

## DIET BREADTH AND HOST PLANT RELATIONSHIPS OF SOUTHEAST-ASIAN SPHINGID CATERPILLARS

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*Abstract.* We investigated larval host plant relationships of hawkmoth species (Lepidoptera: Sphingidae) from Southeast-Asia and Malesia, using a compilation of published and unpublished host plant records. We found that diet breadth (the number of recorded host plant families) and the diversity of utilized host plants differ between sphingid subfamilies and tribes. In addition, significant variation in host plant composition can be found between subfamilies. Our data suggests an influence of sphingid phylogeny on host plant utilization. We found no differences in diet breadth between tropical, SE-Asian sphingids and temperate, European species, confirming earlier results from several butterfly families, although there may be differences between the two regions in the host spectrum utilized. There is no indication that host plant distribution limits the geographical distribution of sphingid moths. Sampling biases, the possibility of local host plant adaptation and their potential impact on the use of host plant compilations from different regions are discussed and illustrated by examples from our data. *Accepted 15 March 2006.*

*Key words:* hawkmoths, hornworms, host plant specialization, insect-plant interactions, Lepidoptera, Malesia, phylogenetic signal, Sphingidae.

### INTRODUCTION

The relationship between herbivorous insects and their host plants is a much-discussed issue in community ecology, particularly when addressing speciose tropical assemblages (e.g., Fiedler 1998, Novotny *et al.* 2002a,b,c; Novotny *et al.* 2004). It is an important parameter in the estimation of global biodiversity (Ødegaard *et al.* 2000) and a central issue in the discussion of niche breadth and the role of competition in the structuring of communities (e.g., Denno *et al.* 1995, Hartley & Jones 2003). Diet breadth is an essential niche dimension for herbivorous insects (e.g., Novotny *et al.* 2002b) and has been used to explore

the influence of niche breadth on variables such as body size (Loder *et al.* 1998), range size and abundance (Gaston *et al.* 1997). The distribution of host plants can restrict the distribution of a herbivore, but is generally not the only factor that limits a herbivore's range size (Quinn *et al.* 1997, 1998; Lawton 2000) or its local abundance (Gaston *et al.* 2004).

Janzen (1981, 1984, 1988) studied in detail the caterpillar communities of bombycoid moths in northwestern Costa Rica, characterizing them as relatively host-specific folivores under local conditions. Furthermore, he noted that the dichotomy in life history traits between the families Sphingidae (feeding, long-lived adults) and Saturniidae (non-feeding, short-lived adults; Janzen 1984) also extends to the larval feeding patterns of these groups. Janzen char-

acterized Neotropical sphingids as typically feeding on the young leaves of plants that contain small toxic molecules, which can be detoxified by specialized enzymes, whereas Saturniidae feed on tough, older leaves of plants with a high content of tannins or other molecules that negatively interfere with digestion (Janzen 1981, 1984). As a result, Sphingidae caterpillars eat many more nutrients ‘per bite’ and need less time to reach full size (Bernays & Janzen 1988). However, this dichotomy cannot be transferred directly to the Oriental and Australasian regions, where Saturniidae are much less speciose and their ‘ecological role’ might be taken over in part by the sphingid subfamily Smerinthinae (Holloway 1987a, b).

Data for studies on insect diet breadth have been produced either through laborious feeding trials of sampled insects in local field studies, allowing the comparison of food spectra and host specialization at one site (e.g., Barone 1998, Novotny *et al.* 2004, Janzen & Hallwachs 2004), or by using records compiled from published data that cover a larger spatial as well as temporal scale. The latter is particularly an option for those Lepidoptera taxa that can be reliably identified, allowing consistent cross-referencing between studies. Such data have been largely accumulated from caterpillars found and raised by enthusiasts for more than 150 years, and often from many different parts of a species’ range. However, even data of very well-sampled tropical taxa must still be suspected of being biased by undersampling to an unknown degree, no matter which of the two approaches is employed (Fiedler 1998, Basset *et al.* 2004).

We used host plant records of hawkmoth caterpillars (Lepidoptera: Sphingidae) from Southeast-Asia and Malesia (henceforth “SE-Asia”) to address the following questions:

- 1) Are there systematic differences in diet breadth between taxonomic sub-groups of the hawkmoths? In this context, is the diet breadth of sphingid caterpillars related to their phylogeny, as has been suggested for other taxa (e.g., Holloway & Hebert 1979)?
- 2) Is there a division of the utilized host plant spectrum between taxonomic subgroups of sphingids?
- 3) In comparison with European taxa, do SE-Asian sphingid species utilize a larger or smaller number of larval host plants (cf. Fiedler 1998), and do they utilize a different set of host plants?
- 4) Do host plant ranges have the potential to limit the geographical distribution of SE-Asian sphingids?

## METHODS

*Host plant data.* Larval host plant records for sphingids occurring in SE-Asia and Europe were assembled from both published literature and unpublished sources. One “record” refers here to a unique combination of moth species, plant species, location and source; multiple records (if they occur) of a given host plant for a given moth species typically stem from different countries or regions. This collation contains all data published by Robinson *et al.* (2001a, b) together with more recent corrections and additions. SE-Asia in this study is defined as stretching from Burma and Vietnam to the Solomon Islands (Beck & Kitching 2004), whereas we classified species as European if they occur west of the Urals and north of Turkey (species distributions from Pittaway 1997). We did not include summer migrants from tropical regions in the European data. For the purposes of Europe vs. SE-Asia comparisons we assigned the mainly Palearctic species *Deilephila elpenor* to the European data, whereas *Hyles livornica* was excluded from both data sets for regional diet breadth comparisons (see Beck & Kitching 2004 for distributions). No other non-migratory species are shared between both regions.

