

Host specialization of leaf-chewing insects in a New Guinea rainforest

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Summary

1. Data on host use by herbivorous insects in the tropics cannot be cross-referenced between the studies as only a fraction of the species can be formally identified. It is thus imperative for each study to include a wide range of plant and insect taxa, but this requirement has rarely been met because of logistical difficulties.
2. A novel approach using mass insect collecting and rearing by parataxonomists was applied to study the use of 59 species, 39 genera and 18 families of woody plants by 58 588 individuals and 1010 species of leaf-chewing insects in a lowland rainforest.
3. Most species had wide host plant ranges with reference to congeneric plants. The modal host range for a herbivore feeding on a particular genus (*Ficus*, *Macaranga* or *Psychotria*) included >90% of congeneric species studied. Only 3·7% of species feeding on these genera were monophagous.
4. Most herbivores were specialized with respect to confamilial plant genera, with modal host range of 1 genus from 9 studied in Euphorbiaceae and 13 in Rubiaceae. This pattern was corroborated by modal host range of 1 plant family from 18 studied.
5. Because of the overlap among the herbivore communities on congeneric plants, the total number of herbivores on speciose plant genera was relatively small. For example, although 336 species of leaf-chewers used the 13 study species of *Ficus*, the 35 additional *Ficus* species present locally would support only estimated 163 additional species.
6. Since large genera constitute a significant proportion of tropical floras, these results have implications for regional estimates of herbivore species richness. Our estimate of 10·6–24·1 leaf-chewing species effectively specialized to a rainforest tree species is an order of magnitude lower than previously suggested.
7. The number of new herbivore species (y) resulting from the addition of the x th plant species to the compound community ($x = 1, 2, 3, \dots, n$ where n is the total number of plants studied) can be described as $y = cx^k$, where c and k are constants. k is a useful descriptor of similarity among herbivore communities from different hosts.

Key-words: herbivore communities, insect–plant interactions, Papua New Guinea, species richness, tropical forests.

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Introduction

Host plant range is a key ecological characteristic of herbivore species as it defines their resource base,

which in turn is an important factor influencing their population dynamics and interactions with other herbivorous species, predators and parasites. At the same time, host plant range represents a record of past evolutionary interactions between the herbivore and plant lineages, thus providing clues about the role of historical processes in shaping contemporaneous ecological communities.

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Despite its theoretical and practical importance, research on the host specificity of insect herbivores has progressed slowly in the tropics (Basset 1992; Gaston 1993). Detailed information on host plant range is available only for a few conspicuous and comparatively species-poor groups of tropical insects, such as butterflies (Ackery 1991; Fiedler 1995, 1998). Insufficient taxonomic knowledge of tropical insects and, to a lesser extent, plants renders host plant data particularly prone to biases due to inadequate sampling of rare or unpopular plant or insect species (Janzen 1993; Kitching 1993). Although even relatively comprehensive studies of temperate areas are imperfect (Owen 1987; Ward 1988), information on tropical species, outside agricultural and forestry systems, is typically only anecdotal.

Patterns of local host plant use by herbivore communities have been studied in several tropical forests (Janzen 1988; Marquis 1991; Marquis & Braker 1993; Basset 1996, 1999; Barone 1998). Such local studies, using standardized sampling protocols, can produce quantitative data for both common and rare plant and insect species including those of uncertain taxonomic affiliation. However, host plant data generated by these studies cannot be supplemented by information from other sources as usually only a fraction of the insect material can be formally identified and the species cross-referenced with other studies. Since the host specificity patterns they reveal are contingent on the selection of plant and insect species sampled, it is imperative for such studies to include a wide range of local plant and insect taxa. This requirement has rarely been met, owing to logistical difficulties. With the exception of Janzen's (1988) study, limited to macrolepidoptera, existing data sets describe herbivore communities from a limited number of plant species, or are restricted to either closely (Marquis 1991) or distantly (Basset 1996) related plants.

Recently, a novel approach using mass insect collecting by parataxonomists has allowed an expansion of the scope of ecological studies of rainforest insects (Janzen *et al.* 1993; Basset *et al.* 2000). The present study, based on such large-scale insect collecting, examines local host specialization in the communities of leaf-chewing insects on a selection of 59 rainforest species of woody plants, including both closely and distantly related hosts from 39 genera and 18 families. It describes host specificity patterns with particular emphasis on the relative importance of specialists and generalists in herbivore taxa and communities, the overlap in the composition of herbivore communities between closely and distantly related hosts, and methodological problems of estimating host specificity in rainforest communities.

Methods

STUDY AREA AND HOST PLANTS

The study area extended from the coast to the slopes of the Adelbert Mountains, Madang Province, Papua New Guinea. Fieldwork was concentrated in primary

and secondary lowland forests near Baitabag, Ohu and Mis Villages (145°41'–7'E, 5°08'–14'S, *c.* 0–200 m). The average annual rainfall in the Madang area is 3558 mm, with a moderate dry season from July to September; mean air temperature is 26.5 °C and varies little throughout the year (McAlpine, Keig & Falls 1983).

Fifty-nine locally common species of trees and shrubs, including 13 species of *Ficus* and 1 species of *Artocarpus* (Moraceae), 6 species of *Macaranga* and 8 species representing 8 other genera of Euphorbiaceae, 4 species of *Psychotria* and 12 species representing 12 other genera of Rubiaceae, and 15 species representing 15 other families of flowering plants were selected for the study of their insect herbivores (Appendix). This selection included the major lineages of flowering plants as recognized in a recent phylogenetic classification (APG 1998), viz. gymnosperms, monocotyledons, basal eudicots, euasterids I and II, and eurosids I and II. Further, it included locally common plants from all main habitats within the study area, including early and late stages of forest succession as well as riverine habitats (Leps, Novotny & Basset 2001).

Moraceae, Euphorbiaceae and Rubiaceae are important components of tropical floras (Gentry 1988). They are also abundant and species-rich in the Madang area, as well as in other lowland rainforests in New Guinea (Oatham & Beehler 1998; Miller *in press*).

