vegetation between the rocks in the upper middle of the photograph down to the tree and ridge in the lower middle of the photograph. The light-colored vegetation in the upper left and along the left-hand side of the photograph is a dense stand of *Espeletia schultzii* much like that in the lower figure. Lower.—The sweep sample site at 3550 m elevation. Most of the taller vegetation is *Espeletia schultzii* but there is one bush of *Hypericum laricoides* in the lower foreground.

grazing, and is probably burned at about 10 to 20 year intervals (see Janzen 1973c).

MID-ELEVATION EVERGREEN FOREST (Andes 1600 m, fig. 2a).—The site is locally known as the Potrero de Enrique Carillo and it is on the south side of careterra El Arenal and 0.8 km from the bridge over the Rio Chama near the intersection of the El Arenal road with the Trasandina highway 6 km east of Mérida. It is on old river terraces at the base of the hills rising to 4500 m in the Sierra Nevada. It is about 1 km downhill from apparently undisturbed montane forest. There are fields of sugar cane and truck crops in the area. The site is truly an old field ("barbecho"). The vegetation swept was a lightly grazed 80 acre horse pasture made up of herbaceous and woody vegetation 0.3 to 1 m tall regenerating on land that had once been a coffee plantation; scattered 30 m tall *Erythrina* shade trees were still present. The site is on a slightly north-facing slope. The vegetation was highly mixed on a large and small scale. At least the following plants were present and tall enough to be contacted by the sweep net: *Stachytarpheta, Thunbergia alata, Lantana camara,* and 2 other species of Verbenaceae; *Eupatorium, Taraxacum,* and 4 other species of Compositae; *Borreria* (Sterculiaceae); 2 species of Labiatae; *Sida* (2 spp.), and 1 other species of Malvaceae; 4 species of Solanaceae; 2 species of *Psidium, Eugenia* and 1 other species of Myrtaceae; *Commelina* (Commelinaceae); *Briophyllum* (Crassulaceae); *Castilleja* (Scrophulariaceae); *Jatropha, Ricinus,* and 1 other species of Euphorbiaceae; *Piper* (2 spp., Piperaceae); *Crotalaria* and 1 other species of Leguminosae; *Miconia* (Melastomataceae); *Coffea* (Rubiaceae); *Rubus* (Rosaceae); *Asclepias* (Asclepiadaceae); 2 species of grass, 1 species of sedge, 2 species of ferns and 3 unidentified species (47 species).

At least half of the plant species listed for this site had flowers on them, but no flowering species was common enough to give the site the aspect of being a "field full of flowers."

At the time of the sweep (9:30 to 11:45 pm, 19 October 1973) there was light dew on some of the lower vegetation. The sky was clear with scattered clouds and the air temperature was 21° C (66% RH). The monthly maximum and minimum temperatures, based on weather records from Fuerza Aerea Venezolana, Aeropuerto Merida, are about 23.0° C and 14.0° C respectively for the coldest month and 24.3° C and 15.3° C for the warmest month (March). The time of the sweeps is regarded as the wet season. The average annual rainfall (1921 to 1972) is 1722 mm. This site never has snow or freezing weather.

LOW ELEVATION EVERGREEN FOREST (Andes 200 m, fig. 2b).—The site is owned by Don Miguel and is about 1 km north of the village of Mucujepe, which is about 10 miles northeast of El Vigia on the El Vigia-Caño Zancudo road, Estado de Mérida. The general area was once covered with well-developed evergreen rainforest but is now converted almost entirely to pasture, sugar cane, and truck crops. It is about 3 km from the foothills of the Andes, and between them and Lake Maracaibo. The vegetation swept was a dense stand of 0.4 to 1.5 m tall herbaceous and woody regeneration ("barbecho") following use of the site for yuca (*Manihot*) cultivation; a dense stand of yuca bordered two sides of the sweep area and a sugar cane field and dense living fence bordered the third side. The vegetation type swept occupies about 20 acres. The site is flat ground. The vegetation was highly mixed in species and height. At least the following plants were present and tall enough to be contacted by the sweep net: *Piper* (2 spp.); *Sida* (2 spp.); *Manihot, Hura* and 2 other Euphorbiaceae; *Musa; Iresine*; 2 species of Malpighiaceae; *Commelina*; 1 species of Cucurbitaceae; *Malvaviscus*; *Stachytarpheta, Lantana* (2 spp.); *Waltheria*; 2 species of Asclepiadaceae; *Lochocarpus, Indigofera, Cassia* (2 spp.), *Gliricidia* and 3 other Leguminosae; 1 species of Acanthaceae; 1 species of Convolvulaceae; *Bursera*; *Solanum*; 2 species of Myrtaceae; *Guazuma*; 1 species of Rutaceae; *Spondias*; *Cuphea*; 2 species of Compositae; 1 species of grass; 1 species of sedge and 2 undetermined species (44 species). About one-quarter of the plant species listed had flowers on them, and no flowering species was common enough to give the field the appearance of being massively in flower. There was no sign of livestock in the field.

