
Local Species Richness of Leaf-Chewing Insects Feeding on Woody Plants from One Hectare of a Lowland Rainforest

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Abstract: *Local species diversity of insect herbivores feeding on rainforest vegetation remains poorly known. This ignorance limits evaluation of species extinction patterns following various deforestation scenarios. We studied leaf-chewing insects feeding on 59 species of woody plants from 39 genera and 18 families in a lowland rainforest in Papua New Guinea and surveyed all plants with a stem diameter at breast height of ≥ 5 cm in a 1-ha plot within the same area. We used two extrapolation methods, based on randomized species-accumulation curves, to combine these two data sets and estimate the number of species of leaf-chewing herbivores feeding on woody plants from the 1-ha area. We recorded 58,483 feeding individuals from 940 species of leaf-chewing insects. The extrapolation estimated that there were 1567–2559 species of leaf-chewing herbivores feeding on the 152 plant species from 97 genera and 45 families found in 1 ha of the forest. Most of the herbivore diversity was associated with plant diversity on the familial and generic levels. We predicted that, on average, the selection of 45 plant species each representing a different family supported 39% of all herbivore species, the 52 plant species each representing a different additional genus from these families supported another 39% of herbivore species, and the remaining 55 plant species from these genera supported 22% of herbivore species. Lepidoptera was the most speciose taxon in the local fauna, followed by Coleoptera and orthopteroids (Orthoptera and Phasmatodea). The ratio of herbivore to plant species and the estimated relative species richness of the Lepidoptera, Coleoptera, and orthopteroids remained constant on the spatial scale from 0.25 to 1 ha. However, the utility of local taxon-to-taxon species ratios for extrapolations to geographic scales requires further study.*

Riqueza de Especies Locales de Insectos Masticadores de Hojas en Plantas Leñosas de una Hectárea de Selva Lluviosa

Resumen: *Se conoce poco de la diversidad de especies locales de insectos herbívoros que se alimentan de la vegetación de selvas lluviosas. Esta escasez de información limita la evaluación de patrones de extinción de especies después de varios escenarios de deforestación. Estudiamos insectos masticadores de hojas que se alimentan de 59 especies de plantas leñosas de 39 géneros y 18 familias en vestigios de selva lluviosa en Papua Nueva Guinea y examinamos todas las plantas con un diámetro ≥ 5 cm a la altura del pecho en una*

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parcela de 1 ha en la misma zona. Utilizamos dos métodos de extrapolación, basado en curvas aleatorias de acumulación de especies, para combinar estos dos conjuntos de datos y estimar el número de especies de herbívoros masticadores de hojas que se alimentan de las plantas leñosas de la parcela de 1 ha. Registramos un total de 58,483 individuos de 940 especies de insectos masticadores de hojas. La extrapolación estimó que había 1567-2559 especies de herbívoros masticadores de hojas alimentándose de las 152 especies de plantas de 97 géneros y 45 familias encontradas en 1 ha de bosque. La mayor parte de la diversidad de herbívoros estaba asociada con la diversidad de plantas a nivel de familia y género. Predijimos que, en promedio, la selección de 45 especies de plantas, cada una representando a una familia diferente, soportaba al 39% de todas las especies herbívoras, las 52 plantas, cada una representando a un género adicional diferente de estas familias, soportaba a otro 39% de las especies herbívoras y las restantes 55 especies de plantas de estos géneros soportaban al 22% de las especies herbívoras. El taxón con más especies en la fauna local fue Lepidoptera, seguido por Coleoptera y ortopteridos (Orthoptera y Phasmatodea). La relación herbívoros - planta, y la riqueza relativa estimada de especies de Lepidoptera, Coleoptera y ortopteridos permaneció constante en la escala espacial de 0,25 a 1 ha. Sin embargo, la utilidad de proporciones de especies de taxón - taxón para extrapolaciones a escalas geográficas requiere de mayor estudio.

Introduction

Plant ecologists have made significant progress in mapping the local species richness of tropical rainforests, particularly when using standardized census protocols for 1-ha and 50-ha plots (Condit 1997). In contrast, insect ecologists have yet to accomplish even a baseline description of their subject. For example, despite Erwin's (1982) pioneering effort to formulate an estimate of the local species richness of insects in the tropics, they still do not know what and how many insect species live in any single hectare of a tropical rainforest (Godfray et al. 1999). The value of cataloging and understanding species before attempting to conserve them is obvious, and our inability to do so is damaging the credibility of the conservation movement (e.g., Mann 1991). One example of the problems faced by conservation biologists is the controversy surrounding Lomborg's (2001) optimistic estimates of low extinction rates caused by habitat destruction. These estimates are hard to disprove because of the lack of data on tropical diversity patterns (Pimm & Harvey 2001; Lovejoy 2002).