Ficus is an exceptionally large, pantropical genus, with over 700 species (Berg 1989). New Guinea is one of the main centres of its diversity with 135 described species (Corner 1965). In the lowlands around Madang, there are at least 48 species of *Ficus* (G. Weiblen personal communication), from which 13 were selected for the present study. Species richness of Moraceae other than *Ficus* is rather low both in New Guinea (22 species in 11 genera, Höft 1992) and in the Madang area (V. Novotny personal observation).

There are 461 species of Euphorbiaceae reported from New Guinea, 73% of them being endemic (Airy Shaw 1980; van Welzen 1997). *Macaranga*, with over 280 species distributed from West Africa to the western Pacific, is the largest genus of early successional (pioneer) trees in the world (Whitmore 1979). New Guinea is the main centre of diversity for this genus, with 82 described species (van Welzen 1997). It is also the most species-rich genus of Euphorbiaceae locally, with a conservative 12 species present in the study area (V. Novotny personal observation). The other eight species of Euphorbiaceae, one per genus, include species from four out of the five subfamilies of Euphorbiaceae recognized by Webster (1994).

Rubiaceae, with 838 species, is the most species-rich family of woody plants in New Guinea (Höft 1992). *Psychotria*, with 124 New Guinean species described (Höft 1992) and perhaps as many as 200–300 species in New Guinea (Sohmer 1988), is the largest genus of the family, and New Guinea is a major centre of its diversity in the Old World (Sohmer 1988). The other 12 species of Rubiaceae, one per genus, included

species from all three currently recognized subfamilies (Bremer, Andreasen & Olsson 1995).

INSECT SAMPLING

All externally feeding, leaf-chewing insects (Orthoptera, Phasmatodea, Coleoptera and Lepidoptera), including leaf rollers and leaf tiers, were collected by hand or by the use of an aspirator. Both young and mature foliage from shaded and sun-exposed locations was sampled from each plant species. Taller trees were climbed or lower, more accessible branches were examined. Five collecting teams, usually including three people per team sampled insects. All tree species were sampled for the period of at least one year: *Ficus* from July 1994 to March 1996, Euphorbiaceae from August 1996 to August 1997, Rubiaceae from March 1998 to April 1999 and the remaining species from May 1999 to May 2000.

Sampling effort was recorded as the time spent searching the foliage of each plant species for insects, which was approximately proportional to the leaf area examined. The foliage area sampled was identical for all plant species and amounted to 1500 m² per species. The number of tree inspections, that is, a particular tree sampled at a particular time, exceeded 1000 per plant species. This sampling effort represented approximately 1500 person-days of fieldwork.

In the laboratory, each insect was provided with fresh leaves of the plant species it was collected from and kept on it until the insect fed or died (Basset *et al.* 2000). Only the specimens that fed were considered in the analyses. Caterpillars were reared to adults whenever possible. The feeding tests produced 1010 insect morphospecies and 58 588 individuals with confirmed ability to feed on the plant species from which they were collected. All morphospecies were subsequently verified by specialist taxonomists and identified as far as possible so that they correspond to species, except that they have not been formally described and named. Part of the taxonomic information is detailed in Novotny *et al.* (1999) and on the web at http://www.nmnh.si.edu/new_guinea/. Voucher specimens are deposited in the Bishop Museum (Honolulu) and Smithsonian Institution (Washington).

The body length multiplied by thorax width was used as an index (in cm²) of the species' biomass. Only the largest leaf-chewing stages, i.e. caterpillars in Lepidoptera and adults in other taxa, were measured. Average value was estimated from 10 measurements whenever possible, but only the largest available measurement was used for caterpillars, in order to approach the size of the last instar. Measurements were performed on dry, mounted specimens, except for caterpillars that were measured when alive (Novotny & Basset 1999).

HOST SPECIFICITY

Only those plant species on which a particular herbivore species was collected and able to feed in the laboratory

were considered host plants. Host specificity was measured as the number of host plant taxa ascertained for each insect species, viz. the number of host *Ficus* species, *Macaranga* species, *Psychotria* species, Euphorbiaceae genera, Rubiaceae genera and plant families. This measure was chosen over indices measuring the variance of the distribution of individuals among the host plants, such as the Shannon–Weaver index (Futuyma & Gould 1979) or Lloyd's index (Novotny & Basset 1998), since it was more amenable to further analysis of phylogenetic relationships and ecological similarity among hosts. However, because they require decisions about whether a particular plant is a host species or not, these approaches are also more sensitive to sampling error. Rare insect species were therefore excluded from the analysis, to avoid artificial inflation of host specificity estimates due to insufficient opportunity to detect rare hosts.

The average proportion of herbivore species feeding on a particular host plant, which is unique (or 'effectively specialized') to this plant, was estimated as the ratio of the total number of herbivore species found on all hosts studied, divided by the number of host plant records involving these hosts (May 1990).

For an adequate description of the host plant range of a polyphagous species, it is necessary to collect substantially more individuals than the number of the potential host plant taxa analysed. For instance, for a herbivore that is equally abundant on all its *H* hosts, a random sample of $N = 2H$ individuals will record, on average, 88% of its hosts (V. Novotny unpublished results). In order to describe the host plant range with more than 95% accuracy, approximately three times as many individuals as hosts would be needed. In reality, the underestimation of the true host plant range will be higher because this simulation did not account for the fact that herbivores are often distributed unevenly among their hosts.

Data filtering using a high minimum abundance threshold, although adequate for polyphages, may selectively exclude specialized herbivores, thus underestimating their importance. Most sampling protocols, including the present one, maintain constant sampling effort per plant species studied so that the combined sampling effort on their host plants is lower for specialists than for generalists. The number of individuals needed to characterize host ranges of specialists is lower than that for generalists. For example, although 30 individuals may not be enough to characterize the host range of a polyphagous species feeding on 15 hosts, it is more than enough to confirm monophagy of a species with respect to these hosts. For specialists, minimum abundance per host species, rather than per all species studied, is a more appropriate selection criterion.

