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6 • Determinants of local diversity in phytophagous insects: host specialists in tropical environments

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This symposium illustrates that insect diversity may be viewed from various taxonomic and geographical perspectives. An aspect of insect diversity receiving considerable attention recently involves the study of taxonomically heterogeneous faunas delimited by sampling methods (see Taylor, this symposium, Chapter 1), by host plant taxa (Strong, 1974; Lawton, Chapter 7), or by geographical boundaries (Simberloff, Chapter 9 and references therein). The primary goal of all such studies has been to explain observed variation in overall insect faunal diversity between different traps, plant species, or islands.

Simberloff (this volume) has elegantly shown that rates of build-up, turnover and equilibrium numbers of species on small mangrove islands are predicted by island biogeography theory. Strong (1974) likewise, has rekindled interest in the relationship, first explored by Southwood (1961), that area occupied by a plant taxon predicts the size of the total insect fauna associated with it over its range.

In this paper we are concerned with explaining patterns of within-habitat (or point) diversity in host-specialist insects. We further limit our scope by emphasising recent work in the neotropics with special reference to our own studies of neotropical butterfly communities. Unfortunately, at this taxonomic and geographic level of resolution, published host records, so useful to broad scale comparisons (e.g. Strong, 1974) are worthless. Most publications giving host records for butterflies and other specialist insects fail to specify precise locality or other potential hosts and herbivores in sympatry. Gilbert and Singer (1975) and Gilbert (1978) provide several examples of extreme discrepancies between the local versus the cumulative regional pattern of host usage by particular butterfly species. Obviously, to distinguish among hypotheses which explain variation in diversity between sites we must know details of interactions between herbivore and host plants locally.

It should be emphasised that the significant correlations between total herbivore diversity and host-plant range is probably not relevant to the very different problem which is of interest to us; i.e., the local diversity of specialist or coevolved herbivores. Gilbert and Singer (1975) provide a general discussion of the various niche dimensions which appear relevant to explaining the diversity of coexisting species of butterflies, and Gilbert (1978) discusses the extension of equilibrium biogeography to the analysis of host plant 'islands' with special reference to butterflies.

While 'small-scale' island biogeography may explain the diversity of some insect groups on local patches, this is undoubtedly not the case with butterflies. Since deliberate egg

placement is the only 'parental care' which these insects exhibit, many cues other than patch size are used in assessing host plant. Females of some *Euptychia* butterflies actually prefer small isolated patches of host plant for oviposition (Singer, personal communication), possibly as a predator escape tactic. Female *Heliconius*, which oviposit on shoots of *Passiflora* vines, can revisit the same patches daily for several months (Gilbert, 1975; Benson *et al*, 1976).

As we have been primarily involved with the behavioral ecology and population biology of neotropical heliconiine butterflies, a group confined to, and coevolved with, the Passifloraceae (Benson *et al*, 1976), we automatically approach community-level problems in a somewhat reductionist fashion. We are specifically concerned with the diversity within local host-plant guilds over areas ideally defined by the size of local heliconiine demes. Some explanations of community diversity in studies of this kind are inspired by direct observation (sometimes involving experiments) of individual insects interacting with their resources, predators, and competitors.

We therefore attempt to account for the host-specialist fraction of phytophagous insect diversity by dissecting coevolved subsystems in which the relevant interactions take place (Gilbert, 1977). Admittedly we do not know what fraction of overall within-habitat diversity is accounted for by specialists, but the increased intensity of biotic selection in tropical regions should shift the balance toward monophagous species.

We know of few analyses of host-specialist tropical insects which would provide adequate information on geographical patterns of local diversity as well as all the necessary ecological information required to explain them. An interesting example from the temperate zone is the study by Opler (1974) on the leaf-mining microlepidoptera of oak in California. According to Opler, *within-habitat diversity* of oak leaf-miners is predicted by the overall range of the host. No similar tropical study to our knowledge leads to this conclusion. Admittedly, none involve leaf-mining lepidoptera.

STUDIES OF TROPICAL HOST SPECIALISTS

HISPINE CHRYSOMELIDS ON ZINGIBERALES

Strong (1977*a*, 1977*b*) has conducted population and community studies of hispine beetles which feed on the Zingiberales. In addition to local studies at the Organization for Tropical Studies 'La Selva' site, Costa Rica, he has sampled several geographically separate habitats of Central America. Strong shows that widely distributed species of Zingiberales have more associated hispines over their range (because of geographical replacement of hispine species). However, the numbers of beetles coexisting locally depend on host size, abundance, and the species diversity of coevolved host families, but not the extent of host distribution outside of the sample area.

BEETLES ON TREE SEEDS

A detailed and long-term study of tropical host-specialist insects is that of Janzen (1977) on the seed-feeding beetles in Guanacaste Province, Costa Rica. Ninety-five beetle species have been identified from seeds of 83 tree species; of these, 73% of the bruchids ($N = 78$) were restricted to a single host and 100% of cerambicids and curculionids ($N = 17$) were on only one host. The maximum number of hosts used by a single bruchid species was only six. In addition, the number of bruchids coexisting on a host ranged from one to three.

Janzen's results rule out both local and regional distribution as factors involved in the number of beetles per tree species. Janzen believes that chemical diversity in tree seeds has been generated by coevolutionary interaction with the beetles. Reciprocally, chemical diversity of these resources leads to a diversity of digestive specialisations and speciation by the beetles. Thus, the number of tree species determine the number of beetles. Ehrlich and Raven (1965) proposed just this kind of feedback system for the generation of tropical insect and plant diversity. It may be argued that Janzen's view of community structure is biassed by his work on such extreme specialists, and that they are specialised partly because they feed internally. However, at least one group of foliage feeders illustrates a similar pattern.