Sphingid species (nomenclature follows Kitching & Cadiou 2000, and subsequent taxonomic developments) were used as the lowest taxonomic level of this analysis, with subspecies data ignored. Host plants were generally identified at least to the level of genus, but we did not analyze them below the level of plant family. Plant family has often proved to be the taxonomically relevant level of host plant specialization in Lepidoptera (Ackery 1991, Ward & Spalding 1993). In addition, the use of higher taxonomic units in the analysis of plant data reduces the risk of artifacts from undersampling. Plant classification follows APG (2003). ‘Higher Taxon Orders’ (HTOs, equivalent to classical plant orders; APG 2003) were used as an additional level of host plant analysis.

The sphingid species *Hippotion boerbaviae* and *H. rosetta* are easily confused and were only confirmed as separate species in 1987 (Holloway 1987a). An unknown number of older *boerbaviae* records might therefore refer to *rosetta*. A similar problem occurs in the genus *Psilogramma*, where several subspecies have been elevated to species rank in recent years (Kitching & Cadiou 2000). We excluded data for problematic taxa from all analyses.

Undersampling can seriously bias analyses of host plant relationships (Fiedler 1998). To minimize such effects we based our statistical analyses on data from

TABLE 1. Number of monophagous (one utilized host plant family), oligophagous (2–3 host plant families), and polyphagous ( $\geq 4$  host plant families) species of SE-Asian sphingid (a) subfamilies and (b) tribes. Data in square brackets indicate additional species with less than 5 host plant records, which were excluded from analyses.

a)	Macroglossinae	Smerinthinae	Sphinginae				
monophagous	14 [43]	8 [14]	1 [3]				
oligophagous	20 [10]	5 [8]	2 [1]				
polyphagous	22	6[1]	6				
b)	Macroglossini	Dilophonotini	Ambulycini	Smerinthini	Sphingulini	Acherontiini	Sphingini
monophagous	14 [43]	0	0 [3]	7 [11]	1	0 [1]	1 [2]
oligophagous	19 [10]	1	2 [3]	3 [5]	0	0	2 [1]
polyphagous	21	1	4	2 [1]	0	3	3

species with at least five host plant records (see Table 1 and discussion for comparison to results from all data).

*Measuring diet breadth and host plant diversity.* We measured dietary niche breadth of moth species as the number of recorded host plant families and HTOs. Non-parametric Kruskal-Wallis ANOVA (StatSoft 2005) was applied to test for differences in diet breadth between higher taxonomic units (sphingid subfamilies, tribes). Highly skewed data (even after transformations) precluded the use of parametric techniques such as nested ANOVA. We calculated Fisher's  $\alpha$  ( $\pm 95\%$  confidence intervals; Southwood & Henderson 2000) as a measure of host plant diversity of subfamilies and tribes, using the cumulated number of records and of utilized host plant families within each higher taxon (software by Kenney & Krebs 1998). Fisher's  $\alpha$  scores were tested for significant differences using Solow's (1993) randomization test (two-sided, computed with software from Henderson & Seaby 2001).

*Phylogenetic independence.* A randomization method (Test for Serial Independence, TFSI; Abouheif 1999) was applied to test the assumption of phylogenetic independence of species' diet breadths. Randomized phylogenies ( $n = 3000$ ) were used to assess the likelihood that observed data relationships were due to chance. An updated version of the taxonomic classification in Kitching & Cadiou (2000) was used, allowing for unresolved nodes where applicable. Computations were executed with software by Reeve & Abouheif (2003).

*Analyzing similarity in host plant use.* We calculated various indices of similarity to quantify differences in host plant family use between pairs of species. Sørensen- and Dice-indices (Southwood & Henderson 2000) consider only presence and absence of a host plant family in a species' diet, whereas CNESS ( $m = 5$ ; Trueblood *et al.* 1994, using COMPAH, Gallagher 1998) also utilizes how often a species was recorded feeding on a given host plant family, i.e. how typical its use is. We used Multidimensional Scaling (MDS) to display the similarity of sphingid species according to their utilized host plant spectra. MDS is a powerful tool to ordinate ecological data that do not follow standard statistical distributions (Legendre & Legendre 1998) and has frequently been employed in biodiversity studies in recent years (e.g., Beck *et al.* 2002, Brehm & Fiedler 2004), whereas it has only rarely been used to analyze host plant relationships (Holloway & Jardine 1968). We tested similarity data for differences between higher taxonomic groupings (subfamilies, tribes) and regions (Europe, SE-Asia) by randomization of the similarity matrices (ANOSIM, 10000 randomizations; Primer-5 2002), using univariate and two-way nested designs.

*Host plant distribution.* To assess the potential impact of host plant distribution on sphingid ranges, we used moth distribution maps that were available through a GIS-supported range estimate (Beck & Kitching 2004). This estimate does not refer to plant distribution except by utilizing large-scale maps of land cover; hence data can be considered independent of host plant distributions. The geographical distribution of

TABLE 2. Frequency of distribution classes for 92 of 107 recorded larval host plant families of SE-Asian sphingids. See text for method of classification and data sources.\*) Occasionally refers to families that are not present in the new world.