The effect of data filtering using increasing minimum total abundance and minimum abundance per host species thresholds on host specificity estimates was explored for herbivore communities from all plant taxa analysed (Fig. 1). With the exception of *Ficus* spp., host specificity estimates stabilized for data sets

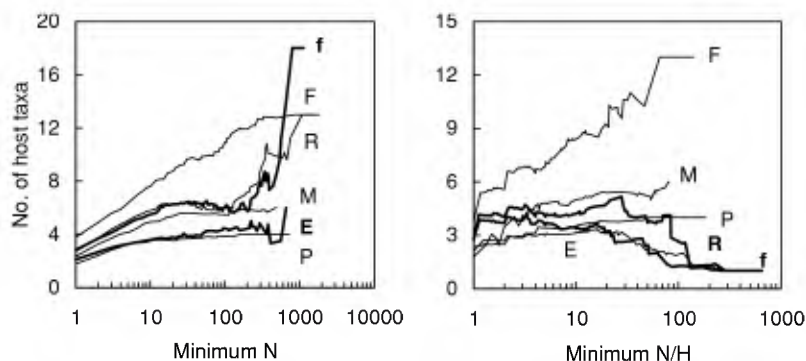


Fig. 1. Relationship between the minimum total abundance (N) and minimum abundance per host species (N/H) thresholds for herbivore species included in host specificity analysis and resulting estimates of the average number of host plant taxa recorded for herbivore species in communities on *Ficus* (F), *Macaranga* (M) and *Psychotria* (P) host species, Euphorbiaceae (E) and Rubiaceae (R) host genera, and different host families (f).

including species with minimum abundance of 10–100 individuals per species and 2–50 individuals per host plant species. Higher thresholds retained only a few species in the analysis, producing thus erratic host specificity estimates.

These results indicated that species from which at least twice as many individuals as plant taxa studied were collected (i.e. 26 individuals for *Ficus* spp., 12 for *Macaranga* spp., 8 for *Psychotria* spp., 18 for Euphorbiaceae genera, 26 for Rubiaceae genera and 36 for plant families) could be analysed. This threshold ensured a minimum of two individuals per host and the minimum total abundance of 8–36 individuals per species was also within the region of stabilized host specificity estimates, with the exception of *Ficus* spp., where host specificity could not be reliably estimated from our data (Fig. 1). Applying this abundance threshold reduced the number of species included in the analysis to 14–22% of the total, which represented 87–93% of all individuals in the compound communities studied.

Herbivore species from *Ficus*, *Macaranga* and *Psychotria* were classified as monophagous if at least 90% of individuals were collected on a single host species. Species collected on Euphorbiaceae and Rubiaceae were also assigned to one of the following categories: genus specialists (at least 90% of individuals feeding on a single plant genus), family specialists (at least 90% of individuals feeding on a single plant family) and generalists (less than 90% of individuals feeding on a single family). Only species for which at least 10 individuals were collected were considered in any of the classifications using the 90% threshold. Although arbitrary, we preferred this threshold to the strict definition, requiring that all individuals feed on a particular plant taxon. It is known that some individuals have anomalous host plant preferences (Dirzo 1980; Marohasy 1998) and numerous feeding tests, performed here on abundant species of herbivores, increase the probability of recording such anomalies.

Host specificity was analysed in component communities (*sensu* Root 1973), which included herbivores from a single host plant species, as well as in compound

communities, combining herbivores from congeneric hosts, from confamilial hosts, each representing a different genus, or from hosts, each representing a different family. For the latter analyses, *Ficus wassa* Roxb. was chosen to represent *Ficus* and Moraceae, *Macaranga quadriglandulosa* Warb., to represent *Macaranga* and Euphorbiaceae, and *Psychotria micralabastra* (Laut. & Schum.) to represent *Psychotria* and Rubiaceae. These species were chosen because their successional optimum and habitus were representative of their respective genus (Leps *et al.* 2001). Species accumulation curves for compound communities of increasing size were estimated by amalgamating community data from individual host species in randomized sequence. One hundred random sequences were created for each such calculation.

Host specificity patterns were analysed for all species, as well as separately for herbivores from three major taxa, Coleoptera, Lepidoptera and the orthopteroids (Orthoptera and Phasmatodea).

Results

HOST SPECIFICITY IN COMPONENT AND COMPOUND COMMUNITIES

Most herbivore species feeding on *Ficus*, *Macaranga* and *Psychotria* were found using most of the congeneric species included in our study (Fig. 2). The modal (median) host range was 12–13 (10) *Ficus*, 6 (6) *Macaranga* and 4 (3) *Psychotria* species, i.e. more than 90 (70)% of the congeneric species studied. Monophagous species were particularly rare. Among 245 species feeding on *Ficus*, *Macaranga* or *Psychotria* and collected as at least 10 individuals, only 9 (3.7%) had at least 90% of individuals limited to a single host. There were 6 species of Lepidoptera and 3 species of Coleoptera among the monophagous species. However, only two (0.8%) of them were entirely limited to a single host: *Rhodoneura aurata* (Butler) (Lepidoptera: Thyrididae) to *M. quadriglandulosa* and *Coenobius* sp. (Coleoptera: Chrysomelidae) to *F. nodosa* Teysm. & Binn. In contrast,