ITHOMIINE BUTTERFLIES ON SOLANACEAE

Ithomiines (Nymphalidae) are conspicuous neotropical insects most species of which specialise on the Solanaceae. A preliminary study in Costa Rica by Gilbert (1969) suggested a one-to-one, host-plant species to butterfly species pattern. More recently Drummond (1976) has completed a detailed analysis of a local ithomiine community in Ecuador. He found 53 ithomiines co-occurring with 44 potential host plants. Of 27 species whose life histories were established, 81% ($N = 22$) were restricted to a single host plant while 19% ($N = 5$) used two to five hosts. Conversely, 85% ($N = 28$) of host plants known to be utilised supported only one ithomine species, the remaining 15% ($N = 5$) supporting two to three species. Even without knowing the ranges of all host plants we can say with certainty that plant geographical distribution does not account for variance in numbers of ithomiines per host within habitats. Moreover, there is no relationship between local abundance of hosts and the number of butterfly species associated with them. As with Janzen's beetles there seems to be almost no opportunity for larval competition on host plants, presumably an outcome of the fact that observed resource partitioning is generated by coevolutionary interaction of host chemical defense and parasite digestive specialisation (see Gilbert and Singer, 1975, for a discussion of this aspect of butterfly community interactions).

Gilbert (1969) noted a positive relationship between local abundances of individual ithomiine species and the corresponding host-plant species. This seemed remarkable given the fact that heavy parasitoid and predator mortality of early stages keeps ithomiines well below food limitation (also noted by Drummond, 1976). Gilbert (1969) suggested an 'indirect food limitation hypothesis' to account for this pattern. Since the effective density of larvae available to foraging ants and wasps is probably measured in number of larvae per unit of leaf area, species using an abundant host should be expected to reach greater absolute numbers before reaching densities which elicit functional response by resident hymenopteran predators and parasitoids. Rare ithomiines may have similar larval densities measured in terms of leaf area but, having rare host plants, they are limited well before host leaves are depleted or a host becomes difficult for females to locate. For example *Pteronymia notilla* is consistently present but in low density (less than 5% of any ithomiine sample) at Finca Las Cruces near San Vito, Costa Rica. The host plant, a forest-understory shrub, *Solanum brenesii* is extremely rare and scattered. Only one small individual of this host plant has been located in the study site (by following ovipositing *P. notilla*). Observations in 1969, 1970, 1971, and 1977 by one of us (L.E.G.) indicate low density persistence of the butterfly, relatively little change in the size or leaf area of the plant, few *P. notilla* eggs or larvae present at each observation period, and evidence of some larval damage on most older leaves (which persist for years).

This example illustrates a pattern of interaction consistent with the 'indirect host limitation' idea. The plant occurs in scattered, small patches but is consistently located by its specialist herbivore. The plant is consistently damaged but no evidence of defoliation has been seen, and it is clear that the butterfly is generally not converting leaves into butterfly as fast as amount of host would allow. It thus remains at a lower relative abundance than an ithomiine specialised on a locally more common host. Strong (1977*b*) has suggested a similar process to account for correspondence between abundances of hispines and abundances of their specific hosts.

It is relevant to mention that ithomiine species richness, equitability, and overall abundance increases as one proceeds from flat lowland to middle elevation montane habitats. Gilbert (1969) suggested that in steep terrain, abundant stream-cuts and land-slips maintain a greater fraction of the available habitat in early successional stages. Solanaceae thrive well along forest edges and in early succession, and are themselves more diverse and on average more abundant than in less disturbed forest. Janzen (1973*b*) noting increases in beetle and moth density at mid-elevations, suggested that plants there are able to increase net productivity because cool nights reduce respiratory losses. Thus without changing number of plant species or climatic predictability, each plant represents a larger resource base allowing more specialists to coexist per plant. Scott (1976) provides good evidence for such a process affecting diversities of the litter herpetofaunas in tropical regions. However, available data on ithomiines from mid-elevation Costa Rica (Gilbert, unpublished; Haber, unpublished) support the hypothesis of increased host diversity rather than that of increased energy available per plant, since numbers of specialists per plant appear not to be different from lowland habitats. Study sites along elevational transects in several areas are required to verify this apparent trend.

SATYRINE BUTTERFLIES ON GRAMINEAE

Singer and Ehrlich (unpublished data) have studied local diversity and host utilisation by 14 species of *Euptychia* (Satyrinae) in Trinidad. Eleven (or 79%) were found to be polyphagous (within the Gramineae) while the remaining three (21%) were found to be host specialists either on sedges or grasses.

In marked contrast to the other examples discussed in this paper, *Euptychia* population and community structure is highly variable in space and time, even in areas such as Andrews Trace, Trinidad where *Heliconius ethilla* exhibits extreme numerical constancy (Ehrlich & Gilbert, 1973). In most *Euptychia* study sites, specifying numbers of host-plant species present does not predict which or how many *Euptychia* species will be present. A graph of numbers of host species against numbers of *Euptychia* species found (lumping several sampling periods) in 10 Trinidadian study sites (Singer & Ehrlich, unpublished data) would show all points on or below the 45 degree line. Thus no local area rich in host plants had fewer than one butterfly species per plant species. However, one of the richest sites for *Euptychia* (10 species) had only one grass species present and a total of four (40%) sites had only half as many host species as butterfly species.