Distribution class	Plant families
Worldwide*	27
Pantropical/subtropical*	41
Temperate (montane if in the tropics)	9
Restricted range	15

plant families for 98 of 107 recorded larval host plant families was found in various literature sources (van Steenis & Holttum 1959–2002, Ridley 1967, Keng 1969, Keng *et al.* 1998, Argent *et al.* 1999; data were converted to ‘classical’ plant families where applicable). We grouped descriptions of each family’s geographical range into four classes (Table 2). More than

two-thirds of the host plant families are either globally distributed or of pantropical range. These data are of little concern when looking for host plant ranges that potentially limit moth distributions, as the northern or southern limits of an equatorial moth species are more likely to be determined directly by climate rather than via host plant availability (Quinn *et al.* 1997, 1998). The remaining distribution classes were scanned for cases of common distribution limits of host plants and moths, i.e., plant families of mainly temperate distribution that do not occur in the tropics or are confined to montane and alpine regions, and plant families that had some other, idiosyncratic distribution limit in the Indo-Australian region. For each of these plant families we systematically examined 1) what species of sphingid feeds on it, 2) if one of the geographical limits of these moth species is congruent with that of the plant family, and 3) if the moth species does not feed on any other plant family that transgresses these limits. We used all available data (including species with fewer than five records) for these assessments.

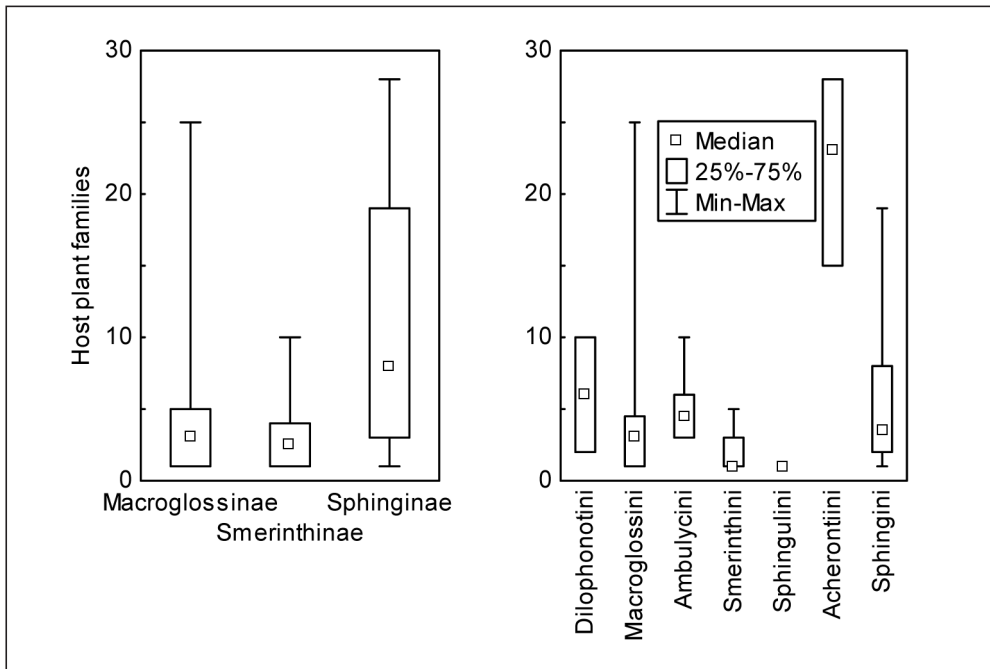


FIG. 1. Medians, quartiles and maxima of the number of utilized plant families per species for SE-Asian sphingid subfamilies (left graph) and tribes (right graph). See main text for test results.

## RESULTS

We had available 3081 host plant records for 165 SE-Asian sphingid species (43% of the known species in the SE-Asian region, Beck & Kitching 2004). The data include 107 plant families; the most commonly recorded families were Rubiaceae (with 55 sphingid species), Vitaceae (41 species) and Araceae (30 species). Our restriction of analyses to species with at least five records reduces these to 2924 records for 85 sphingid species (22% of known species), covering 102 families of plants. Analyzed data for European species refer to 21 sphingid species (1420 records).

*Diet breadth.* The numbers of recorded host plant families range from one to 28 for SE-Asian sphingid species. Frequencies of monophagous, oligophagous, and polyphagous species in each sphingid subfamily and tribe are shown in Table 1. The median number of host plant families per species for sphingid subfamilies and tribes is displayed in Fig. 1. Non-parametric KW-ANOVA indicates differences between sphingid subfamilies ( $N = 85$ ,  $H_{df=2} = 6.04$ ,  $p < 0.05$ ) as well as tribes ( $H_{df=6} = 17.30$ ,  $p < 0.01$ ); the results are significant after applying the sequential Bonferroni correction of Hochberg (1988). Multiple post-hoc  $z$ -tests after significant KW-ANOVA results indicate a higher diet breadth in Sphinginae than in Smerinthinae ( $z = 2.42$ ,  $p < 0.05$ ), which is mainly caused by the tribe-level difference between Acherontiini and Smerinthini ( $z = 3.40$ ,  $p < 0.02$ ). Very similar patterns of diet breadth are repeated at the level of HTO (data not shown), suggesting that the results are not artifacts of undersampling biases. Furthermore, subfamilies and tribes do not vary significantly in the number of host plant records (KW-ANOVA,  $N = 85$ ; subfamilies:  $H_{df=2} = 4.89$ ,  $p = 0.087$ ; tribes:  $H_{df=6} = 10.39$ ,  $p > 0.10$ ).