At the time of the sweep (10:00 to 11:00 am, 25 October 1973) the sky was clear, there was a light breeze, and there was no moisture on the vegetation. The air temperature ranged from 28° C at the beginning to 29° C at the end of the sample. The monthly maximum and minimum temperatures, based on weather records from Estaciones MOP-CLIMA, for the coldest month (January) are 26.0°

FIGURE 2. Upper.—The sweep sample site at 200 m elevation. Dark vegetation in the background is a 5-meter wide strip of trees. Lower.—The 1600 m elevation sweep sample site. Most of the area swept was past these trees on the right and in an area that has no trees overhead. These large trees are scattered *Erythrina* left after coffee had been removed from the site.

C and 16.4° C respectively and for the warmest month (October) are 34.5° C and 23.9° C. This site never has snow or freezing weather. The average annual rainfall is 1823 mm (1946 to 1972) and October is regarded as the wet season.

RESULTS

NUMBER OF SPECIES.—All three high-elevation samples have less than a quarter of the number of species found in the mid- and low-elevation samples (table 1, fig. 3). As found in a previous Costa Rican elevational transect (Janzen 1973a,b), the mid-elevation sample is richer in species than the low-elevation sample (540 as opposed to 449 species). However, the previous Costa Rican samples were from primary forest understory rather than secondary vegetation.

TABLE 1. *Species richness distribution among insect groups in four Venezuelan and one Costa Rican sweep samples.*

	Number of Species				
	Venezuelan Andes				Costa Rica, Cerro
	200 m	1600 m	3550 m	3600 m	3380 m
Adult					
Coleoptera	86	91	7	7	11
Hemiptera	44	43	3	4	0
Homoptera[a]	46	52	1	10	6
Orthoptera	6	13	1	1	0
Diptera	129	181	36	62	20
Lepidoptera	13	29	2	2	1
Hymenoptera					
Ants	13	13	0	0	0
Bees & wasps	15	19	2	1	0
Parasitic Hymenoptera	95	96	27	22	10
Neuroptera	2	3	0	0	0
	449	540	79	109	48

[a] Excluding aphids.