Numerous studies, using insecticide fogging, light trapping, and other mass-collection methods, have provided insect samples from rainforests that included large numbers of species (Stork et al. 1997) but yielded only limited information on the ecology of these species. Thus, it remains unclear which species are genuine members of local food webs and which are but transients, inflating the species richness of the samples (Novotny & Basset 2000). A different approach focuses on sampling and studying live insects from selected plant species (Janzen 1988; Marquis 1991; Basset 1996; Barone 1998; Ødegaard 2000a; Novotny et al. 2002a, 2002b). These studies provide a novel source of information on the food webs in rainforest communities but are often restricted to a small number of plant or herbivore taxa, limiting their usefulness for inferring the size of the local pool of herbivore

species in rainforests. One study relatively free of these limitations investigated a food web including all locally coexisting species of macrolepidoptera in a dry forest in Costa Rica (Janzen 1988; Janzen & Gauld 1997).

With such fragmentary information available at present, only indirect estimations of local herbivore diversity in rainforests are feasible. Missa (personal communication) estimated the local species richness of weevils from an asymptotic species-accumulation curve, obtained from samples from diverse vegetation within a 1-km² area of a lowland rainforest in New Guinea. Novotny and Missa (2000) estimated the local species richness of several hemipteran families in a New Guinea rainforest from the overlap between a complete census of these taxa from a limited part of the vegetation (15 species of *Ficus* trees) and more comprehensive but incomplete samples from mixed vegetation. Ødegaard (2003) extrapolated data on herbivorous beetles from 50 species of trees and lianas sampled from a canopy crane in Panama to estimate the number of beetle species feeding on 500 woody plant species present in the rainforest ecosystem. Hammond et al. (1997) estimated the species richness of beetles in a 500-ha tract of rainforest in Sulawesi from samples collected by various sampling methods. Despite various spatial scales involved, a 1-ha standard is often used for extrapolation on the local scale (Erwin 1982; Ødegaard 2003), in correspondence with many botanical studies.

We used novel methods based on species-accumulation curves (Novotny et al. 2002a) to extrapolate data on herbivore assemblages feeding on 59 species of woody plants to the assemblages occurring on the vegetation surveyed within a 1-ha area of a lowland rainforest in New Guinea. The estimate is based on a particularly detailed data set, including quantitative ecological information on 940 species of insect herbivores obtained through mass collection and rearing of insects by parataxonomists (Basset et al. 2000).

Methods

Study Area and Plant Census

Our study area situated in the Madang Province is part of the lowlands (0–400m above sea level) of Papua New Guinea that stretch from the coast to the slopes of the Adelbert Mountains. The study area has a humid tropical climate with average annual rainfall of 3558 mm, a moderate dry season from July to September, and mean air temperature of 26.5° C (McAlpine et al. 1983). Field work focused in a mosaic of primary and secondary lowland forests near the villages of Baitabag, Ohu, and Mis (145°41–7'E, 5°08–14'S, approximately 50–200 m). At each site, the study area included 5–10 km² of primary and secondary forests. The study sites were <20 km from one another and had nearly identical vegetation (Laidlaw et al. 2003) and herbivore communities (Novotny et al. 2002c). The data from all sites were therefore analyzed together.

All plants with a diameter at breast height (dbh) of ≥5cm were censused in a 1-ha, 100 × 100 m plot in a primary rainforest at our Baitabag site. The location of each plant above the threshold size was mapped and the plant identified if possible. Plant vouchers are deposited in Papua New Guinea's National Herbarium in Lae.

Sampling of Insect Herbivores

We selected 59 locally common species of trees and shrubs (13 species of *Ficus* and 1 of *Artocarpus* of the Moraceae, 6 species of *Macaranga* and 8 representing 8 other genera of Euphorbiaceae, 4 species of *Psychotria* and 12 representing 12 other genera of Rubiaceae, and 15 species representing 15 other families) for the study of their insect herbivores (listed in Novotny et al. 2002a). This selection included representatives of all major lineages of vascular plants (Angiosperm Phylogeny Group 1998). Further, we included locally common plants from all main habitats, including early and late stages of forest succession and riverine habitats (Leps et al. 2001). The 3 families and 3 genera studied in greater detail are important general components of tropical floras including lowland rainforests in Papua New Guinea (Corner 1965; Whitmore 1979; Sohmer 1988; Oatham & Beehler 1998).