In contrast, the occurrence in an area of a plant species used by a monophagous *Euptychia* practically assures that the butterfly will be found there. For example, in 12 instances in which such host plants were found among 10 study sites, the appropriate *Euptychia* species was found to co-occur 11 times. Thus, the component of *Euptychia* diversity due to the host-specialist species (an average of 15% of the diversity of any site) is, in effect, determined when the host plant survey is completed. A similar pattern was found

in Costa Rica where 79% ($N = 14$) of species studied were relatively polyphagous on grass species, and the remaining 21% ($N = 3$) were specialists on palm seedlings (one) and *Selaginella* (two) (Singer *et al*, 1971).

Singer's observations of numerous bizarre oviposition behavior patterns by *Euptychia* species (e.g., preferences by several species for the same isolated clump of grass over extended periods!) combined with the observation that *Euptychia* larvae have greater phenotypic diversity than do adults (the reverse of European satyrines) suggest that structure of the grass-feeding component of *Euptychia* communities may be affected much more by predation and unknown aspects of microsite heterogeneity than by direct competitive interaction (or coevolutionary interaction with host).

As species-rich *Euptychia* communities overlap in space and time with ithomiines, heliconiines, and hispine chrysomelids, they provide an interesting contrast and should be studied more intensively. Their distinct pattern of host utilisation at the species level may reflect a relative lack of chemical distinctiveness among grass species. This is also indicated by the lower incidence of species-specialists among grass-feeding, as opposed to Umbelliferae-feeding agromyzids (Price, 1977).

Further study may well show *Euptychia* communities to be structured along the lines of the stem boring guild studied by Rathcke (1976).

THE HELICONIINE-PASSIFLORACEAE SYSTEM

Heliconiine butterflies are conspicuous and constant components of neotropical butterfly communities. In any area they account for only about 3–7% of total butterfly diversity. Yet, even more than the similarly aposematic ithomiines, heliconiines are one of those conspicuous attributes of neotropical forests which invariably have caught the attention of tropical naturalists since H. W. Bates. Consequently, accumulated information on behavior (Gilbert, 1976), reproduction (Dunlap-Pianka *et al*, 1977), genetics (Turner, 1976), biogeography (Brown *et al*, 1974), systematics (Emsley, 1965; Brown, 1976), host relations (Benson *et al*, 1976), population biology (Ehrlich & Gilbert, 1973; Gilbert, 1975) and community ecology (Gilbert, 1977; Benson, 1978) of this group rivals that available for any group of insects.

All heliconiines are restricted in larval feeding to the family Passifloraceae, which contains one major New World genus, *Passiflora*, and several minor genera including *Tetrastylis, Dilkea,* and *Mitostemma*, which occasionally serve as hosts to heliconiines (Benson *et al*, 1976).

Since we have been studying the entire food web based on *Passiflora* (Gilbert, 1977), we know that flea beetles (e.g. *Altica, Disonycha, Monomacra, Strabala*) are the principal host specialists aside from the heliconiines which are significant herbivores of these plants. For particular *Passiflora* species coreid bugs of the genera *Anisocelis* and *Holymenia* can be important locally. Our data on flea beetle communities is less extensive than that for heliconiines, yet adequate beetle data exist from our primary study site (the O.T.S. 'La Selva' field station in Costa Rica) to allow useful comparisons between host specialists of rather distinct life histories which live on the same host-plant family.

PATTERNS OF HELICONIINE DIVERSITY

Of the 66 heliconiine species, up to 30 have been found in an area along the Rio Negro, Meta, Colombia (Brown, 1972), but this figure may involve some between-habitat

component. Local site diversity rarely exceeds 20 species and drops to eight in the northernmost semi-evergreen neotropical forests in Tamaulipas, Mexico (L.E.G., personal observation). Brown's (1972) remarkable data based on intensive daily sampling of butterfly faunas in numerous Brazilian localities reveal a high degree of consistency in the species richness of particular butterfly taxa from region to region within Brazil. This is particularly true of heliconiines in that they are represented by 12, 14, 16, 13, and 17 species respectively for five regions sampled in extra-Amazonian Brazil (see Brown's Table 1, p. 191). Region totals for heliconiines equal 60–81% of the 21 species available in all of extra-Amazonian Brazil. In contrast, riodinid butterflies with more local endemism are represented at a regional level by only 24–44% of the total of 350 species known to exist in extra-Amazonian Brazil.

A similar comparison may be made between local diversity and regional diversity. Brown's data show that cumulative sampling period totals of 15–40 days over a year or more at a locality typically reveal 80–100% of heliconiines known from the region. Over a period of years, the number of heliconiine counted daily samples are remarkably constant at locations such as Sumaré (Brown's (1972) Table 1), where 14 daily counts from 1967 to 1971 yielded from eight to 10 species of the total of 16 known from Sumaré. These data are superficially consistent with the hypothesis that eight to 10 species represents a dynamic balance between colonisation and extinction in the Sumaré study site. However, observations of single species populations (Ehrlich & Gilbert, 1973) and our experience in Trinidad and Central American localities suggest that such a pattern is more likely the outcome of the presence of six to eight constant, conspicuous species, plus six to seven species which, because of rarity, arboreal flight habits, or mimicry association are less likely to be 'counted' on a particular day, but have a constant probability of being counted. Finally there are likely to be two to four species which would not persist in the area if it were cut off from adjacent habitats (of a different elevation) from which they disperse at some regular flow rate.