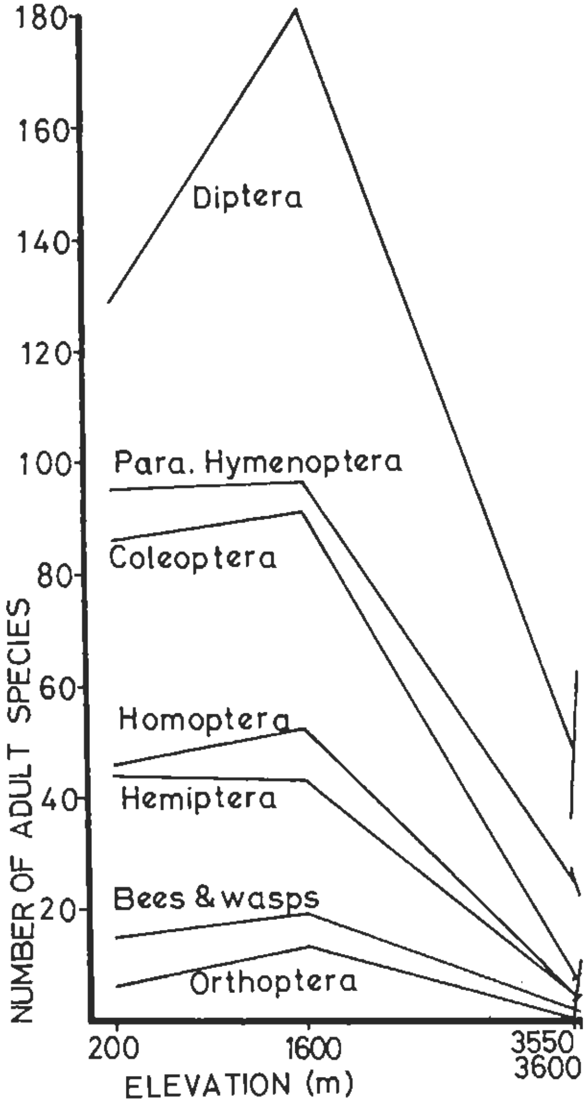

FIGURE 3. Distribution of species of adult insects with elevation at four Venezuelan sites. The right-hand end of the graphs joins the midpoint of the range of values for the two high-elevation sites.

Diptera display the greatest range of numbers of species between the two high-elevation Venezuelan samples (fig. 3) and they are the most species-rich order at all elevations (table 1). Diptera and parasitic Hymenoptera are notable for being the two groups whose species-richness is proportionately least reduced by high-elevation conditions (table 1). Conversely, in agreement with the previous Costa Rican elevational transect (Janzen 1973b), ant species-richness declined to zero at the high-elevation Venezuelan sites (table 1).

SPECIES DIVERSITY.—Owing to the dubious significance of inter-habitat differences in H′ (species diversity) indices (De Benedictus 1973), we are reluctant to develop their analysis; however, for workers who do believe that they have value we include them here. The H′ (base 2) values for adult Coleoptera, Hemiptera, Homoptera, Diptera, parasitic Hymenoptera, and these five groups pooled are, respectively, 3600 m: 1.63, 1.03, 0.22, 3.30, 2.71, and 1.83; 3550 m: 0.78, 1.10, 0.00, 2.51, 2.70, and 2.82; 1600 m: 3.47, 2.86, 3.00, 3.85, 4.19, and 4.98; and 200 m: 3.63, 3.11, 2.76, 3.36, 4.06, and 4.83. The pattern displayed by these H′ values does not conflict in any dramatic way with the pattern of the number of species over this elevational transect (table 1, fig. 3).

TABLE 2. *Distribution of individuals among arthropod groups in four Venezuelan and one Costa Rican sweep samples.*

	Number of Individuals				
	Venezuelan Andes				Costa Rica, Cerro
	200 m	1600 m	3550 m	3600 m	3380 m
Adult					
Coleoptera	531	542	350	30	161
Hemiptera	333	418	3	22	0
Homoptera[a]	457	329	1	848	24
Orthoptera	13	30	2	2	0
Diptera	1157	1176	416	208	124
Lepidoptera	34	172	27	2	1
Hymenoptera					
Ants	331	128	0	0	0
Bees & wasps	58	37	3	2	0
Parasitic Hymenoptera	289	224	97	67	13
Neuroptera	7	4	0	0	0
Subtotal	3210	3060	899	1181	323
Immature					
Hemiptera	57	177	1	5	0
Homoptera[a]	60	60	0	3	40
Aphids	6	47	8	7	1
Orthoptera	49	207	7	2	0
Lepidoptera	34	27	27	7	1
Psocoptera[b]	0	0	3	4	0
Thysanoptera[b]	8	11	1	5	34
Neuroptera	1	0	0	1	0
Subtotal	215	529	47	34	76
Spiders	109	259	22	27	32
Grand total	3534	3848	968	1242	431

[a] Excluding aphids.
[b] Includes adults and immatures.

NUMBER OF INDIVIDUALS.—All three high-elevation samples have less than one-third the number of individual arthropods that were found in the mid- and low-elevation samples (table 2). Additionally, the high-elevation samples had a greater proportion of their individuals represented by only a few species than was the case at lower elevations. For example, of the 350 beetles in the 3550 m sample, 265 were a curculionid apparently feeding in the abundant inflorescences of *Espeletia schultzii*, while the other six species were represented by 55, 24, 3, 1, 1, and 1 individuals. The most abundant beetle at 1600 m had only 95 individuals, but the next six most common had 83, 39, 34, 27, 14, and 11 individuals. At 200 m elevation, the most common beetle had 65 individuals, and the next six most common had 58, 46, 27, 16, 16, and 15 individuals. Of the 848 Homoptera in the 3600 m sample, 818 belonged to one species of Psyllidae. At 1600 m elevation, the most abundant Homopteran was a cicadellid with 68 individuals. At 200 m elevation, the most abundant Homopteran was a membracid with 146 individuals. Of the 161 beetles in the Cerro 3380 m sample, 116 were a hispine chrysomelid that feeds on the very common *Chusquea* at the site.

