LYCAENID BUTTERFLIES AND PLANTS:
HOSTPLANT RELATIONSHIPS, TROPICAL VERSUS TEMPERATE

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Abstract. Hostplant ranges, scored as number of plant families utilized by the caterpillars, are reviewed for 1068 species of the butterfly subfamily Lycaeninae. The majority of species are oligophagous, being restricted to one plant family or genus. Polyphagous species account for a significantly larger proportion among tropical species than in temperate-zone faunas. This difference is independent of influences of myrmecophily on hostplant relationships. A strong correlation between polyphagy and use of woody hostplants, as well as between oligophagy and connections with herbaceous hostplants, suggest that the more strongly developed chemical defense of herbaceous plants constrains the amplification of hostplant ranges of herb-feeding Lycaeninae butterflies. Specializations on unpredictable ephemeral food resources (young foliage, inflorescences) in unseasonal tropical environments, in contrast, may have favoured the more frequent rise of polyphagy. *Accepted 16 May 1995.*

Key words: Butterflies, herbivores, host specificity, myrmecophily, species diversity.

INTRODUCTION

The degree to which herbivorous insects are specific to certain hostplants has played a central role in estimating tropical species richness, and hence global biodiversity. For example, Erwin's (1982) estimates of insect species numbers are based on the assumption that a large portion of the beetle fauna to be collected from any given tropical tree species is specific to that plant. However, most studies on tropical species communities employ sampling techniques like canopy-fogging or light-trapping, from which hostplant ranges or host specificity of the animals sampled can at best be indirectly inferred. A notable exception is the study by Basset (1992) of the herbivore fauna of an Australian Sterculiaceae tree species, where faunal sampling was subsequently supplemented by feeding trials and a systematic evaluation of the available literature records on hostplant relationships.

Differences in host ranges have hitherto been documented between tropical and temperate members of various taxonomic groups (such as chrysomelid beetles) or ecological guilds (such as parasitoids or particular phytophagous insects, see references in Basset 1992), but larger taxa of herbivorous insects have rarely been analyzed in detail. One reason for this deficit is that for most herbivores, especially from tropical regions, information on hostplant relationships is still very scant. Hostplant relationships of butterflies (superfamily Papilionoidea), however, are probably better

known than those of any other insect taxon of comparable diversity and distribution. Due to their conspicuousness and aesthetic appeal, butterflies have attracted the interest of numerous naturalists throughout the last 200 years. Accordingly, butterflies are relatively well known with respect to taxonomy, and life-history data are available for a considerable portion of the species, including tropical faunas. Recent reviews of hostplant relationships cover the African and Australian butterfly fauna (Ackery 1991), or the world fauna of the largest butterfly family, Nymphalidae (Ackery 1988), but do not specifically address the comparison of tropical versus temperate hostplant ranges.

Here I investigate the hostplant relationships of the second-largest butterfly family, the Lycaenidae. The lycaenids comprise approximately 4500 described species worldwide (Bridges 1988), with life-history data available for more than 1200 of these (Fiedler 1991, 1995).

I treat the Riodinidae, often assigned to the lycaenids as a subfamily, as a separate family for the reasons given by DeVries (1991) and Robbins (1988, 1989). Patterns of hostplant use within the Riodinidae have been discussed by Harvey (1987) and DeVries *et al.* (1994). Following Scott & Wright (1990), the Lycaenidae can be divided into four subfamilies (Poritiinae, Miletinae, Curetinae, and Lycaeninae). Two subfamilies of lycaenid butterflies have aberrant life-cycles; larvae of Poritiinae mostly feed on lichen, fungi, algae or

similar substrates, while those of Miletinae are entirely aphytophagous, preying on Homoptera and ant broods, or thriving as guests in ant societies. The Oriental Curetinae consist of the single genus *Curetis* with less than 20 species (Eliot 1990), whose larvae feed on plants of the order Fabales. The subfamilies Poritiinae, Miletinae, and Curetinae are almost entirely tropical in distribution and, to avoid taxonomic bias, these have been excluded from the following analyses of latitudinal patterns of hostplant use.