If any collection data is to reflect some underlying reality about butterfly faunas, that of Brown should. However, the highly consistent patterns in space and time revealed in his samples of butterfly communities, heliconiines in particular, cannot be explained without further knowledge of the fine structure of these communities including ecological interactions among component species and their resources.

PATTERNS OF PASSIFLORACEAE DIVERSITY

In contrast to heliconiines, the Passifloraceae contain vastly more species in the neotropics than would ever be found in one locality. Killip (1938) describes about 350 *Passiflora* species and there may be as many as 500. General floristic surveys are of little value in estimating local species densities because few individuals and species of *Passiflora* are likely to be in flower at any given time and are thus not well sampled by botanists. Therefore we must rely on data from those areas where we and/or our colleagues have followed ovipositing heliconiines and have located most of the non-flowering *Passiflora* species. In a dozen or so sites intensively sampled by ourselves or Benson and Brown in South America, nowhere to our knowledge has the number of locally coexisting *Passiflora* species exceeded 15, and 10–12 is a more typical figure for moist to wet habitats favored by heliconiines.

In spite of the large number of species in the genus *Passiflora*, there are reasons to believe that the number to heliconiines may be much less. It may well be that *Passiflora* taxonomy, like that of *Heliconius* 80 years ago, contains many 'species' which will turn out to be racial

variants of widespread species. For example, what were about 70 'species' of silvaniform *Heliconius* in 1894, are now known to be about seven species (Brown, 1976). Also, a substantial fraction of *Passiflora* species occur at higher elevations of Central and South America so that they are not potential invaders of the mid to low elevation habitats occupied by most heliconiines. We can also eliminate the few dry-adapted and temperate zone species. Even so, it is reasonable to estimate that 100–150 *Passiflora* species exist which are potential colonisers of any moist neotropical habitat below 1500 meters. Yet the maximum number which locally coexist is consistently 10% or less of that number. The relationship of within habitat diversity of *Passiflora* to regional diversity is not adequately understood because local diversity is accurately known in so few cases. Since *Passiflora* diversity appears to be a major factor regulating heliconiine diversity at a local level (see below), it is crucial to learn more concerning the geographical ecology of the group.

LOCAL HERBIVORE DIVERSITY ON *PASSIFLORA* SPECIES

We have examined the heliconiine and flea beetle communities on nine species of Passifloraceae which occur at the La Selva field station in Costa Rica, and have used strictly heliconiine data from Trinidad, Costa Rica and Brazil summarised by Benson, 1978. Host records are obtained slowly and interactions between rare herbivores and rare plants are probably still to be made. However, the La Selva data represent our accumulated observations over a four year period and we feel confident that the major interactions of *Passiflora* species and the herbivore community are known. At least one of us has conducted field studies in Arima Valley, Trinidad, and/or Rincon, Costa Rica, and have supplemented Benson's data for both areas in constructing graphs for this paper. The data collected by Benson and Brown near Rio de Janeiro are likely to represent a nearly complete picture of *Passiflora*-heliconiine interaction there, as their studies were specifically directed to host utilisation by heliconiines.

We ask the following question: How do geographical distributions, local abundance, plant size, and successional status of a *Passiflora* species correlate with the number of heliconiine and/or flea beetles which will be associated with it?

Geographical distribution

It can be hypothesised that plant species with larger distributions are larger targets for evolutionary colonisation by host specialists and that these subsequently spread throughout the total range of the plant. It could be predicted then, that local diversity on a host would be an indirect result of this more global process. This effect might be particularly likely if competitive interactions were unimportant in the local herbivore guild as was probably the case in Opler's (1974) study.

We examined this possibility by plotting numbers of heliconiines found on each *Passiflora* species (including *Tetrastylis*) against the area occupied by the plants. Areas were estimated from rough distributional ranges given in Killip (1938). Fig. 6.1 shows data plotted from the four areas. Since many plants in the Rio de Janeiro locality were endemic and of uncertain distribution we simply distinguish endemics (E) from widespread species (W). Correlation coefficients calculated for the remaining three areas were not significantly different from zero.

It is worth noting that the open circle in the La Selva graph is *Tetrastylis lobata*, a species possessing hooked trichomes (Gilbert, 1971) and avoided by all heliconiines but *H. charitonius*. Thus its position reinforces the weak positive trend in the La Selva data not