As with the number of species, the number of individuals at the mid-elevation site was slightly larger than at the low-elevation site (table 2), rather than smaller, as would be expected if there were a linear decrease in harvestable productivity from low to high elevation. Likewise, the proportional distribution of adult insects among the more common orders is very similar in the low- and mid-elevation sites. The ants and Lepidoptera are the notable exceptions to this statement. The discrepancy in numbers of individual ants may be a sample error due to the patchy nature of ants on foliage; however, in view of the total absence of ants at high elevations, it is in the direction expected. The two mid-elevation secondary vegetation samples in Janzen 1973b had much lower numbers of ants than either of the lowland rainforest secondary succession samples. The higher numbers of Lepidoptera in the mid-elevation site were due to large numbers of moths, a phenomenon also conspicuous at the San Vito Costa Rican mid-elevation site (Janzen 1973b).

The largest numbers of spiders were associated with the largest numbers of prey (table 2) and with the largest dry weight of prey (table 3). However, spider numbers are poorly correlated with numbers of potential prey since there are 32 prey items per spider in the 200 m sample and only 15 per spider in the 1600 m sample. At the two Venezuelan high-elevation sites there are 44 and 46 potential prey items per spider, but in the Costa Rican Cerro 3380 m sample there are only 14 per spider. There were 42 per spider in the 3340 m Costa Rican sample (Janzen 1973b). Parasitic Hymenoptera are equally confusing. The 200 m and 1600 m samples have 12 and 17 potential prey items per adult parasitic hymenopteran. At 3550 and 3600 m the figures are 10 and 18. The Costa Rican 3380 sample has 33 and the Costa Rican 3340 sample (Janzen 1973b) has 38 potential prey items per adult parasitic hymenopteran.

There were more aphids in the four Venezuelan samples (table 2) than were encountered in all the mainland Costa Rican samples recorded in Janzen 1973b. However, the highest number, 47 in the 1600 m sample, was recorded at about the same elevation as the several that were seen in a Costa Rican sample. While aphids are very abundant in mid-latitude sweep samples of secondary vegetation (e.g. Janzen and Pond 1975), they did not increase dramatically at Venezuelan (or Costa Rican) high elevations. However, Psyllidae (*Trioza* sp., det. D. Hollis) were extraordinarily abundant in the 3600 m sample, just as they often are in mid-latitude samples (Janzen and Pond 1975), but there was only 1 Psyllidae in each of the 200 m and 1600 m samples.

DRY WEIGHT.—The dry weight of total arthropods (table 3) follows the same trend noted earlier for numbers of species and individuals. There is nearly twice as much dry weight of arthropods in the 1600 m sample as in the 200 m sample, and the high-elevation Venezuelan samples contained about one-twelfth as much as the mid-elevation sample. The dry weight at high elevations probably differs conspicuously from that lower down in respect to palatability as well as amount. While not quantified, a very substantial fraction of the individuals in the mid- and low-elevation samples were aposematic insects or their mimics. In the high-elevation samples, there were only five aposematic insects and no mimics. However, the 5 black and red bumblebees *(Bombus)* and 4 black, blue, and red adult acridid grasshoppers together constituted 48 percent and 43 percent of the total dry weight in the 3550 m and 3600 m samples.

Though the number of individual potential prey may not be closely related to the number of spiders, we might expect the dry weight of potential prey to be related. There are 0.06, 0.05, 0.05, and 0.03 gms of potential prey dry weight per spider in the 200 m, 1600 m, 3550 m, and 3600 m samples, respectively. The comparable figures for parasitic Hymenoptera are 0.02, 0.05, 0.01, and 0.01 gms.

SIZE OF INDIVIDUALS.—The overall size distribution of arthropods (fig. 5) holds few conspicuous surprises. The average arthropod length is 3.45, 4.05, 3.45 and 2.94 mm for the 200 m, 1600 m, 3550 m, and 3600 m samples. The difference in the two high-elevation samples probably has no biological meaning as it is the outcome of the commonest species being 3 mm long in the 3600 m sample. The difference between the 200 m and 1600 m samples is primarily due to the presence of many more small flies in the former sample.