Hereafter, only the Lycaeninae (*sensu* Scott & Wright 1990) are considered, which account for over 80 % of the present-day Lycaenidae species diversity. Lycaeninae are worldwide in distribution except Antarctica. They occur in all terrestrial habitats from the subarctic tundra to the humid tropical rainforests, where their diversity reaches a maximum.

A special feature of lycaenid butterflies is their widespread association with ants, termed myrmecophily. The larvae of more than 50 % of all lycaenid species are myrmecophilous, and certain species, the so-called obligate myrmecophiles, even depend on the presence of specific host ants for their survival (Fiedler 1991). Myrmecophily interacts in various and complex ways with many life-history traits of lycaenid butterflies. In many obligate myrmecophiles, for example, the females use the appropriate host ants as oviposition cues (Atsatt 1981, Pierce & Elgar 1985). As a consequence, the hostplant ranges of such obligate myrmecophiles tend to be broadened as compared to their facultatively myrmecophilous or non-myrmecophilous relatives (Pierce & Elgar 1985, Fiedler 1994). Pierce (1985) also suggested that myrmecophily selects for certain hostplant preferences among lycaenid butterflies, but this idea has recently been challenged (Fiedler 1995).

As in many other herbivore taxa, hostplant relationships of lycaenid butterflies show distinct taxonomic patterns (Fiedler 1991), which are most likely governed by hostplant chemistry. Therefore, myrmecophily as well as taxonomic affinities must be taken into account as factors when comparing hostplant ranges of tropical and temperate lycaenid butterflies.

In this paper I address the following questions: (1) Are there differences in the hostplant ranges between lycaenid butterflies living in tropical and in temperate realms? (2) Are these latitudinal patterns independent of the myrmecophilous relationships of the larvae? (3) Are the patterns consistent across the major taxonomic subgroups? (4) What is the significance of the hostplant growth form (woody *versus* herbaceous)?

DATA BASE AND ANALYTICAL PROCEDURE

Hostplant data were extracted from the literature for 1068 species of Lycaeninae butterflies. A previous version of this database has been published (Fiedler 1991), and this has been extended using recent faunal treatments, publications on the life-histories of individual species, and own fieldwork in Europe and Malaysia (a full list is available upon request). Only reliable hostplant records were accepted, whereas results of feeding experiments (e.g., Pratt & Ballmer 1991) were discarded.

As in a previous study (Fiedler 1994), hostplant ranges were essentially scored as number of plant families utilized. Meaningful numbers of hostplant species are unavailable even for the well-studied European or North American lycaenid fauna, as evidenced by the continuous additions to the hostplant lists of butterflies in these areas. Comparisons at genus level are obscured by the broadly divergent delimitations of plant genera as used by different taxonomists when dealing with different regional floras. Family delimitations, in contrast, are more widely accepted in a congruent manner, here following the list of plant families in Groombridge (1992).

Butterflies are categorized in 5 groups with regard to hostplant range: one hostplant family, two hostplant families, three hostplant families, 4-5 hostplant families, and more than 5 hostplant families recorded ("5-classes analysis" hereafter). In addition, butterflies known only from a single host genus within one plant family are scored as a separate category in a parallel analysis ("6-classes analysis" hereafter). Because obligate myrmecophiles may have amplified hostplant ranges due to ant-dependent oviposition (Pierce & Elgar 1985, Fiedler 1994) all comparisons are calculated twice (once considering all relevant species, once excluding the obligate myrmecophiles). To further investigate taxonomic patterns, I separately analyze the two most speciose groups: "blue butterflies" (tribe Polyommatini) and "hairstreak butterflies" (tribes Theclini and Eumaeini *sensu* Scott & Wright 1990). It must be emphasized, however, that the monophyly of these tribes requires thorough documentation employing cladistic techniques.