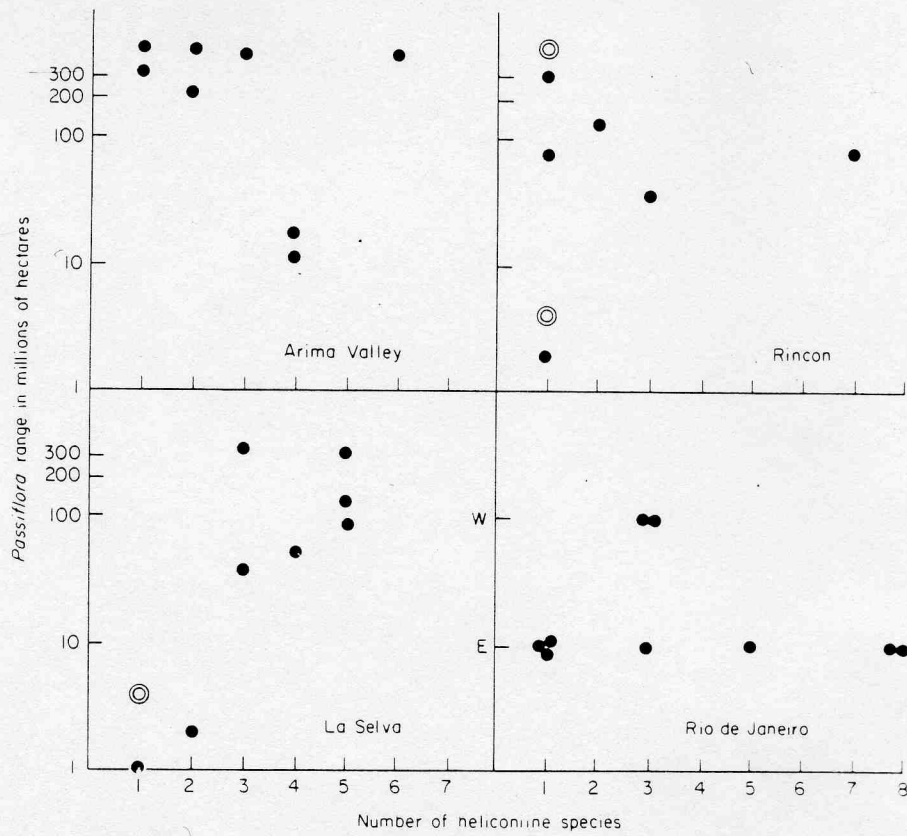*L. E. Gilbert and J. T. Smiley*

FIG. 6.1. Number of heliconiine species found locally using species of Passifloraceae as a function of their total geographical range. Data for Arima Valley, Trinidad; Rincon, Costa Rica; and Rio de Janeiro, Brazil, taken from Benson (1978); that of La Selva, Costa Rica, from J. Smiley (1978*b*). Janzen (1973*c*) provides descriptions of the two Costa Rican sites.
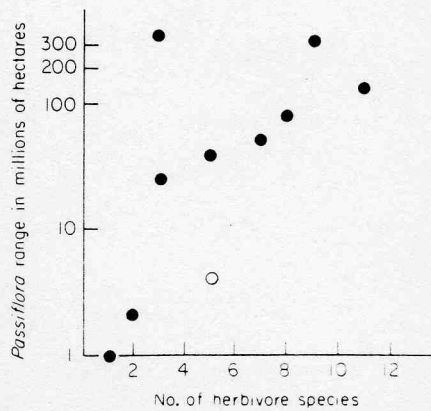

FIG. 6.2. Number of herbivorous insect species on La Selva Passifloraceae as function of plant geographical range. La Selva heliconiine data (Fig. 6.1) are combined with La Selva flea beetle host records (J. T. Smiley, 1978*b*).

because it is narrowly distributed, but because of its heliconiine deterrents. These trichomes do not deter flea beetles. The *Tetrastylis* point moves to the right when La Selva flea beetle data is combined with La Selva heliconiine data (Fig. 6.2), but significant correlation is not obtained ($r = 0.32$).

Local abundance

In cases where strong chemical coevolution has resulted in extreme monophagy at the level of host species (as in seed beetles and many ithomiines) changing the local abundance of a host is unlikely to increase the diversity of specialist herbivores associated with it. Rather, those that already use it simply become more abundant as was suggested above for ithomiines.

At another extreme are family-restricted herbivores which are relatively unconcerned with chemical distinctiveness, if any, among potential host species (within the family). In this case any host species which becomes abundant is likely to attract many of the herbivore species available. *Euptychia* and grasses probably involve this type of interaction.

Heliconiines and *Passiflora* flea beetles fall between the two above extremes. Depending on the area, 40–80% of these specialists utilise two or more host plants. Even some host specialists such as *H. melpomene* at La Selva turn out to be specialist for ecological not chemical reasons (Smiley, 1978a), and this has been termed 'ecological monophagy' as opposed to 'coevolved monophagy' (Gilbert, 1978).

Increasing the local abundance of a particular host plant should, in the case of *Euptychia,* and to a lesser extent the heliconiines, increase the number of species which feed on it since many species of these groups are not chemically restricted to a single host. A correlation between numbers of herbivores per *Passiflora* species and local *Passiflora* abundance (measured in numbers of new shoots per hectare) at La Selva (Fig. 6.3) is significant ($r = 0.69, P < 0.05$).

Thus we tentatively suggest that the local abundance of a *Passiflora* measured in terms which reflect productivity (e.g. new shoots available) determines the number of heliconiines and flea beetles found on it within a habitat, even if a substantial part of the herbivore guild is strictly monophagous.
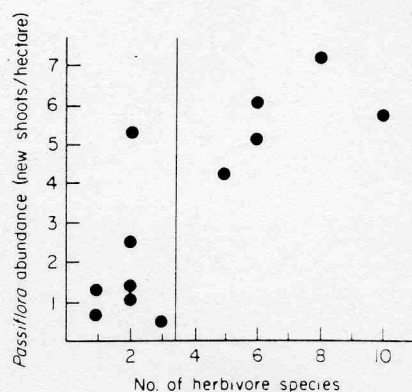

FIG. 6.3. Number of heliconiine plus flea beetle species per host-plant species at La Selva as a function of local abundance of host. Data from J. T. Smiley (1978b).

Plant size

Large *Passiflora* vines attract a complex fauna of omnivorous and predaceous insects which exploit their extra-floral nectar production. Field observations and time-lapse cinema photography of leaf or petiolar nectaries of several species (Smiley and Gilbert, in prep.) leaves little doubt that the larger species, and larger individual plants within a species, are occupied by larger general assemblages of insects.