Perhaps the most interesting difference between the high elevation and the lower samples is in the length of the upper tail of the size distribution. At 3550 m and 3600 m, there were only 6 and 4 individuals greater than 10 mm in length (0.63 and 0.32%, respectively). In the 1600 m sample, there were 153 such arthropods (3.98%), and in the 200 m sample, 104 (2.94%). These differences in sizes

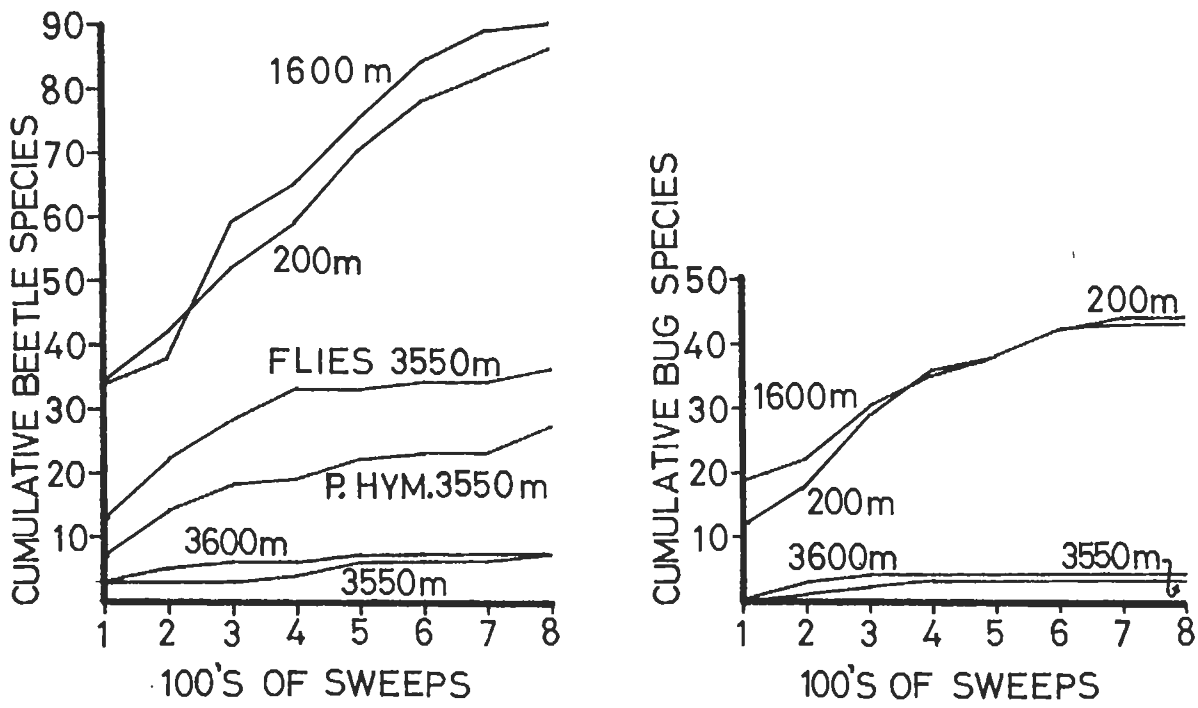

FIGURE 4. Cumulative numbers of adult beetle, fly and parasitic Hymenoptera species (left figure) and overall insect species (right figure) at the various sites.

should be of importance to the insectivores in the habitats sampled, but we know nothing of them.

DISCUSSION

The results of these sweep samples serve largely to confirm the patterns displayed in an elevational transect taken earlier in Costa Rica (Janzen 1973b). However, further discussion of the possible underlying processes is in order.

There are two ways to examine the possibility that the large number of species in the mid-elevation sample is merely a sample error. First, we may ask if it is a consequence of just one taxonomic group being extraordinarily species-rich at 1600 m elevation. From the elevational trends for each species in figure 3, it is clear that all the major orders of insects are contributing to the mid-elevation increase. Furthermore, the taxonomic universality of the trend suggests that the causal factor is capable of influencing several trophic levels. Second, we may ask