*Diversity of host plants.* The diversity of utilized host plant families differs significantly between subfamilies (Solow-test,  $p < 0.05$ ; see Table 3 for Fisher's  $\alpha$  scores): Smerinthinae use a much less diverse array of host plants than Macroglossinae or Sphinginae. Within subfamilies, we found significant differences between the tribes Dilophonotini (based on 2 species only) and Macroglossinae, but not between the Ambulycini and Smerinthini or the Acherontiini and Sphingini (although confidence intervals are non-overlapping in the latter pairing, Table 3). Results are significant after applying the sequential Bonferroni correction of Hochberg (1988).

TABLE 3. Diversity of host plants (Fisher's  $\alpha$ ) for SE-Asian sphingid subfamilies and tribes; insufficient data did not allow a computation of Fisher's  $\alpha$  for the tribe Sphingulini.

	Fisher's $\alpha \pm 95\%$ CI
Macroglossinae	15.9 $\pm$ 1.7
Macroglossini	15.9 $\pm$ 1.8
Dilophonotini	2.8 $\pm$ 0.9
Sphinginae	14.2 $\pm$ 2.1
Sphingini	7.5 $\pm$ 2.1
Acherontiini	12.0 $\pm$ 2.0
Smerinthinae	6.7 $\pm$ 1.5
Smerinthini	4.2 $\pm$ 1.1
Ambulycini	5.7 $\pm$ 2.5

*Phylogenetic signal in diet breadth.* TFSI simulation results indicate that the null hypothesis of a phylogenetic independence of diet breadth can be rejected with an error probability of  $p < 0.001$ . Closely related taxa use a more similar number of plant families than do less related taxa (note that this test does not refer to the identity of plant taxa).

To account for the possibility of subfamily-specific undersampling (see discussion), we also tested the largest subfamily separately for phylogenetic independence. Diet breadths were found to be dependent on phylogeny within the Macroglossinae ( $p < 0.01$ ), hence confirming the results found for the whole family Sphingidae.

*Differences in host plant composition: phylogeny and region.* A dietary segregation at plant family level between higher taxa of the Sphingidae is not directly evident. We did not observe entirely exclusive diets for subfamilies or tribes. We use MDS based upon Dice indices to display similarities of SE-Asian and European species according to the overlap in their host plant families (Fig. 2). One-way ANOSIM results indicate significant effects of subfamily association (Global  $\rho = 0.361$ ,  $p < 0.0001$ ; Macroglossinae differ significantly from both Smerinthinae ( $\rho = 0.435$ ) and Sphinginae ( $\rho = 0.271$ , both  $p < 0.0001$ )) and tribes (Global  $\rho = 0.350$ ,  $p < 0.0001$ , see Fig. 2 legend for details). Regional differences, on the other hand, have only a weak, non-significant effect on host plant spectra (Global  $\rho = 0.066$ ,  $p = 0.075$ ), but become significant if controlled for subfamily association in a two-way cross design (Region:  $\rho = 0.148$ ,  $p = 0.005$ ;

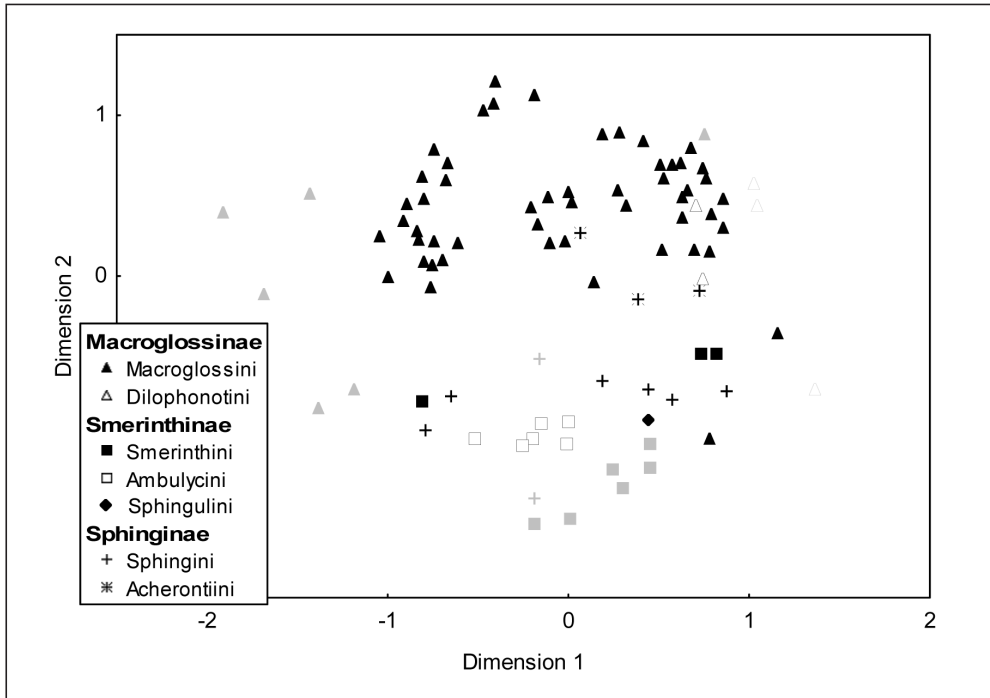


FIG. 2. Two-dimensional MDS plot (stress = 0.290) of 75 SE-Asian (black) and 15 European (grey) sphingid species ordinated by larval host plant family use. Due to computational constraints only 90 species could be included in the MDS plot, but all 105 species were used for statistical testing. Significant differences (one-way ANOSIM,  $p < 0.05$ ; Primer-5 2002) were found between the tribes Smerinthini *vs.* Macroglossini; Ambulycini *vs.* all non-Smerinthinae tribes; Sphingini *vs.* both tribes of the Macroglossinae (see main text for further data, two-way testing and results based on CNESS).