However, the impact of size on the diversity of heliconiines and flea beetles is not so clear. For shoot-feeding *Heliconius* (Benson *et al*, 1976), smaller plants are frequently preferred over adjacent large plants. Females can assess egg loads (Williams and Gilbert, in prep.) and presumably predator activity. Old-leaf feeders such as *Eueides aliphera*, or the cluster-laying *Heliconius doris*, prefer the large plants of their host species, while *H. cydno* might be found only on small plants of the same species.

Thus *Passiflora* species which mature as large woody lianas may support a longer list of herbivores because juvenile and adult plants are effectively different resources from a herbivore viewpoint. However, our data suggest that population productivity measured as active meristems per unit area is more significant than maximum size attainable in predicting heliconiine and flea beetle diversity on a plant species. Better sampling of canopy emergents of the lianas *P. vitifolia*, *P. ambigua*, and *P. auriculata* might alter this conclusion.

Successional status

Most *Passiflora* species begin as seedlings in early successional areas (stream banks, road-cuts, land slips) or in light-gaps caused by tree falls. While some species such as *P. biflora* drop out as succession proceeds, others grow up with the forest and become emergent lianas (*P. ambigua*, *P. vitifolia*, *P. auriculata*). In Fig. 6.3, the five points to the right of the line are all from secondary successional areas at La Selva, while six to the left are from the forest. We have separated juveniles (successional area) from adults (in forest) for *P. vitifolia* and *P. auriculata* in this graph. It appears that *Passiflora* populations which occupy later succession have fewer herbivores because they are less abundant and less productive per unit area.

Implications for total diversity of herbivore guild

Given the interest in the diversity of herbivores on particular host-plant species (e.g. Southwood, 1961; Strong, 1974; Lawton, Chapter 7) it is worth asking the following question: Does an understanding of the factors which determine the number of family-specialist herbivores on a plant species help our understanding of the determinants of diversity in a local herbivore guild sharing many species of the host family?

For example, if geographical range of a host determined the local faunal diversity of specialists on that host, then the total specialist herbivore diversity of habitats dominated by widespread plant taxa would be greater than those dominated by relatively endemic plants. We see no evidence in our studies, or in those of others for such a pattern.

As we have indicated, the local abundance of productive biomass explains most of the variance in family specialist faunas *between plant species* within a habitat; but it explains little of the between site variance in local diversity of a family-specialist guild unless: (1) little overlap occurs between faunas of each host species, and (2) there exists regionally a pool of species for each host capable of invading when local concentrations of particular

hosts are high (this is what is not happening in Janzen's system). Note that if only one plant species of a family is available locally, and if (2) above holds, we have a special case exemplified by Simberloff's islands. Even if the local diversity of coevolved mangrove specialists correlates nicely with the area of the island, this result would be relevant only to the problem of herbivore loads *on individual plant species* in more botanically complex communities. It fails to provide any general explanation for pattern of diversity in local specialist herbivore guilds based on species rich host assemblages. Likewise, as we deal with increasingly generalist faunas, we expect island biogeography theory to predict diversity more accurately from plant abundance or habitat area alone since biotic interactions are of lesser significance.

DETERMINANTS OF LOCAL HELICONIINE DIVERSITY

The wealth of taxonomic, ecological and geographical information available on heliconiines allows us to make an attempt at factoring out major causes of local diversity. However, these conclusions must be tentative until many additional local communities are studied in detail.

Historical factors: biogeography and evolution

Heliconiines and the genus *Heliconius* in particular underwent considerable adaptive radiation, in terms of aposematic color patterns, while isolated in the glacial forest refuge areas of South America (Turner, 1976).

Species pairs such as *Heliconius melpomene* and *H. cydno* probably diverged as races on different habitat islands. They now coexist over a large region where *H. cydno* is restricted to forest and *H. melpomene* occupies forest edges and successional areas.

Not all heliconiine species generated by this process of cyclic refuge isolation (Turner, 1976) have spread over the entire range of potential habitats. Thus, while species like *H. erato* range from northern Mexico to southern Brazil, most others occupy a fraction of that range, and historical factors come into play in accounting for between site differences in diversity (if sites are compared between regions differing in the total available pool of heliconiine species). In particular, local sites proximate to numerous Quaternary refugia (see maps in Brown *et al*, 1974) have many more potential species available for colonisation. For example, the previously mentioned Rio Negro site in Colombia (Brown, 1972) as well as other extremely rich heliconiine sites in the Manaus, Brazil, area (Brown, personal communication) are in the overlap zones for the geographically expanded faunas of four to five surrounding refugia. Since forest plants also underwent differentiation in Quaternary refugia (see references in Brown *et al*, 1974) it is possible that sites in zones receiving input from several previously separate refugia may well have higher *Passiflora* diversity than sites in more homogeneous regions.

Clearly, to minimise historical factors in seeking explanations for local diversity we should compare local sites within regions homogeneous for the influence of refugia.