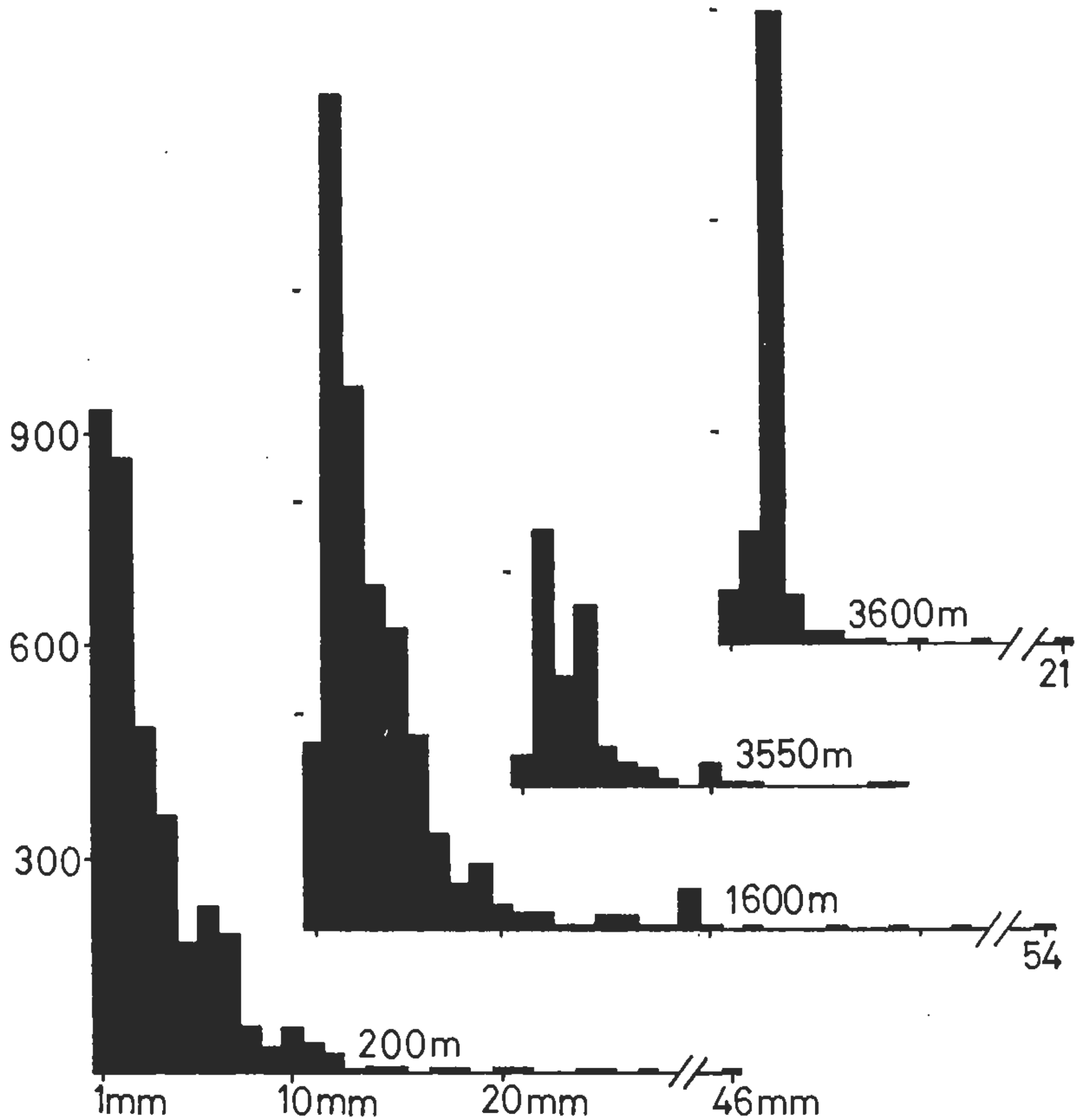

FIGURE 5. Distribution of body-lengths of adult and immature insects at four points along a transect from 200 to 3600 m elevation.