Subfamily:  $\rho = 0.398$ ,  $p < 0.0001$ ). A two-way nested design of subfamilies and tribes does not yield significant results for either group ( $\rho = 0.338$ ,  $p = 0.105$  and  $\rho = 0.132$ ,  $p = 0.083$  respectively). Results based on Sørensen indices are almost identical.

Analyses based upon CNESS take into account the abundance of records for an assessment of similarity and are supposedly more robust against under-sampling biases. One-way ANOSIM results confirm the effects of subfamilies (Global  $\rho = 0.175$ ,  $p < 0.0001$ , significant differences between all three subfamilies) and tribes (Global  $\rho = 0.175$ ,  $p < 0.0001$ ), but also indicate a significant difference between regions (Global  $\rho = 0.081$ ,  $p < 0.0001$ ): In an MDS plot (not shown), European Macroglossini appear far distant from all other species. Furthermore, a two-way cross design confirms significant effects of both sub-

family and region (Region:  $\rho = 0.168$ ; Subfamily:  $\rho = 0.226$ , both  $p < 0.0001$ ), and a nested two-way design of taxonomic grouping yields a significant difference between subfamilies ( $\rho = 0.625$ ,  $p = 0.029$ ), independently of the non-significant differences between tribes ( $\rho = 0.065$ ,  $p = 0.102$ ). Hence, phylogenetic effects on host plant use are probably mostly found at the subfamily level. Nested ANOVA analysis of MDS scores (not shown) led to similar conclusions.

*Diet breadth in European and SE-Asian species.* Average numbers [ $\pm$  SD] of recorded host plant families are not different in 83 SE-Asian ( $4.9 \pm 5.8$ ) and in 21 European species ( $5.6 \pm 5.8$ ; Mann-Whitney U-test:  $z = -0.615$ ,  $p = 0.538$ ). However, even in this data set (only species  $\geq 5$  records) European species have a significantly larger number of host plant records ( $z = -3.22$ ,  $p < 0.01$ ). The inclusion of species

with fewer than five records (data not shown) would lead to a much lower score of diet breadth for SE-Asian species, which is almost certainly an under-sampling artifact.

*Host plant distributions and their effect on SE-Asian sphingid ranges.* We did not find a single case suggesting an influence of plant family range on moth distributions among the temperate or tropical-montane plant families (Table 2). Most sphingid ranges were either considerably more equatorial than the respective food plant (because they also fed on other plants) or they also fed on other food plants with a tropical distribution, so their temperate range was not due to food limitation in tropical areas (e.g., *Deilephila elpenor*, which only barely stretches into tropical regions, but is frequently recorded on plant families of tropical distribution such as Araceae or Balsaminaceae). The closest case to a potential distribution limit due to food plant availability is the genus *Sphinx*, where two species that occur in SE-Asia feed exclusively on Pinaceae. This plant family does not commonly occur in most lowland regions in tropical Asia and *Sphinx* species are not found below 1000 meters altitude south of 25°N latitude (the genus is found as far south as 18°N in Thailand and 15°N in Vietnam; some records have no altitude information, but all locations are in mountainous regions). However, some species of pine trees (genus *Pinus*, which is frequently recorded as a host plant genus for *Sphinx*) do naturally occur in some lowland areas of Sumatra, Luzon, and Mindoro, where *Sphinx* is not found.

Among the 'restricted range' distribution class (Table 2) we found only one potential candidate for a host plant limitation of moth range: *Eupanacra malayana* feeds apparently exclusively on Hypoxidaceae (three records from Java and the Malay Peninsula, all from the genus *Curculigo*). The host plant family is distributed in the Southern Hemisphere and tropical Asia, whereas the moth occurs from Sikkim in the Indian Himalaya foothills eastwards to the Wallace line, on the Lesser Sunda Islands as far east as Sumbawa (Beck & Kitching 2004). Thus there is a possibility that the moth is limited in its northern distribution by the range of the host plant, but a direct influence of climate might also produce the observed distribution. There is no host plant family range that would explain any of the prominent biogeographic boundaries within the Malasian archipelago (Hall & Holloway 1998), which appear to be less influential on plant distribution (Roos *et al.* 2004) than on sphingids (Beck *et al.* 2006a, in press).

## DISCUSSION

*Differences between taxonomic groups.* Subfamilies and tribes differ in the number of plant families that are utilized per moth species (Fig. 1) and even show strong tendencies to differ in the number of HTOs (data not shown). In particular, many species of the subfamily Sphinginae are recorded on a large number of plant taxa, some of which are not used by any other oriental sphingid. The diversity of utilized plant families for whole subfamilies indicates a slightly different trend: Smerinthinae are recorded from a much less diverse array of plant taxa than other subfamilies, although average number of host plant families per species does not differ significantly from that of Macroglossinae. Thus some ecological or phylogenetic constraint may limit the diversification of Smerinthinae host plant choice. Phylogenetic conservatism in the adaptation of herbivores to plant secondary compounds, for example, can have a great influence on insect-plant interactions (Mitter *et al.* 1991, Farrell & Mitter 1993, Miller & Wenzel 1995). Hilt & Fiedler (2006) recently suggested that preferences of arctiid moth species for disturbed *vs.* undisturbed montane sites in Ecuador might be connected to their degree of polyphagy. Our data superficially indicate similar trends (Fig. 1), since Smerinthinae, for example, are typically associated with undisturbed forest in Borneo (Beck *et al.* 2006b).