The scoring of a butterfly species as either tropical or temperate in distribution inevitably calls for some arbitrariness. I here adopt a categorization which follows the well-established boundaries between zoogeographical realms (e.g., Heppner 1991 for Lepidoptera). Hence, I score a lycaenid as "temperate" if its main dis-

tribution is in the Nearctic (North America north of Mexico) or Palearctic zone (including the Himalayas), in New Zealand or in high-altitude Patagonia. As a corollary, a species is scored as "tropical" if its main distribution is in the Neotropics (Central and South America, including the Caribbean region, but except Patagonia), the Ethiopian region (Africa from the Sahara southwards plus Madagascar), the Oriental region (including the Indian subcontinent, but excluding the Himalayas), or Austro-Melanesia. Species which mainly occur in one region, but marginally extend into another (less than 10 % of the range), are scored according to their main range. The very few species (n = 9) which have substantial portions of their range in tropical as well as temperate regions are omitted from all calculations.

While the "temperate" species categorized in the above way truly inhabit ecosystems with a temperate or cold climate, the climatic conditions are more variable for the "tropical" group. Parts of South America (e.g., high Andes) and southern Australia (Tasmania) have a distinctly temperate climate. However, hostplant data of only two Patagonian lycaenids (*Pseudolucia* spp.) are available, and these are included in the temperate species. Only 4 Australian species (*Neolucia* 3 spp., *Pseudalmenus chlorinda*) have their main distributions in the temperate zone of southern Australia. This small species number is negligible in view of the large database. In southern Africa, the species-rich Cape fauna of lycaenid butterflies does not indicate a long separate history (in contrast to the famous Cape flora), but is clearly derived from the Ethiopian region (Cottrell 1985). Hence, the use of the straightforward subdivisions of "temperate" and "tropical" using zoogeographic boundaries with few alterations appears sufficiently robust for the following approach.

All quantitative analyses are conducted using Chi^2 contingency tables to test for homogeneity (Sachs 1992; for a similar approach cf. Fiedler 1994). Tests are carried out on absolute species numbers, and are restricted to groups with sufficiently large species numbers. Hence, in the taxonomic comparisons, the tribes Lycaenini (hostplant information available for 46 spp.) and Aphnaeini (76 spp.), were not analyzed separately.

RESULTS

The quantitative data are summarized in Table 1. On subfamily level, there is a significant difference in the hostplant range distributions between tropical and temperate zone lycaenid butterflies (5-class analysis,
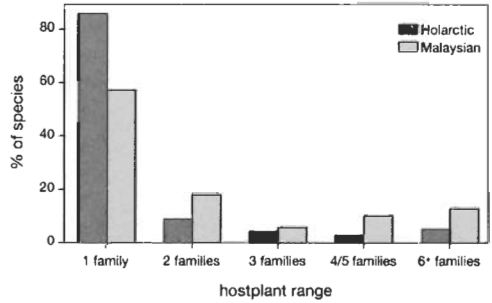

FIG. 1. Comparison of hostplant ranges of Holarctic (n = 342 spp.) versus Malaysian (Peninsular Malaysia and Borneo, n = 109) Lycaeninae species. The Holarctic fauna comprises a very high proportion of hostplant specialists, whereas in South East Asia almost a quarter of the species utilizes two or more hostplant families.

excluding obligate myrmecophiles: $Chi^2_{4\,df} = 12.851$, $P < 0.02$; 6-class analysis, excluding obligate myrmecophiles: $Chi^2_{5\,df} = 14.345$, $P < 0.025$). This difference is caused by a greater proportion of highly polyphagous species (3+ hostplant families used) in the tropics (13.6 % vs. 9 %). The great majority of lycaenid butterfly species, however, is restricted to one hostplant family (tropical: 74.7 %; temperate: 84.4 %), and more than half of the species even to one hostplant genus (tropical: 58.3 %; temperate: 61.4 %).

This same pattern is observed when the obligate myrmecophiles are included (5-class analysis: $Chi^2_{4\,df} = 13.056$, $P < 0.02$; 6-class analysis: $Chi^2_{5\,df} = 16.194$, $P < 0.01$). Neither the percentages of polyphages nor those of oligophages change distinctly. Hence, irrespective of myrmecophily, there is a significant heterogeneity in hostplant ranges of Lycaeninae butterflies, with tropical species showing a greater proportion of polyphages than temperate-zone inhabitants.