TABLE 3. *Dry weight distribution of arthropods among four Venezuelan sweep samples.*

	200 m	1600 m	3550 m	3600 m
	Dry Weight (gms)			
Adult				
Coleoptera	0.99	1.66	0.15	0.03
Hemiptera	1.31	1.34	0.006	0.02
Homoptera[a]	1.55	0.45	0.0006	0.25
Orthoptera	0.37	1.04	0.11	0.18
Diptera	0.29	0.64	0.24	0.09
Lepidoptera	0.20	2.45	0.03	0.002
Hymenoptera				
Ants	0.17	0.11	—	—
Bees & wasps	0.15	0.12	0.40	0.18
Parasitic Hymenoptera	0.07	0.14	0.03	0.03
Neuroptera	0.01	0.01	—	—
Subtotal	5.11	7.96	0.9666	0.782
Immature				
Hemiptera	0.13	0.46	0.002	0.0006
Homoptera[a]	0.09	0.03	—	0.002
Aphids	0.002	0.01	0.003	0.003
Orthoptera	0.25	1.89	0.01	0.002
Lepidoptera	0.25	0.25	0.04	0.02
Psocoptera[b]	—	—	0.001	0.0009
Thysanoptera[b]	0.006	0.006	0.0005	0.0008
Neuroptera	0.002	—	—	0.002
Subtotal	0.730	2.646	0.0565	0.0313
Total Insects	5.840	10.606	1.0231	0.8133
Spiders	0.23	1.12	0.05	0.03
Total Arthropods	6.070	11.726	1.0731	0.8433

[a] Excluding aphids.
[b] Contains adults and immatures.

if 800 sweeps is enough for the "species-sweep" curve to have leveled off. If the species-sweep curve has leveled off for 1600 m but is still rising in the 200 m sample, this could explain the apparent anomaly. Figure 4 shows that for adult beetles and bugs the species-sweep curves are behaving almost identically for the 200 and 1600 m elevation samples. We conclude, therefore, that the mid-elevation increase in insect species richness is probably not a simple sample error. We have no improvement to add to the causal explanation offered by Janzen (1973b) which postulates that the mid-elevation bulge in herbivore, and dependent carnivore, species-richness is due to the highest net plant productivity at the intermediate elevations in the tropics. It was further postulated that the increased net productivity at this elevation is due to the plants burning up less of their daily photosynthate in nocturnal respiration because of the cooler night-time temperatures than in the hot lowlands. The species-richness of herbivores was expected to respond positively to this increase in net productivity, because plants with higher net productivity should have more parts (seeds, flowers, shoot tips, etc.) with sufficient biomass or turnover rate to support host- and part-specific species of insects.

Why is the dipteran species-richness proportionately much less depressed at Venezuelan high elevations than insects in general? One factor may well be that Diptera, whose larvae and adults are comparatively defenseless, are exposed to lower predation at high-elevation sites. High-elevation sites have an overall low biomass (and, we suspect, turnover rate) of arthropods (table 3) and attendant vertebrate and invertebrate predators, much as under arctic conditions. In addition, at least half of the Diptera in these samples are not directly dependent on living macrophytes for food (e.g. chironomic detritus feeders). Such animals may not be as severely affected by a reduction in net productivity at high elevations as the direct phytophages (Coleoptera, Hemiptera, Homoptera, Lepidoptera, Orthoptera) would be.

The parasitic Hymenoptera species-richness was also not so severely depressed as that of the phytophagous groups at high elevation. We suggest that this is probably due to the following phenomena. At high elevations, those prey species that do persist tend to become quite abundant. For example, a single species of microlepidoptera larva was present in many of the very common inflorescences of *Espeletia schultzii* (24 of the 27 Lepidoptera larvae in the 3550 m sample, table 2). Such common prey species should support relatively many more species of parasitic Hymenoptera than the same amount of biomass subdivided into very many prey species, since many of the prey species would have too small a population to sustain a parasite. For the same reason, mid-latitude parasitic Hymenoptera species-richness should not be depressed as severely as that of phytophageous species over an equator-pole latitudinal transect, and this is in fact the case (Janzen and Pond 1975).

Our results would appear to be of importance to theoretical examinations of tropical agriculture, but we urge extreme care in their use in specific cases. While species-richness of insects may be unexpectedly high at intermediate elevations, it does not follow that a specific crop may have more species of pests at intermediate elevations. For example, there was a severe drop in species-richness from forest understory to secondary vegetation at the mid-elevation Costa Rican site (Janzen 1973b); two forest samples had 969 and 767 species of adult insects while the secondary succession site only a few meters away had only 409 species. Equally, the higher arthropod dry weight in the Venezuelan mid-elevation sample may not necessarily mean greater pest pressure on a crop at that elevation; the hypothesized greater harvestable productivity for insects may mean likewise a greater harvestable productivity for man, especially if the insect community has been severely disrupted by cropping schemes.

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