To investigate in more depth if there is a relationship between diet breadths, local abundance and habitat disturbance we carried out a comparative analysis, using light-trapping data from 47 sites in Borneo (see Beck *et al.* 2006b for details). Within each site we correlated the number of host plant families used by a species with its relative local abundance (omitting species without any host plant information). We then used categorical meta-analysis (Rosenberg *et al.* 2000) to test if there are differences in the strength or direction of this relationship, depending on the habitat type (in three classes of disturbance). Results indicate that there are no differences between habitats (effect size Fisher's  $z_t \pm 95\% \text{ CI} = -0.07 \pm 0.14$  for primary forests,  $z_t = -0.17 \pm 0.19$  for secondary forests,  $z_t = 0.00 \pm 0.25$  for open, agricultural habitats); testing for data heterogeneity revealed no differences between categories other than expected due to sampling error ( $Q_{T(df=46)} = 32.7, p = 0.93$ ). Furthermore, summarized effects are not significantly different from zero in any habitat category, with a trend to a negative relationship (i.e., abundant species have narrow diet breadths) in secondary forests. However, it has to be noted that

all species with any host plant information were used in this analysis to maximize statistical power, which might bias results due to incompletely known host records (see below). Data were also not corrected for phylogenetic non-independence.

Holloway (1987a) suggested that host plant utilization of Smerinthini *vs.* Macroglossini in Borneo does not overlap much. Although we could not confirm exclusive diets between any investigated groups, we found a strong separation of host plant taxa between Macroglossinae and the other subfamilies (Fig. 2). Interestingly, Holloway (1987a) argued that the discrepancy between the 'slight overlap' in his data (Bornean species, but host plant data of these species from their Indo-Australian range) and the strict separation in host plant families in Janzen (1984) may be a result of the larger geographical scale of host plant data acquisition. If this is correct for whatever reason (e.g., incompleteness of data from small regions, or local adaptation of species), it might explain why data for SE-Asian species, using global host plant data for these species, produce even more overlap between subfamilies and tribes.

Our analyses do not allow conclusions on the quality of host plants, e.g., if there are common traits (in structure or chemistry) among the food plants of certain taxa. Smerinthinae might utilize trees more often than other subfamilies (Holloway 1987a), which is a common trait among species with a reduced proboscis (Miller 1997). However, host plant data await further analyses in order to confirm hypotheses on a relationship between host plant availability and diversity patterns along habitat gradients (Beck *et al.* 2006b, Schulze 2000).

*Temperate-tropical comparison.* The diet breadths of insects from tropical and temperate regions might differ for various reasons: tropical species might be expected to be more specialized (explaining the high diversity of equatorial regions by a finer separation of niche space), or they might be more generalist in order to compensate for a higher floristic diversity, hence lower abundance of specific plants, in the tropics (see Fiedler 1998 for references and thorough discussion). Our results corroborate Fiedler's (1998) assessment of no difference in diet breadth between SE-Asian and European butterflies, but show, on a large set of data, the importance of phylogeny. Sphingidae, despite being of the same insect order as butterflies, are substantially different in many life-history traits, which justifies a generalization of our results. Assumptions of very high host specificity in herbivorous tropical

beetles may have led to overestimates of tropical invertebrate diversity in the past (Ødegaard *et al.* 2000 and references therein). Judged by the evidence that is so far available for Lepidoptera (Fiedler 1998, this paper), it might be reasonable to use known figures of host plant specificity for well-sampled temperate taxa to extrapolate to taxonomically related, tropical groups (but see discussion on local adaptation below). Our results are less conclusive regarding utilized host plant spectra, where regional differences are clearly weaker than phylogenetic effects (i.e., differences between subfamilies), but are still significant if controlled for subfamily association, or if quantitative similarity measures (e.g., CNESS) are used.

*Host family range as a limiting factor for moth range.* We could find no evidence corroborating the hypothesis that host plant range is a limiting factor for sphingid distribution with the preliminary approach that is presented here. This supports the conclusion of Quinn *et al.* (1997, 1998) on British Lepidoptera that food plant presence is a necessity for moth presence, but other factors such as climate or dispersal barriers keep a moth's range considerably smaller than the combined range of its host plant families. However, a more careful approach, including a more thorough compilation of host plant distribution records and subsequent GIS-based analysis might, in the future, bring further and more detailed insights into this matter.

Our results may be affected by flaws in data quality due to undersampling biases and local adaptation of host plant use. We will show in a detailed discussion below why we believe that both issues can be tentatively ruled out as strong caveats on our conclusions, but the limited completeness of host plant data makes all analyses of this kind preliminary.