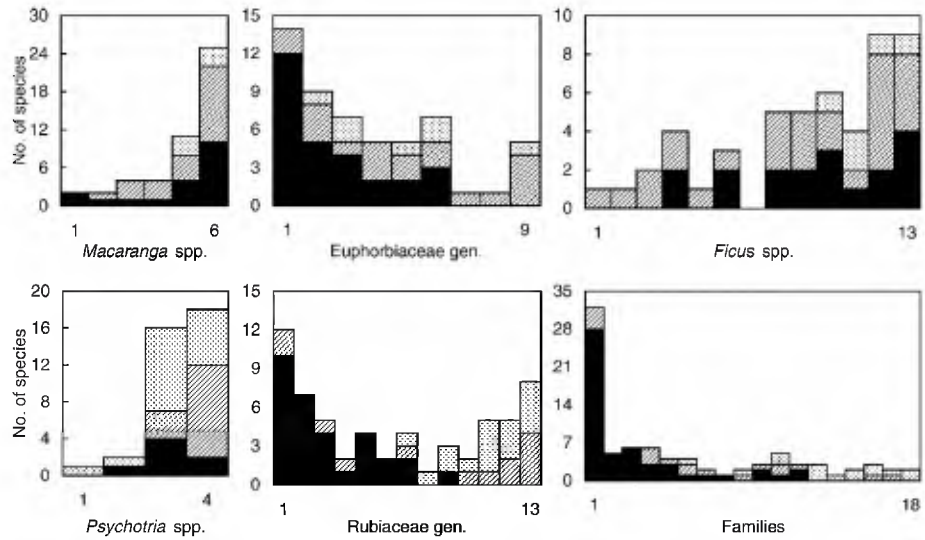


Fig. 2. Host plant range of leaf-chewing insects on congeneric species of *Macaranga*, *Psychotria* and *Ficus*, on confamilial hosts from different genera of Euphorbiaceae and Rubiaceae, and on hosts from different families of flowering plants. Lepidoptera (black), Coleoptera (hatched), orthopteroids (stippled).

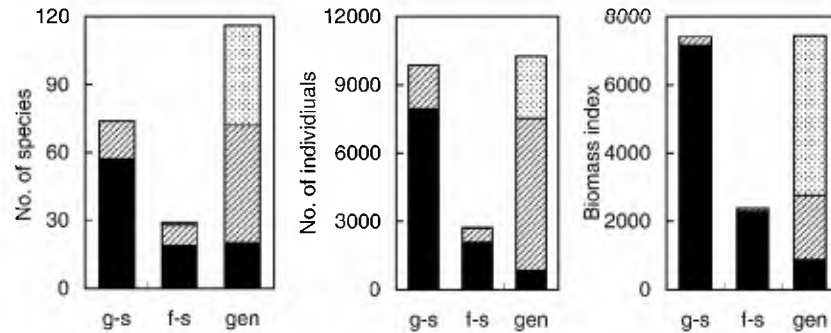


Fig. 3. The importance of Lepidoptera (black), Coleoptera (hatched) and orthopteroids (stippled) among genus specialists (g-s), family specialists (f-s) and generalists (gen) in a compound community from 22 host species, each from a different genus of Euphorbiaceae and Rubiaceae. The importance is measured as the number of species, number of individuals and biomass index (in cm², see Methods).

the modal (median) host range at the generic and familial levels was quite low: 1 (3) Euphorbiaceae genera and 1 (5.5) Rubiaceae genera, i.e. at most 10 (42)% of the confamilial genera studied, and 1 (3.5) of the 18 families studied (Fig. 2).

The genus specialists were mostly Lepidoptera, while the category of generalists was dominated by Coleoptera and orthopteroids (Fig. 3). The host specificity decreased in the order Lepidoptera > Coleoptera > orthopteroids (Kruskal–Wallis test with Dunn’s pair-wise comparisons, all pair-wise comparisons between taxa significant, $P < 0.05$). Generalists were the most species-rich group in herbivore communities, but their share of individuals and biomass was equaled by genus specialists, while family specialists were always of marginal importance (Fig. 3).

The communities on individual plant species included, on average, 5–6 genus specialists, 4 family specialists and 31–32 generalists (Fig. 4). The number of generalist

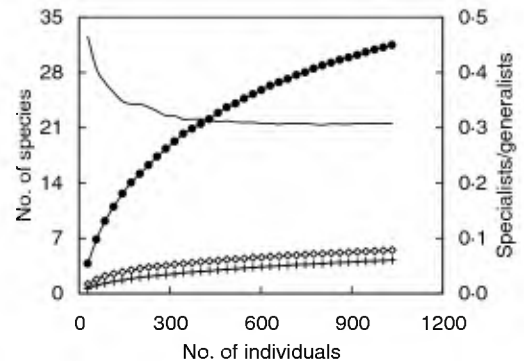


Fig. 4. Average species accumulation curves for genus specialists (diamonds), family specialists (crosses) and generalists (dots) in component communities. Smooth line – the ratio of genus- and family specialists to generalists. Each species accumulation curve is an average of 22 randomized curves, representing herbivore communities from 22 host species, each from a different genus of Euphorbiaceae and Rubiaceae.

Table 1. Taxonomic composition of herbivores feeding on Moraceae, Euphorbiaceae, Rubiaceae and other 15 families. Only insect families with 10 or more species are listed separately (except Eumastacidae which is the only other Orthoptera family sampled). Orders and families with species richness significantly different from a 1 : 1 : 1 ratio among the three separately listed plant families are marked by asterisk (χ^2 -test; only taxa with expected frequency ≥ 5 species per family were tested; results with $P < 0.01$ were considered significant since multiple tests, 24 in total, were performed)

Taxa	Moraceae	Euphorbiaceae	Rubiaceae	Other	Total
Coleoptera	163	157	197	132	371
Brentidae	1	4	5	4	13
Cerambycidae*	78	43	61	47	111
Chrysomelidae	63	61	54	44	124
Curculionidae*	19	28	52	23	78
Elateridae	1	8	8	7	16
Other 10 families*	1	13	17	7	29
Lepidoptera	136	138	159	218	513
Choreutidae*	20	4	0	5	22
Crambidae*	28	8	16	14	53
Geometridae*	2	25	20	42	76
Limacodidae	3	5	4	8	17
Lycanidae	3	3	1	11	15
Lymantriidae	11	14	8	17	40
Noctuidae	14	14	17	20	57
Psychidae	7	6	6	8	16
Pyralidae	1	4	7	5	16
Sphingidae*	3	0	14	2	19
Tortricidae	26	24	33	51	80
Uraniidae*	0	4	18	3	24
Other 18 families	18	27	15	32	78
Orthoptera	58	58	73	69	103
Acrididae	9	8	15	14	17
Pyrgomorphidae	12	12	17	15	18
Tettigoniidae	35	35	38	37	65
Eumastacidae	2	3	3	3	3
Phasmatodea	11	5	17	15	23
Heteronemiidae	5	2	9	8	12
Phasmatidae	6	3	8	7	11
Total	368	358	446	434	1010

species increased faster with sample size than the number of specialists so that the ratio of specialists to generalists in the community decreased with sample size (Fig. 4). The compound community combining herbivores from 22 Euphorbiaceae and Rubiaceae hosts from different genera had a much higher ratio of specialists to generalists as it consisted of 74 genus specialists, 29 family specialists and 116 generalist species. The generalists were thus the most species-rich group in the compound community, as they represented 53% of all species.