A comparison of two subsets of Lycaeninae species exemplifies this difference (Fig. 1). The lycaenid fauna of the Malay Peninsula and the island of Borneo has been the subject of intensive taxonomic and faunistic research (Seki et al. 1991, Eliot 1992), and hostplant data are available for 109 (30.6 %) of the roughly 356 Lycaeninae species known from this region (Fiedler 1991, and unpubl.). About 24 % of the Malaysian Lycaeninae species for which hostplant information could be traced are known from at least two hostplant families. In contrast, among the 342 Holarctic Lycaeninae species with available hostplant information, only 11 % are yet known to utilize two or more hostplant families.

TABLE 1. Hostplant ranges of Lycaeninae butterflies as scored by numbers of plant families recorded as utilized. Absolute species numbers are given, figures in parentheses are percentages of row totals. Lycaeninae include the 5 tribes Aphnaeini, Lycaenini, Theclini, Eumaeini and Polyommatini sensu Scott & Wright (1990), "hairstreaks" comprise the tribes Theclini + Eumaeini. "Tropical" species are those from the Neotropical (except Patagonia), Ethiopian, Oriental, and Austro-Melanesian faunal regions. Butterfly species of the Holarctic region, Patagonia and New Zealand are categorized as "temperate".

Hostplant range	1 gen	1 fam	2 fam	3 fam	4/5 fam	6+ fam
tropical Lycaeninae	428	120	86	38	26	36
(n = 734)	(58.3)	(16.4)	(11.7)	(5.2)	(3.5)	(4.9)
obligate myrmecophiles	97	15	13	11	5	9
others	331	105	73	27	21	27
temperate Lycaeninae	205	77	22	10	8	12
(n = 334)	(61.4)	(23.1)	(6.6)	(3.0)	(2.4)	(3.4)
obligate myrmecophiles	11	1	0	1	2	0
others	194	76	22	9	6	12
all Lycaeninae	633	197	108	48	34	48
(n = 1068)	(59.3)	(18.4)	(10.1)	(4.5)	(3.2)	(4.5)
tropical "hairstreaks"	253	53	42	15	13	30
(n = 406)	(62.3)	(13.1)	(10.3)	(3.7)	(3.2)	(7.4)
obligate myrmecophiles	25	0	2	4	2	8
others	228	53	40	11	11	22
temperate "hairstreaks"	59	32	11	5	4	6
(n = 117)	(50.4)	(27.4)	(9.4)	(4.3)	(3.4)	(5.1)
obligate myrmecophiles	1	0	0	0	0	0
others	58	32	11	5	4	6
tropical Polyommatini	127	60	33	17	12	5
(n = 254)	(50.0)	(23.6)	(13.0)	(6.7)	(4.7)	(2.0)
obligate myrmecophiles	34	8	2	1	2	0
others	93	52	31	16	10	5
temperate Polyommatini	113	35	8	4	4	6
(n = 170)	(66.5)	(20.6)	(4.7)	(2.3)	(2.3)	(3.5)
obligate myrmecophiles	7	0	0	0	2	0
others	106	35	8	4	2	6

A separate comparison of the larger tribes reveals important differences. Among the "hairstreak butterflies" (tribes Theclini and Eumaeini), no disparity in host-range distributions between tropical and temperate species can be found in the 5-class analyses (without obligate myrmecophiles: $Chi^2_{4 df} = 0.794$, $P > 0.9$; including obligate myrmecophiles; $Chi^2_{4 df} = 0.916$, $P > 0.9$), while the difference becomes significant in the 6-class analyses (without obligate myrmecophiles: $Chi^2_{5 df} = 11.594$, $P < 0.05$; including obligate myrmecophiles: $Chi^2_{5 df} = 14.421$, $P < 0.025$). Among the Polyommatini, in contrast, a highly significant heterogeneity emerges throughout (5-class analysis, without obligate myrmecophiles: $Chi^2_{4 df} = 20.820$, $P < 0.001$;

6-class analysis: $Chi^2_{5 df} = 25.00$, $P < 0.001$), and this pattern remains unchanged when obligate myrmecophiles are included (5-class analysis: $Chi^2_{4 df} = 15.906$, $P < 0.005$; 6-class analysis: $Chi^2_{5 df} = 18.877$, $P < 0.01$). Only 8.2 % of temperate zone Polyommatini feed on 3 or more hostplant families, whereas among tropical Polyommatini the respective proportion is 13.4 %.