*Biases due to incomplete and erroneous data.* Food plant records for tropical Lepidoptera are generally incomplete – even for well-sampled butterfly taxa, life-history information is available only for about 50% of the species in Malaya and Borneo (Fiedler 1998). It must be assumed that locally common, widespread species have a higher chance of being investigated. Furthermore, much of the host plant data stem from relatively old sources (e.g., almost 45% of records on Sphingidae were published earlier than 1950). The completeness of the host plant range of species might be influenced by the choice of sampling sites of early researchers (often amateur European expatriates) – it is unlikely that the host plant range of a species oc-



curing in an inaccessible area (e.g., forests and mountains of central New Guinea) is as well known as that of a taxon feeding on garden ornaments in former colonial strongholds (e.g., the 'hill stations' of India and Malaya). The use of higher taxonomic units of host plants helps to diminish the effects of undersampling, but a dependence of recorded host plant families and even HTOs on the number of records is still evident in data even after exclusion of species with less than five records (Fig. 3). This relationship might be due to undersampling, but it might just as well be caused by a publication bias against 'duplicate' rearing records from already known host plants. The true magnitude of these biases is extremely difficult to assess or correct for, as species with an ecological preference for disturbed areas (e.g., gardens) might genuinely have a wider geographical range and be more generalist than primary forest specialists (see, e.g., Ricklefs & Bermingham 2002 and references therein). However, while the above mentioned biases

have the potential to produce artifact results (Smerinthinae, for example, are apparently less polyphagous than other subfamilies, but are also less abundant and less speciose in disturbed habitats in Borneo; Beck *et al.* 2006b), we did not find specific indications of undersampling biases, such as significant differences in the number of records between tested groups, in our data. However, all our conclusions are based on less than a quarter of the species present in the SE-Asian region. The inclusion of 80 species with fewer than five records did generally lead to similar conclusions, but yielded more significant results due to increased statistical power, particularly in tests on tribe level. Some of these are ecologically very interesting, e.g., a dietary segregation between Ambulycini and Smerinthini (data not shown) that might relate to differences in life history between these taxa (cf. Beck *et al.* 2006b).

Errors in host plant data are common in the Lepidoptera literature (see Fiedler 1998 for discussion and

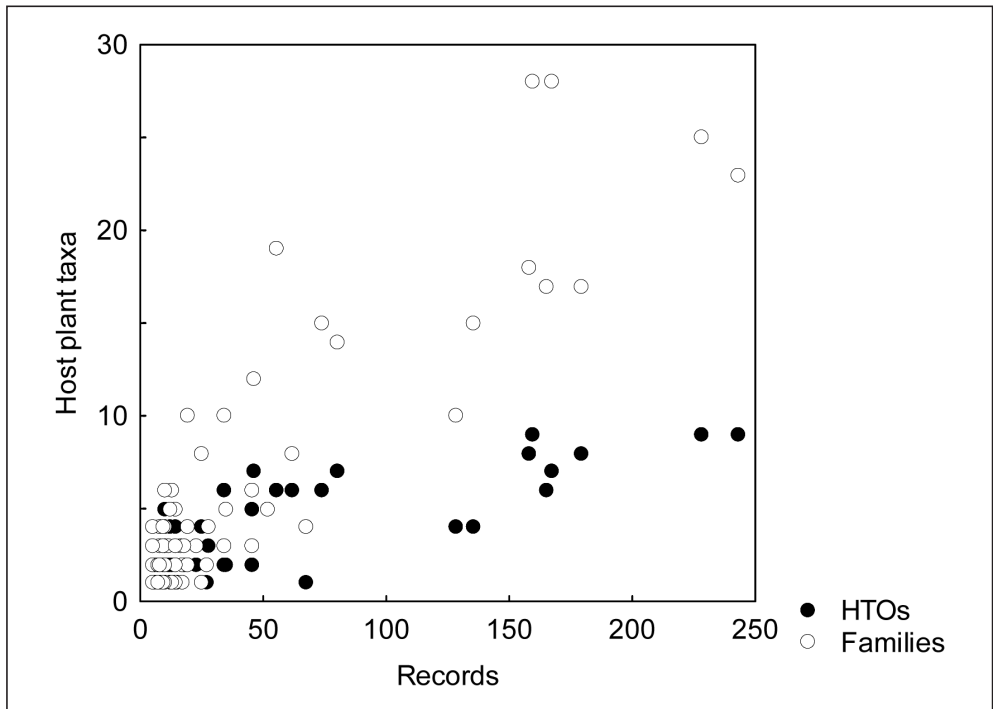


FIG. 3. Numbers of host plant taxa for SE-Asian sphingid species are not independent, but increase with the number of records at Higher Taxonomic Order ( $N = 165$ , Spearman's  $R = 0.826$ ,  $p < 0.001$ ) and plant family level ( $R = 0.835$ ,  $p < 0.001$ ).

references on butterflies) and might refer to misidentification of the moth, or the plant, or incorrect information on the location. All data for 'confirmed' errors were excluded from the analyses, but about 2.5% of the utilized data remain unconfirmed or questionable (I.J. Kitching, unpubl.). Thus erroneous reports might still be contained in the data, but probably not at a frequency that could produce serious biases.

*Local adaptation.* Janzen (1988) suggested that species with long lists of host plant records might actually be fairly specific under local conditions, but accumulate a lot of records over their wide geographical range (i.e., their fundamental niche is much wider than their realized niche, Fiedler 1998; see Kawecki & Ebert 2004 for theoretical aspects). Generally, geographic variation in local resource utilization behavior is known from a number of animal species (e.g., Foster 1999). Furthermore, browsing Janzen & Hallwachs' (2004) online databank of Sphingidae caterpillar host plant records from Costa Rica (a small country) gives the impression that most species are quite specific to one or two plant families. Host plant feasibility for a herbivore insect can differ significantly between regions (even within the same plant species) on a much smaller scale than considered here (Mody 2003, see also Bangert *et al.* 2005). Indeed, species with a wide range of recorded host plants are more wide-spread than host-specific species (Beck *et al.* 2006c), but the cause of this relationship might also be the other way around: polyphagous species might be able to extend their range more easily than host-specific taxa (Gaston *et al.* 1997).