Herbivorous communities were dominated by a few large families, viz. by moths from Tortricidae, Crambidae, Geometridae and Noctuidae, beetles from Chrysomelidae, Cerambycidae and Curculionidae, and orthopteroids from Tettigoniidae and Phasmatidae (Table 1). No orders and only a few families showed a strong preference to a particular host plant family. In Lepidoptera, Geometridae avoided and Choreutidae were predominately concentrated on Moraceae, Crambidae (Pyraustinae) preferred Moraceae but avoided Euphorbiaceae, and Uraniidae (Epipleminae) and Sphingidae were concentrated on Rubiaceae. In

Coleoptera, Curculionidae preferred Rubiaceae to other families while Cerambycidae preferred Moraceae and avoided Euphorbiaceae.

HOST SPECIFICITY AND SPECIES RICHNESS

Species accumulation curves for compound communities, combining various numbers of component communities from individual plant species, were used to describe the relationships between estimates of species richness and the taxonomic breadth of host plant sampling. It was found that the number of additional herbivore species (y) resulting from the addition of the x th plant species to the compound community ($x = 1, 2, 3, \dots, n$ where n is the total number of plants studied) could be accurately described by the power function $y = cx^k$, where c and k are constants (Table 2). For instance, the species richness of herbivores on *Ficus* was described by the equation $y = 95.50x^{-0.911}$ (Fig. 5). There were, on average, 95.5 herbivore species on the first *Ficus* species sampled, 50.8 additional species when the second *Ficus* was sampled, and 9.2 new herbivore species obtained when the last, 13th, species of *Ficus*

Table 2. Power functions describing the number of additional species of herbivores (y) resulting from the addition of the x th plant species to the study, $y = c \cdot x^k$, where n = total number of plants studied ($x = 1, 2, 3, \dots, n$); R^2 = variance explained

	n	c	k	R^2
<i>Ficus</i> species	13	95.5	-0.911	0.99
<i>Macaranga</i> species	6	79.0	-0.770	0.95
<i>Psychotria</i> species	4	77.7	-0.842	0.97
Euphorbiaceae genera	9	72.2	-0.628	0.93
Rubiaceae genera	13	88.2	-0.673	0.98
Plant families	18	84.3	-0.547	0.99

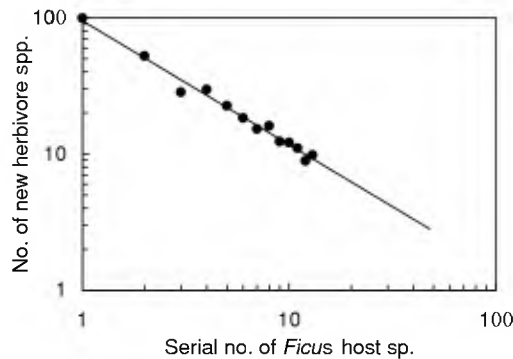


Fig. 5. The number of new herbivore species obtained by sampling a new *Ficus* species. The average number of new herbivore species collected from 1st, 2nd, ... , 13th *Ficus* species is depicted (circles) and fitted by a power function (line) to estimate new herbivore species expected on additional 35 *Ficus* spp. which have not been studied.

was included. According to this equation, sampling of the remaining 35 species of *Ficus* found in the Madang area should produce 163 new species of herbivores, in addition to the 336 species collected in our study.

The same power function also proved to be a good model for communities on other plant taxa, viz. *Macaranga* and *Psychotria* species, Euphorbiaceae and Rubiaceae genera, and the plant families, as indicated by the high R^2 values (Table 2). The k -value is inversely proportional to the overlap in species composition among herbivore communities, while the c -value is the species richness of an average component community. The exponent k was lower for congeneric plants than for plants from different genera and families, which indicates a greater overlap among the communities on closely related than on distantly related plants.

Discussion

HOST SPECIFICITY AND SAMPLING ARTEFACTS

As in other insect community data sets from rainforests, the majority of species in the samples were sufficiently rare so that their host plant range could not be adequately estimated. When using Lloyd's index and other quantitative measurements of host specificity

that account for abundance, it is possible to remove a positive and supposedly spurious correlation between sample size and estimated host specificity (Leps 1993; Novotny & Basset 1998). As shown in the present study, however, such correlations can be more difficult to remove when the number of host plant taxa is used as the measure of the host specificity (cf. Wright 1991).

Data filtering criteria that balance the conflicts between the adequate description of polyphages, the retention of specialists in the data set, and the retention of most species in the analysis, represent a compromise that is dependent on sample size and community composition. In the present study, only 14–22% of species were sufficiently abundant for host specificity analysis. Despite its limited scope, the analysis characterized host specificity of 87–93% of all individuals in the herbivore communities studied, providing thus a sufficiently comprehensive estimate of their host specificity.

The classification of herbivores as specialists and generalists is also dependent on the number of plant species studied and their phylogeny. While the hypothesis of monophagy can be easily rejected for polyphagous species, often on the basis of data from a limited number of plant species, its absolute confirmation requires study of all plant species present. Therefore, it is likely that studies focusing on a small part of the local flora, including the present one, overestimate the number of specialized herbivores.

Host specificity may have been overestimated in herbivore communities since many species of herbivores were not collected in sufficient numbers of specimens and many species of plants were not studied. Finally, only a single guild of herbivores was studied, viz. free-living leaf-chewers, which is probably one of the least host-specific herbivorous guilds. In particular, internal feeders are likely to be more host-specific than external feeders (Janzen 1970, 1980).