Previous studies (Pierce & Elgar 1985, Fiedler 1991, 1994) have shown that, in general, hairstreak butterflies tend to be more polyphagous than Polyommatini species. The present analysis only partly confirms this result. When the obligate myrmecophiles are excluded, the hostplant range distributions of [Theclini + Eumaeini] and Polyommatini (tropical plus tem-

perate species combined) are homogeneous (5-class analysis: $Chi^2_{4 df}$ = 5.86, P = 0.29) or marginally heterogeneous (6-class analysis: $Chi^2_{5 df}$ = 11.08, P < 0.05). Species known from more than 5 hostplant families are disproportionately more common among the hairstreak butterflies, but overall differences are small. The pattern becomes more distinct when obligate myrmecophiles are included (5-class analysis: $Chi^2_{4 df}$ = 9.99, P < 0.05; 6-class analysis: $Chi^2_{5 df}$ = 15.25, P < 0.01).

Between temperate zone Polyommatini and [Theclini + Eumaeini], no differences in hostplant ranges can be observed (with or without obligate myrmecophiles, $Chi^2_{4 df}$ < 5.24, P > 0.26, for 5-class analysis; $Chi^2_{5 df}$ > 8.4, P > 0.1, for 6-class analysis). Tropical [Theclini + Eumaeini], in contrast, comprise a significantly larger proportion of polyphagous species than tropical Polyommatini (P < 0.01 in all 5- and 6-class analyses, irrespective of the inclusion of obligate myrmecophiles). Hence, the greater "taxonomic" tendency towards amplified hostplant ranges of hairstreak butterflies is more pronounced in the tropical faunas.

DISCUSSION

Like most other herbivores (Jaenike 1990), and particularly like other families of butterflies (Miller 1987, Ackery 1988, Scriber *et al.* 1995), the Lycaeninae embrace a high proportion of oligophages which are specialized on one hostplant genus (c. 60% of all species) or family (c. 78%). This high degree of host specialization in herbivores is most certainly governed by phytochemical barriers (Jaenike 1990, Berenbaum 1990), although studies on the chemical ecology of hostplant relationships in lycaenid butterflies are still scant (Fiedler *et al.* 1993, Wiesen *et al.* 1994). Superimposed on the preponderance of hostplant specialization is the well-documented, contrasting effect of obligate mutualistic relationships towards ants. Due to ant-dependent oviposition, such species tend to utilize amplified hostplant ranges (Pierce & Elgar 1985, Fiedler 1994). Furthermore, as shown above, a greater proportion of tropical lycaenids has polyphagous larvae as compared to temperate-zone species. This difference is pronounced among the Polyommatini, but absent in the [Theclini + Eumaeini].

This result raises three questions: (a) Is the pattern real? (b) What might be the causal factors responsible for this tropical-versus-temperate difference in hostplant specialization? (c) Why is this difference not universal among lycaenid butterflies?

The reliability of the pattern observed can be assumed for five reasons. First, the number of species in the analysis is high. Minor inconsistencies in the life-history data of individual species, or forthcoming additions of a few species, therefore, are unlikely to cause severe changes. Second, the analysis was restricted to a single, speciose, cosmopolitan subfamily. This should reduce possible effects of taxonomic heterogeneity or of highly uneven geographical distributions of the taxa under investigation. Third, although less than 30% of the extant species diversity is represented in the database, all major subordinated taxa of the subfamily Lycaeninae are covered to a roughly equal extent. Fourth, with only a single exception the outcome of the statistical calculations was identical in the 5- and 6-class analyses, which shows that the method of scoring of host ranges did not flaw the results. Fifth, the hostplant relationships of tropical species are less well recorded than are the hostplant ranges of temperate zone lycaenid butterflies. As a consequence, the documented hostplant ranges of tropical lycaenids will probably become larger, but certainly not smaller, when the tropical faunas become better known. Hence, further additions to the database are likely to corroborate or even strengthen, instead of diluting, the pattern.