Ecological factors: resource variety

At a first level of approximation, the taxonomic diversity of Passifloraceae locally accounts for much of the variation in heliconiine species richness between 10 sites (Fig. 6.4) for which reasonable data exist ($r = 0.82$, $P < 0.05$). The number of plant species is an even better indication (Fig. 6.4) of how many *Heliconius* species can be expected ($r = 0.87$, $P < 0.01$).
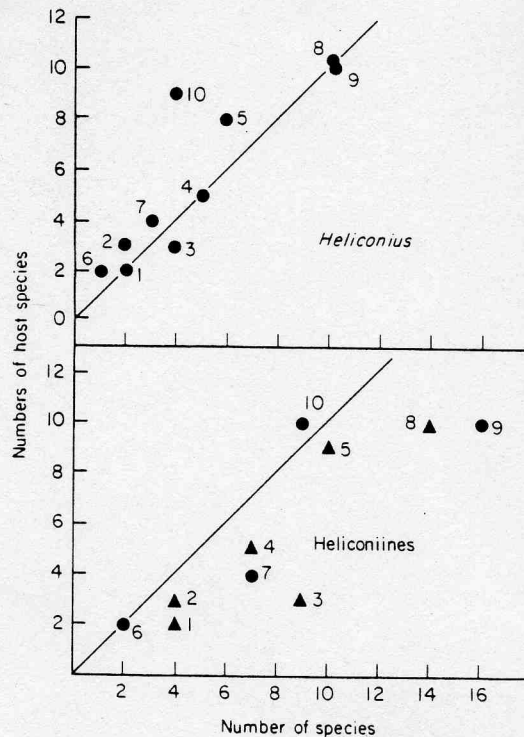
FIG. 6.4. Number of *Heliconius* (above) or heliconiine (below) species as a function of host plant diversity for 10 different locations. Triangles indicate areas for which the most abundant heliconiines are clearly associated with the most abundant *Passiflora* species. Localities are: 1, Headquarters, Santa Rosa Park, Costa Rica; 2, Airstrip hill, Palo Verde Field Station, O.T.S., Costa Rica; 3, Andrews Trace, Arima Pass, Trinidad; 4, Guanapo Dump, near Arima, Trinidad; 5, Monteverde, Costa Rica; 6, Rancho Cielo, Tamps., Mexico; 7, Gomez Farias, Tamps., Mexico; 8, La Selva Field Station, nr. Puerto Viejo, Costa Rica; 9, Rincon, Costa Rica; 10, Rio de Janeiro, Brazil. Sources: Sites 1–7, unpublished field observation of L. E. Gilbert; site 8 unpublished field observations of J. T. Smiley and L. E. Gilbert; sites 9 and 10, data from Benson (1978).

The fact that 90% ($N = 10$) of the *Heliconius* data points fall on or above the 45° line, while 90% ($N = 10$) of heliconiine points fall below the line (Fig. 6.4) reflects the partitioning of *Passiflora* species into two different resources: new shoots (most *Heliconius*) and older leaves (other heliconiines). Benson *et al* (1976) and Benson (1978) give detailed discussion of how heliconiines subdivide *Passiflora*.

The observed correlation between numbers of *Passiflora* and numbers of heliconiines raises two important questions: (1) What determines the number of *Passiflora* species which coexist locally? (2) What determines their distinctiveness from a herbivore point of view?

Janzen's (1973*a*) answer to the first question would be that host-plant diversity is locally regulated by counter-balancing mortality due to density-dependent response by host specialists. This model, like the strictly stochastic models of community structure, is attractive for its convenient lack of complexity. As the extent to which heliconiines kill or reduce the growth of *Passiflora* plants is not known, it is not possible to evaluate their role in regulating the diversity of their hosts. However, the regular patterns of *Passiflora* species locally (see above) suggest some sort of biotic limitation on diversity.

A solution to this problem may be suggested by Gentry's (1976) study of tropical Bignoniaceae. This family is remarkably like Passifloraceae in containing many vine

species, having a variety of pollinators, and in exhibiting regular patterns with respect to local site diversity. Gentry was able to account for most variation in local diversity of Bignoniaceae by establishing: (1) the number of pollination niches available, (2) rainfall and edaphic features of the site, (3) the degree of seasonality and climatic predictability, and (4) the balance of successional stages locally. Gentry's study exemplifies the sort of work needed to help unravel a major aspect of resource diversity which contributes to heliconiine diversity.

In spite of the significant correlation between taxonomic diversity of hosts and numbers of heliconiines, we know of other family specialists (e.g. *Euptychia*) for which no such correlation exists. Clearly a more important aspect of resource diversity is the degree of distinctness between available host species.

Gilbert (1975) suggested that the behavioral sophistication of foraging female *Heliconius* accounts for the remarkable leaf-shape diversity of *Passiflora* species. Gilbert (1975) and Benson *et al* (1976) discuss other traits of *Passiflora*, apparently evolved in response to heliconiine herbivory, which increase differences among *Passiflora* species and, in effect, generate new niches for specialists. For example, the hooked trichomes which defend some *Passiflora* and *Tetrastylis* species from heliconiine attack (Gilbert, 1971) make these species resources for *Dione moneta* and *Heliconius charitonia,* both of which are able to utilise these plants in spite of the trichomes. Benson (1978) notes that this feeding specialisation by *H. charitonia* allows it to coexist with similar species such as *H. erato.* This observation indicates that some combinations of *Passiflora* species might maintain higher heliconiine diversity than others, and that qualitative as well as quantitative differences in *Passiflora* communities between local areas may affect differences in heliconiine species density between them.