HOST SPECIFICITY IN COMPONENT AND COMPOUND COMMUNITIES

Only nine species were found to be monophagous on *Ficus*, *Macaranga* and *Psychotria*. Since some locally present species from these genera were not studied, it is possible that a more extensive study would further reduce this number. It is also possible that these apparently monophagous species also fed on plants from other genera that we did not sample. For instance, *Coenobius* spp. have been previously reported to be polyphagous (Jolivet & Hawkeswood 1995) so that the *Coenobius* sp. that were found restricted to *F. nodosa* may also use other hosts. Thus, very few truly monophagous herbivores probably exist on these speciose plant genera in New Guinea rainforests. In contrast, the proportion of monophages reported by other studies of large plant genera was higher than that in the present study. In particular, 30% of species were monophagous in the herbivorous communities on 9 species of *Passiflora* (Thomas 1990a) and 10% of

Geometridae and 26% of Curculionidae were found to be monophagous on 45 species of *Piper* (Marquis 1991). It is not clear whether these differences are due to differences in sampling methods or in the communities studied.

A large proportion of Lepidoptera species are restricted to a single host plant species in Neotropical forest communities (Janzen 1988; Marquis & Braker 1993; Barone 1998), while detailed data for other herbivorous groups and areas are not available. This pattern probably owes more to the absence of closely related (congeneric) plants within these plant communities than to the inability of herbivores to feed on more than a single species. For instance, Barone (1998) reported 12 monophages among his set of 46 herbivores studied, but only three of these apparently monophagous species were tested on alternative congeneric plants. Rainforest vegetation often has a high proportion of species that do not have any close relatives present in the same community. For instance, a 1-ha survey of plants with stem diameter ≥ 5 cm at one of our study sites, Baitabag, recorded 152 species, 64% of which belonged to locally monotypic genera while only 23% belonged to locally speciose genera with at least 5 coexisting species (Laidlaw *et al.*, in press). Surveys from another lowland rainforest in New Guinea indicated similar results (Reich 1998). A diet restricted to numerous host species from a single genus, which was the predominant pattern found in the present study, would result in de facto monophagy of many herbivores feeding on such vegetation.

Specialized herbivores represent a conspicuous element of herbivore communities, often targeted for detailed ecological and phylogenetic studies (Farrell & Mitter 1993; Basset, Novotny & Weiblen 1997). However, a typical community of tropical herbivores on a single host species is dominated by generalists. This was the case for component communities in the present study, on *Passiflora* (Thomas 1990a), *Piper* (Marquis 1991), as well as 10 tree species studied in Panama by Barone (1998). Likewise, there were seven component communities with more generalists than specialists among 10 tree species studied in New Guinea (Basset 1996). Low host specificity was documented also by Tavakilian *et al.* (1997) and Berkov & Tavakilian (1999) for Cerambycidae beetles reared from trees in French Guiana.

Even substantial sampling effort combined with the exclusion of transient species by feeding experiments does not reduce the number of rare species, as shown by the present study, as well as those by Marquis (1991), Basset (1996), Price *et al.* (1995) and Barone (1998). Many herbivore species that are rare on a particular host species are sustained there by immigration from other hosts that are their main resource base (Novotny & Basset 2000). Most of the rare species are therefore probably oligophages or polyphages. With increasing sample size, the proportion of specialist species is thus likely to decrease in any component community, as was

found in the present study, as well as by Barone (1998). This stresses the challenge of delineating meaningful component communities in tropical rainforests, in terms of constituent insect species (Basset 1997).

Higher host specificity of Lepidoptera compared to other groups is consistent with results from other rainforest communities (Thomas 1990a; Marquis 1991), as well as with rather narrow host ranges reported for tropical Lepidoptera (Janzen 1988) and butterflies (Fiedler 1998). It should be noted that while the host ranges in Lepidoptera included only food plants used by caterpillars, those in Coleoptera often, or exclusively, included plants used by adults during maturation feeding, when such insects tend to be less specific. The majority of Coleoptera species from our study performed only maturation feeding on the foliage, while their larvae develop in wood or on roots (Novotny *et al.* 1999). The larvae are likely to be more host-specific than the adults, but information on their host range is very limited (Jolivet & Hawkeswood 1995). No monophages or genus specialists were found among Orthoptera in the present study, while numerous specialized acridids were reported from a Neotropical rainforest by Marquis & Braker (1993). In their world review of Acridomorpha, Chapman & Sword (1997) report more than half of the species as generalists (feeding on more than one family).

Patterns of host specificity and taxonomic composition of herbivore communities evaluated in terms of species richness, abundance and biomass can radically differ from each other. This was the case for genus specialists in our study, which were represented by relatively few species but were important in terms of individuals and biomass. Similar differences probably underlie often-reported lack of correlation between species richness of herbivore communities and damage they inflict on plants (e.g. Marquis 1991). Biomass can be particularly informative in the assessment of herbivore impact on host plants. Lepidoptera, which had the largest share of biomass, were probably the most important cause of leaf damage in leaf-chewing communities. A similar pattern was also found in a rainforest in Panama (Barone 1998).

HOST SPECIFICITY AND PLANT TAXONOMY

Contrasting patterns of host specificity with respect to congeneric plants and those from different genera and families indicate that plant genera can be used as relatively independent units in the analysis of tropical herbivore communities. This is not self-evident since assignment of higher taxonomic ranks, such as genera or families, is somewhat arbitrary and their delimitation often varies among taxonomists (Mabberly 1997).