Therefore, it must be taken as valid that tropical Lycaeninae species comprise a larger proportion of polyphages than their temperate-zone counterparts. What reasons can be responsible for this trend? I will discuss three potentially important factors: (a) myrmecophily, (b) the preference of lycaenid caterpillars for young growth and inflorescences of their hostplants, and (c) the hostplants' growth form.

(a) Myrmecophily is clearly not the major selective force behind the higher proportion of polyphages among tropical lycaenid butterflies. Although obligate myrmecophiles tend to utilize a larger range of hostplants (Fiedler 1994), all results in the analyses presented above remain unchanged when obligate myrmecophiles are excluded.

(b) Among the Lycaenidae, there is a widespread preference to utilize inflorescences, immature seeds, or young tender foliage as larval food (Pierce 1985, Fiedler 1991). This preference has been related to the possibility of more frequent "oviposition mistakes", eventually followed by successful colonizations of novel hostplants (Chew & Robbins 1984). Furthermore, especially in unseasonal tropical rain forests, the spatial or temporal availability of inflorescences or young foliage is often unpredictable. For example, subsequent generations of a given lycaenid butterfly population at

the same locality can be forced to switch between a set of hostplant species (Seufert & Fiedler, unpublished).

Most Holarctic lycaenids also prefer such plant organs (Fiedler 1991), but due to the pronounced seasonality and thus temporal predictability of young foliage or inflorescences, even the narrowest food specialists can tightly synchronize their phenology with that of their hostplant. Accordingly, utilization of "ephemeral" resources like young foliage or inflorescences does not exert a selective force towards amplification of the hostplant diversity among lycaenids in seasonal environments with predictable plant phenology, whereas unpredictability of appropriate plant organs together with increased likelihood of oviposition mistakes may have favoured the evolution of broader hostplant ranges among lycaenids in tropical rainforests.

(c) Another factor potentially shaping hostplant diversity is growth form of hostplants. Overall, the majority of lycaenid butterflies feed on woody plants (trees, shrubs, lianas) or epiphytes (especially on parasitic mistletoes). Within the Theclini and Eumaeini, the great majority of tropical as well as temperate-zone hairstreak butterflies utilize woody hostplants. Among the few exceptions there are all-monocot feeders (subtribe Loxuriti, some orchid-feeding *Hypolycaena* species, a few Neotropical Eumaeiti), African *Leptomyrina* and certain American *Callophrys* on succulent plants, or Neotropical *Arawacus* on Solanaceae. All these, as well as most mistletoe feeders (Fiedler 1995), are oligophagous and utilize one plant family or, rarely, hostplants in two families. Therefore, because tropical as well as temperate-zone Theclini and Eumaeiti consistently prefer woody hostplants, no tropical-versus-temperate disparity would be expected if hostplant growth form is a major causal factor in shaping hostplant ranges. This is in full concordance with the pattern observed.

Among the Polyommatini, the trend towards polyphagy in tropical regions is particularly pronounced. This finding is paralleled by the patterns of hostplant use within this tribe. The temperate Holarctic Polyommatini fauna is dominated by members of the *Cupido, Glaucopsyche,* or *Polyommatus* sections (*sensu* Eliot 1973), and only 25 of 148 species (16.9%) feed on woody shrubs or trees. In contrast, most tropical Polyommatini with known hostplant associations belong to the subtribe Lycaenesthiti, or to the *Nacaduba, Prosotas, Jamides,* or *Lycaenopsis* sections within the Polyommatiti, and these species predominantly utilize woody hostplants (164 of 254 species, 64.6%).