Gilbert (1975) has argued that for *Heliconius,* which as adults utilise pollen resources for maintaining a long reproductive life (Gilbert, 1972; Dunlap-Pianka *et al,* 1977), the presence of abundant pollen allows particular *Heliconius* to persist in a local habitat at lower densities than would non-pollen feeders. Gilbert (1975) has suggested that selection for improved pollen foraging led to many of the individual and population traits of *Heliconius* which allow them to exploit other scattered, low density resources such as new shoots of *Passiflora.* In ecological time, areas which differ only in pollen abundance and/or predictability might differ in numbers of *Heliconius* present because lacking pollen, no *Heliconius* would be able to specialise on lower density, less predictable plants. It is difficult to imagine, for example, a non-pollen feeding heliconiine specialised on the low density *Passiflora pittieri* at La Selva. However, a pollen feeder, *H. sapho,* is able to persist at low densities using only this host plant.

Ecological factors: habitat structure

Heliconiine species have definite preferences for particular successional stages (Benson, 1978) and for particular levels within the forest (Papageorgis, 1975). Papageorgis builds a case for the vertical structuring of mimicry complexes (ithomiines and heliconiines) being related to different color patterns being optimum (from the standpoint of escape from predation) at different levels in a forest. Unfortunately, how these species differences in average height of flight relate to utilisation of host plants is unknown.

Smiley (1978b) has studied similar habitat selection by members of mimicry complexes at La Selva. He has demonstrated that the closely related *H. melpomene* and *H. cydno* differ in host preferences (at the ovipositional level) because they encounter different levels of *Passiflora* abundance in the habitats they choose. *H. melpomene* flies with its co-model *H.*

erato along forest edges and in second growth. *H. cydno* is restricted to the forest where its co-model *H. sapho* flies. Smiley has shown that while *H. melpomene* only uses a single host plant, *P. oerstedii*, its larvae are fully capable of using the same array of *Passiflora* species used by the generalist, *H. cydno*. Thus, vertical or horizontal partitioning of habitat between members of different mimicry complexes can increase *Heliconius* diversity without an increase in host-plant diversity. The butterflies simply adjust host preferences to fit with diversity and abundance of host species encountered in habitat chosen for predator escape reasons.

The extent to which structural differences (balance of successional stages, etc.) between sites accounts for differences in heliconiine species richness between them cannot be estimated from existing data. However, what is known about mimicry, habitat preference and host-plant ecology (Smiley, 1978*b*) emphasises the need to control for habitat structure in diversity studies.

Ecological factors: climatic predictability

Benson (1978) has compared sites having similar numbers of coexisting *Passiflora* species and exposed to similar regional pools of heliconiine species, but differing in the predictability of edible foliage on host plants. He found that in the least predictable site (Rio de Janeiro) average niche breadths with respect to host plants were twice those of sites with more predictable resource availability (Rincon, Costa Rica; Arima Valley, Trinidad). Benson also found fewer heliconiines than predicted from number of host-plant species at the Rio de Janeiro site (see point No. 10 of Fig. 6.4). He points to probable cases of competitive exclusion as accounting for the fewer species.

Ecological factors: topography

As one proceeds from lowlands to the highest heliconiine habitats, ecological replacement occurs for both *Passiflora* and heliconiines. Benson (1978) has documented several examples where heliconiines replace one another over a narrow elevational zone (see Gilbert and Singer, 1975, for other examples in butterflies).

Therefore, sites chosen near transition zones are likely to have higher diversity than sites well within an elevational zone. For example, *Heliconius hecalesia*, a Costa Rican species common in mid-elevation where its primary host, *P. lancearia*, is abundant, occurs in low density at La Selva. As La Selva is within a few miles of montane habitat, and has appropriately cool and wet conditions, some *P. lancearia* and *H. hecalesia* occur there. However, as La Selva becomes increasingly isolated by ongoing forest clearing from surrounding habitats of higher elevation, we expect to see *H. hecalesia* and *P. lancearia* disappear from the site.

Conclusion

It is likely that most higher taxa of tropical plants support at least some tightly associated and coevolved insect groups. It is difficult to understand community properties of either the plants or the insects without specifying how they interact with one another and with other organisms such as predators and adult resources of the insects, and pollinators of the plants (Gilbert, 1977).

While manipulations in simple systems such as tide-pools and mangrove islands have been most useful in the development of community ecology, the complexity, and specificity of interaction as described in the heliconiine-Passifloraceae system make suspect any

experimental manipulation of a tropical forest community done in ignorance of the fundamental natural history and geographical ecology of its component coevolved food-webs. In addition to many more field observations of such systems, we must develop general theory (e.g. Southwood, 1977) which will apply to phytophagous insects if we are to understand how to conserve the bulk of tropical diversity.

Acknowledgements

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Note added in proof

Results of W. A. Haber's research on the Ithomiinae ('Evolutionary Ecology of Tropical Mimetic Butterflies (Lepidoptera: Ithomiinae)', PhD Dissertation, University of Minnesota, Minneapolis/St. Paul, 1978) were made available to us in May 1978 by the author. A few highlights are worth mention in the context of our paper:

1. At Monteverde, Costa Rica, 26% ($N = 5$) of the 19 ithomiines with host records were restricted to a single host. While this departs drastically from Haber's own data at other localities, and from data collected by Drummond or Gilbert (see above), the fraction using three or less of available host species at Monteverde (91%; $N = 17$) is consistent. Other localities may show a Monteverde-type pattern with further sampling.

2. Haber has examined Ithomiine/host-plant diversity along an elevational gradient as we suggest above (p. 92). As suspected, the increase in ithomiine species numbers from lowland to mid-elevation sites is closely paralleled by an increase in Solanaceae species richness.

3. Haber plotted numbers of ithomiine species against numbers of Solanaceae species for 12 Costa Rican localities. The resulting graph is virtually identical to that for *Heliconius* x Passifloraceae in our Fig. 6.4.