Thus, the level at which a particular supraspecific taxon is recognized is a convention, and generic concepts are not commensurate across plant lineages (Stevens 1998). The lack of narrow host specificity with respect to congeneric hosts was found even for

Table 3. The effective specialization of herbivore species on various host plant taxa. $S(\text{com})$ = the number of herbivore species sufficiently common for the analysis of host specificity, $H. \text{rec.}$ – the number of host records involving the common species, $S(\text{tot})$ = average number of herbivore species found on a host species from a particular taxon, $S(\text{eff. spec.})$ = average number of herbivorous species effectively specialized to a host plant species, $S(\text{eff. spec.}) = S(\text{tot}) \times \text{Eff. spec.}$, n = the number of host species studied

	$S(\text{com})$	$H. \text{rec.}$	Eff. spec.	$S(\text{tot})$	$S(\text{eff. spec.})$	n
<i>Ficus</i> species	50	462	0.11	98.0	10.6	13
<i>Macaranga</i> species	48	239	0.20	89.5	18.0	6
<i>Psychotria</i> species	37	125	0.30	81.4	24.1	4
Euphorbiaceae genera	54	200	0.27	69.1	18.7	9
Rubiaceae genera	60	383	0.16	85.3	13.4	13
Plant families	90	561	0.16	88.3	14.2	18

large, broadly defined plant genera, such as *Ficus*, *Macaranga* or *Psychotria* (cf. Mabberly 1997). *Ficus* in particular is retained as a single, large genus because it is well defined by its unique reproductive system, involving syconia figs and specialized pollinator wasps. In terms of morphological and ecological variability, which may be more relevant to leaf-chewing herbivores, *Ficus* exceeds the range encountered in many plant families (Chew 1989). The 13 *Ficus* species studied here reflected the ecological heterogeneity of the genus, ranging from small shrubs to canopy trees, from early to late successional species, both deciduous and evergreen species, and their leaves varied in size, specific weight, pubescence, latex content and growth patterns (Basset *et al.* 1997; Basset & Novotny 1999). Therefore, it is of some interest that despite this diversity, leaf-chewing herbivores were found to be rather indiscriminate in their choice of *Ficus* hosts. The other two large genera studied, *Psychotria* and *Macaranga*, were more uniform in appearance, as well as in ecology. All but one species of *Macaranga* were small pioneer trees, while all four species of *Psychotria* were understory shrubs from mature forests. Their homogeneity may explain the wide host ranges by herbivores on these two genera, even wider than those of the *Ficus* herbivores.

Any analysis of host ranges relying on counts of higher plant taxa (e.g. genera and families, such as in the present study) can be potentially misleading and difficult to compare with other studies since the definition of these higher taxa is often inconsistent. Methods for the measurement of host range based on host phylogeny exist (Symons & Beccaloni 1999), but their use in extensive studies on poorly known tropical vegetation is limited, as the requisite information on plant phylogeny is often unavailable. The observation that herbivores apparently specialize on plant genera, rather than on plant species or families, is thus of practical importance, particularly for broad, pilot surveys of insect herbivores on diverse vegetation. Further, if verified as a general pattern, this should be considered in the design of assessment protocols of the potential host range for insects being considered as agents for the biological control of weeds (e.g. Marohasy 1998).

HOST SPECIFICITY AND SPECIES RICHNESS

Data on the regional species richness of insect herbivores are practically nonexistent for tropical areas, with the exception of a few conspicuous taxa, such as butterflies or cicadas (de Boer & Duffels 1996; Parsons 1999). Numerous attempts to estimate the local, regional or even global species richness of insect herbivores have thus involved extrapolation, using samples obtained from local communities on a limited number of host plant species (Erwin 1982; Stork 1988; May 1990; Ødegaard *et al.* 2000; Miller, Novotny & Basset, in press). In many such extrapolations, host specificity is a key, but poorly known, variable (Basset *et al.* 1996). The present study indicates that plant genera may be more appropriate taxonomic entities, harbouring host-specific herbivores, than plant species.

The average proportion of herbivore species effectively specialized (May 1990) varied from 0.11 to 0.30 among plant taxa (Table 3) and lead to an estimate of 10.6–24.1 species of herbivores effectively specialized to a host plant species. Although these calculations are contingent on the number and taxonomic composition of host plants studied and therefore tentative, it is reasonable to conclude that there are tens, rather than hundreds, of herbivorous species effectively specialized to a woody host species in New Guinea. This is an order of magnitude lower value than that suggested by Erwin (1982), but close to analogous estimates by Thomas (1990b), Basset *et al.* (1996) and Ødegaard *et al.* (2000).

The power function $y = cx^k$, used to predict the number of additional herbivore species (y) produced by the study of additional host plants (x) is a purely empirical relationship, justified by a good fit to our data (note that individual data points fitted by this equation are not mutually independent as they represent various combinations of the original samples, each of them used more than once). However, the parameter k is also a useful descriptor of similarity among herbivore communities from different hosts, analogous to the slope of species accumulation curve. The interpretation of k is straightforward only for the simplest case involving communities from two host plants ($x = 1, 2$). In this case, k is a similarity index, related to the Sorensen's

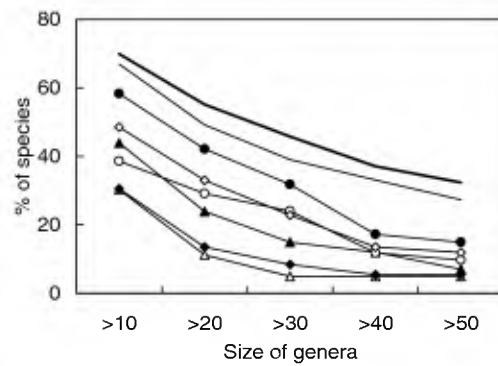


Fig. 6. Proportion of plant species in various floras belonging to genera of various size. Only floras from humid tropical (smooth lines) and temperate (lines with markers) continental areas or large islands were used: smooth thick line, New Guinea; smooth thin line, Peru; solid circles, New Zealand; empty diamonds, Pacific North-west (USA); solid triangles, Japan; empty circles, New England; solid diamonds, Great Plains (USA); empty triangles, British Isles. Data for New Guinea from Höft (1992), others from Fenner *et al.* (1997).

index of similarity ($SI = 2C/(A + B)$, where C is the number of species common to the two samples and A and B are, respectively, the total number of species in each sample) by the equation $SI = 1 - 2^k$. When communities from three host plants are analysed, k integrates the overlap in species composition between all pairs of communities (reflected by the change in y between data points for $x = 1$ and 2) with that between any two amalgamated communities and the third one (reflected by the change in y between data points for $x = 2$ and 3). Analogously, k integrates all higher-level similarity relationships between single and amalgamated samples of various sizes for any larger number of hosts. The overlap between pairs of samples (i.e. data points for $x = 1$ and 2) has the highest influence on the k -value, while the weight of the data points for higher x -values, reflecting higher-level similarities, is becoming progressively smaller. The sensitivity of k to higher-level similarities is a useful feature, but also makes its interpretation less straightforward.