Hence, plant growth form seemingly plays an important role in shaping lycaenid butterfly hostplant ranges. Species feeding on woody plants (most hairstreaks, many tropical Polyommatini) are more likely to accept a broader range of plant families, whereas herb feeders (Lycaenini, most temperate Polyommatini) are more commonly food specialists. This pattern may also explain the observation that Polyommatini tend to be more specialized than hairstreak butterflies (Pierce & Elgar 1985, Fiedler 1994). More frequent shifts towards utilizing herbaceous hostplants may have led to a higher degree of specialization in the Polyommatini. Furthermore, the role of plant growth form fits well into the concept of "hostplant apparency" and the type of chemical defense employed. According to this theory, "apparent" plants such as long-lived woody species tend to produce "quantitative" antiherbivore defenses like tannins and other polyphenolics (Feeny 1976, Rhoades & Cates 1976, Gilbert 1979), which can be further increased in the course of an induced response (Karban & Myers 1989). Non-apparent plants, such as many herbaceous taxa, preferentially use toxic or deterrent allelochemicals as "qualitative" defense.

Accordingly, herb-feeders are selected for effective handling of toxic plant compounds, and given the enormous chemical and pharmacological diversity of such compounds a higher degree of hostplant specialization is to be expected among herb-feeders. Conversely, many tree-feeders encounter a basic set of polyphenolics widely used by numerous and partly unrelated plant taxa. Caterpillars which are able to feed on one such plant group should, therefore, be able to utilize additional hostplants, provided that these do not accumulate additional toxic compounds. As a consequence, polyphagy is expected to be more common and widespread among butterflies feeding on woody plants.

It must be emphasized that the "apparency theory" is a simplification of real patterns. It ignores important defensive mechanisms such as sticky or hairy leaf-surface structures, or resin and latex canals, and neglects individual or organ-specific variation with regard to the accumulation of secondary plant compounds. Nevertheless, in addition to effects of the preference for young foliage and inflorescences, or of symbioses with specific host ants, this concept contributes to an explanation of the observed patterns of host use among lycaenid butterflies.

What significance might the findings on hostplant ranges of lycaenid butterflies have for studies of other

herbivores? Any generalizations should be made with great caution, since lycaenids, or even butterflies as a whole, may be atypical and extrapolations could thus be grossly misleading. Nevertheless, the study of host ranges of butterflies provides us with an almost unique opportunity for large-scale comparisons, since butterflies are one of the few taxa, if not the only larger insect group with a worldwide distribution, whose host-plant relationships are sufficiently well known to furnish a database for such considerations. With all caveats in mind, two consequences emerge:

(a) It is premature to assume that herbivorous insects in tropical regions generally exhibit a similar or even higher degree of hostplant specialization than their temperate-zone counterparts. At least among lycaenid butterflies, a family of moderate species diversity, the opposite is true. Tropical swallowtail butterflies (family Papilionidae), on the other hand, tend to be more specialized feeders than their temperate zone relatives (Scriber *et al.* 1995). Hence, even among butterflies latitudinal hostplant-range patterns differ between families.

(b) As a corollary, a lower degree of specialization among tropical lycaenid butterflies is accompanied by a higher incidence of overlap in hostplant relationships between species. This overlap is further enhanced since only a fraction of the extant tropical floral diversity actually serve as hostplants for butterflies. Hence, floral diversity is often a poor predictor of butterfly species diversity (Vane-Wright 1978). The depauperate butterfly faunas of the Cape Province in South Africa (Cottrell 1985), or of Australia (Common & Waterhouse 1981, Ackery 1991), which contrast sharply with the highly diverse regional floras, are excellent cases in point. On the other hand, many taxonomic groups of butterflies, including speciose clades, "cluster" on specific hostplant taxa (families, orders) with frequent inter-specific overlap (Fiedler 1991 and 1995 for examples among the Lycaenidae).

Hence, although extreme hostplant specializations do occur among tropical lycaenid butterflies, such specialist interactions cannot sufficiently explain their high species diversity in tropical regions. Additional mechanisms, such as partitioning of the plant parts eaten, specific interactions with ants in the case of obligatorily myrmecophilous lycaenids (Pierce 1984, Fiedler 1991, Seufert & Fiedler, *in prep.*), or stochastic colonization events in the temporally and spatially unpredictable mosaic of potentially available hostplants, must play important roles in shaping the outcome of butterfly-plant interactions.

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