Data for SE-Asian sphingid caterpillars with feeding records on a large number of plant families do not support the idea of local specialization for the four species with the largest number of recorded host plants (23–28 families). Using a quite broad definition of 'local', we calculated mean host plant families per country, but used only countries with at least four records. China was treated as two regions (north and south), whereas no such separation was possible for Australia and India due to many unlocalized records. Indonesian records were exclusively from the western part of the country (Java and Sumatra). Data of host plant families per country are (mean  $\pm$  SD [N: number of countries]): *Hyles livornica*: 4.8  $\pm$  2.0 [N = 9], *Acherontia lachesis*: 6.6  $\pm$  4.1 [N = 10], *Hippotion celerio*: 4.5  $\pm$  2.1 [N = 15], *Agrius convolvuli*: 2.3  $\pm$  1.1 [N = 18]. Thus three out of four species would still

be judged as polyphagous at country level even though undersampling biases are evident in these data (often four records refer to 3–4 host plant families). Only *A. convolvuli* appears far more restricted in its country-wide feeding habits than across its global range.

Similarly, we analyzed for differences in the host plant choice of subspecies for two species with a valid subspecies distinction (Kitching & Cadiou 2000) and sufficient host plant heterogeneity and sample sizes. As a species, *Theretra latreillii* (see distribution maps in Beck & Kitching 2004) is recorded from 11 host families, with the eastern subspecies *latreillii* on six families and the western subspecies *lucasii* on ten; five plant families are shared between the subspecies. Both subspecies separately would still be considered polyphagous. The same applies to *Theretra oldenlandiae* (15 host plant families), with subspecies *oldenlandiae* recorded on 13 and subspecies *levini* on nine families (seven families shared). Under the assumption that the number of records in the data bank reflects the preference of moth taxa for a certain plant family, frequency tables of subspecies  $\times$  plant family can be tested for non-random differences that would also serve as an indication of local adaptation. No significant effect was found for *T. latreillii* (N = 76,  $\chi^2_{df=10} = 10.64$ ,  $p = 0.384$ ), whereas there is a difference in *T. oldenlandiae* (N = 153,  $\chi^2_{df=15} = 35.78$ ,  $p < 0.001$ ).

Novotny *et al.* (2004) suggested in an analysis of New Guinean caterpillar communities that local food plant adaptation might be very specific for most species, supporting the idea of 'geographic accumulation' of food plant records in wide-ranging species despite local monophagy. However, it might be worth comparing such studies with temperate European examples, where 250 years of forest zoology and pest control have produced a far better understanding of host plant relationships of herbivorous insects. For example, like most species in the New Guinean community of Novotny *et al.* (2004), in most years >90% of caterpillars of the geometrid moths *Operophtera brumata* and *O. fagata* are found on oak (*Quercus* sp.) and beech (*Fagus* sp.), respectively (both Fagaceae; e.g., Wint 1983, K. Fiedler, pers. comm.). However, both species have the potential to feed on very different plant taxa, particularly if the normal hosts are not available (e.g., in years of oak defoliation by pest insects), such as blueberry (Ericaceae), apple and cherry (Rosaceae; *O. brumata* can be a pest on plantations). Some other studies on widespread, polyphagous but-

terflies also failed to find local host adaptation despite favorable conditions for its evolution (Wehling & Thompson 1997, Bergström *et al.* 2004 and references therein), possibly because variable habitat conditions exhibit selective pressure to retain the ability of utilizing alternative hosts (Bergström *et al.* 2004). Thus it makes a difference if the matter of 'polyphagy' is viewed from the plant's perspective (where certain insect species are typical, apparently specialized predators) or the herbivore's perspective, where some species are truly monophagous by behavioral or physiological constraints, whereas many others might have the potential to switch host if the conditions make it advantageous. Ward & Spalding (1993) noted in a thorough analysis of the known host plant relationships of British phytophagous arthropods that, unlike most other arthropod taxa, the larger-bodied Lepidoptera families contain a relatively high proportion of polyphagous species (about 50% of the species feed on  $\geq 3$  plant families).

It might be argued that our *a priori* assumption of plant family as the relevant taxonomic unit of host plant specialization might be wrong (e.g., Novotny *et al.* 2002c). As a first assessment of this objection we used those species ( $\geq 5$  records) that are recorded as monophagous on one plant family. Of these 23 species (Table 1), we counted how many genera and species within their host plant family were recorded as larval hosts. Means  $\pm$  SD were  $4.3 \pm 2.5$  for plant genera and  $7.0 \pm 3.7$  for species. Hence, specialization on a species or even genus appears uncommon. In our data, only two cases of plant genus specialization were observed: *Hippotion rafflesii* is only recorded from *Impatiens* (Balsaminaceae, 7 records), and *Nephele hespera* seems to feed only on *Carissa* (Apocynaceae, 8 records).

[A list of the species included in our analyses is available at <http://www.gtoe.de/publications/top-publications.htm>; see table of contents of this issue]

## ACKNOWLEDGMENTS

We thank Konrad Fiedler, Jeremy D. Holloway, and an anonymous referee for manifold suggestions and interesting discussions on Lepidoptera host plant relationships. Dayang Siti Nortasha helped with the literature research of host plant distributions. The study was financed by scholarships from the German Research Council (DFG, Graduiertenkolleg), the German Academic Exchange Service (DAAD), and the Sys-Resource program of the European Union.

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