The power function predicted that the 48 *Ficus* species present locally support a total of 499 leaf-chewing species. This result is only approximate because (i) the local species richness on the 13 species of *Ficus* studied was underestimated, (ii) the remaining 35 *Ficus* species were phylogenetically and ecologically more diverse than those sampled so that the extrapolated species richness might be an underestimate, and (iii) the estimate given above ignores hosts other than *Ficus*. A large overlap among herbivore communities on congeneric plants means that the total number of herbivores feeding on large genera is relatively small given their size. This has important consequences for regional and global estimates of herbivore species richness, since a significant proportion of tropical floras is composed of a few large genera. Regional tropical floras seem to have a high percentage of species from large genera (Fig. 6). For example, 32% of plant species in New

Guinea belong to the genera that have more than 50 species in this area (Höft 1992). Further, the three largest genera, *Macaranga*, *Glochidion* and *Phyllanthus*, account for 40% of all Euphorbiaceae, while *Psychotria*, *Timonius* and *Hydnophytum* account for 30% of all Rubiaceae in New Guinea (Höft 1992; van Welzen 1997). A single genus, *Ficus*, represents 84% of all New Guinea Moraceae (Höft 1992).

Differences between tropical and temperate floras, species-rich and species-poor, respectively, are usually smaller in terms of the number of genera and families (Fenner, Lee & Wilson 1997). This is also the case for local plant communities. For instance, the median species to family ratio for trees in 0.1-ha plots was 3.2 for tropical but only 1.7 for subtropical and temperate vegetation ($P < 0.01$, Mann-Whitney test, $n = 74$ plots; data from Gentry 1988). In this data set, tropical plots had five times more species but only three times more families than the temperate plots. These differences between tropical and temperate floras, in combination with low host specificity of herbivores with respect to congeneric plants, suggest that the average overlap among herbivore communities on tropical trees may be higher than that on plants from the temperate zone.

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Appendix: plant species studied

Agavaceae: *Dracaena angustifolia* Roxb., **Apocynaceae:** *Tabernaemontana aurantica* Gaud., **Araliaceae:** *Osmoxylon sessiliflorum* (Lauterb.) W.R. Philipson, **Arecaceae:** *Hydriastele microspadix* (Becc.) Burret., **Euphorbiaceae:** *Breynia cernua* (Poir.) Muell. Arg., *Codiaeum ludovicianum* Airy Shaw, *Endospermum labios* Schodde, *Homalanthus novoguineensis* (Warb.) K. Schum., *Macaranga aleuritoides* F. Muell., *M. brachytricha* A. Shaw, *M. bifoveata* J. J. Smith, *M. densiflora* Warb., *M. novoguineensis* J. J. Smith, *M. quadriglandulosa* Warb., *Mallotus mollissimus* (Geisel.) Airy Shaw, *Melanolepis multiglandulosa* (Reinw. ex Bl.)

Reichb.f. & Zoll., *Phyllanthus lamprophyllus* Muell. Arg., *Pimelodendron amboinicum* Hassk., **Eupomatiaceae:** *Eupomatia laurina* R. Br., **Fabaceae:** *Pterocarpus indicus* Willd., **Flacourtiaceae:** *Casearia erythrocarpa* Sleum., **Gnetaceae:** *Gnetum gnemon* L., **Loganiaceae:** *Neuburgia corynocarpa* (A. Gray) Leenh., **Malvaceae:** *Sterculia schumanniana* (Lauterb.) Mildbr., **Monimiaceae:** *Kibara* cf. *coriacea* (Bl.) Tul., **Moraceae:** *Artocarpus communis* J. R. et G. Forst., *Ficus bernaysii* King, *F. botryocarpa* Miq., *F. conocephalifolia* Ridley, *F. copiosa* Steud., *F. dammaropsis* Diels, *F. hispidioides* S. Moore, *F. nodosa* Teysm. & Binn., *F. phaeosyce* Laut. & K. Schum., *F. pungens* Reinw. ex Bl., *F. septica* Burm., *F. trachypison* K.

Schum., *F. variegata* Bl., and *F. wassa* Roxb.,
Rubiaceae: *Amaracarpus nymanii* Valetton, *Dolicholobium oxylobum* K. Schum., *Gardenia hansemannii* K. Schum., *Morinda bracteata* Roxb., *Mussaenda scratchleyi* Wernh., *Nauclea orientalis* (L.) L., *Neonaclea clemensii* Merrill & Perry, *Pavetta platyclada* Lauterb. & K. Schum., *Psychotria leptothyrsa* Miquel, *P. ramuensis* Sohmer, *P. micralabastra* (Laut. & Schum.) Val., *P. micrococca* (Laut. & Schum.) Val., *Randia schumanni-*

ana Merrill & Perry, *Timonius timon* (Spreng.) Merr., *Versteegia cauliflora* (K. Schum. & Laut.), *Tarenna buruensis* (Miq.) Val., **Sapindaceae:** *Pometia pinnata* Forster, **Ulmaceae:** *Celtis philippensis* Blanco, **Urticaceae:** *Leucosyke capitellata* (Poir.) Wedd., **Verbenaceae:** *Premna obtusifolia* R.Br. Vouchers deposited in Bishop Museum (Honolulu), PNG Forest Research Institute (Lae), Rijksherbarium (Leiden) and Smithsonian Institution (Washington).