We studied the guild of externally feeding, leaf-chewing insects (Coleoptera, Lepidoptera, and orthopteroids [i.e., Orthoptera and Phasmatodea]). Most of the Coleoptera performed only maturation feeding on the leaves, so their larvae were not sampled. Both immature individuals and adults were feeding on the foliage in the orthopteroids.

We collected insects from the foliage by hand. At each sampling occasion, a collector spent 1 day walking throughout the study area and searching the foliage of the target tree species for caterpillars. The sampling

was irregular because it included any tree from the target species encountered during the sampling walk within the study area. Numerous trees were thus sampled on each sampling occasion, and many of the trees were sampled repeatedly at different sampling occasions. The sampling included accessible branches from the forest canopy and understory, which could be climbed or reached from the ground. Particularly poorly accessible trees were not sampled. The approximate area of the foliage sampled was estimated visually and recorded. We kept sampling effort constant for all species at 1500 m² of foliage sampled per species.

We sampled each tree species for at least 1 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 was performed only in daytime.

In the laboratory, each insect was provided with fresh leaves of the plant species from which it was collected until it fed or died. Only the individuals that fed were considered in the subsequent analyses. Caterpillars were reared to adults whenever possible (successful in approximately 40% of individuals and 75% of species; cf. Novotny et al. 2002c). All insects were assigned to morphospecies, which were subsequently verified by specialist taxonomists and identified as far as possible. Thus our morphospecies correspond to species (Basset et al. 2000), which have often been matched to named species and are the subject of further taxonomic research (e.g., Holloway & Miller 2003). Voucher specimens are deposited in the Smithsonian Institution (Washington), Bishop Museum (Honolulu), and National Agriculture Research Institute (Port Moresby).

Extrapolation of Herbivore Species Richness

We used two methods of extrapolation to estimate the number of herbivore species feeding on plants from the 1-ha study plot: (1) extrapolation from 18 plant species from different families studied to the 45 representatives of different families present in the plot, corrected for additional herbivore species feeding on confamilial plant genera and congeneric plant species and (2) extrapolation from subsets of the 59 studied plant species that had an identical taxonomic structure (i.e., the distribution of species among genera and genera among families) as randomly selected subsets of species from the 1-ha forest plot.

Both methods rely on the extrapolation of the number of additional species of herbivores expected from further expansion of the sampling universe beyond plant species actually sampled from species-accumulation curves. The number of additional herbivore species (y) resulting from the addition of the x th plant species to the data ($x = 1, 2, 3, \dots, n$, where n is the total number of plant species studied) is described by the power function $y = cx^k$,

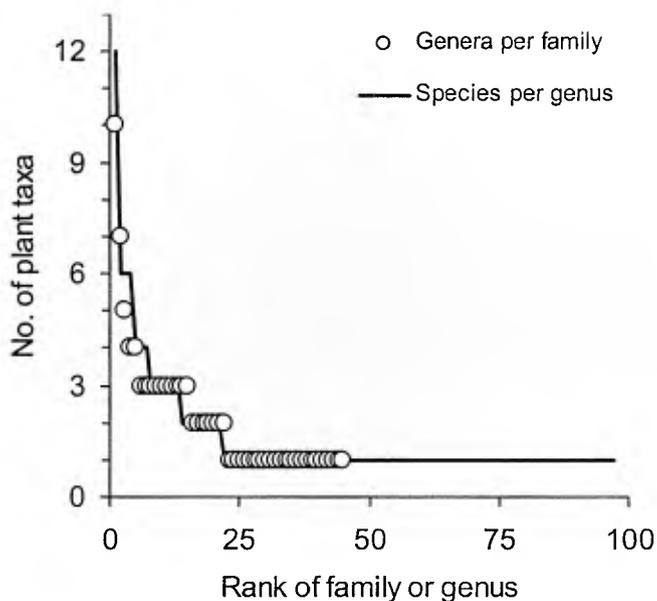


Figure 1. Number of plant genera in each family and of species in each genus recorded in the 1-ha study plot in Baitabag.

where c and k are constants (Novotny *et al.* 2002a). The k is inversely proportional to the overlap in species composition among herbivore assemblages from individual plant species, and the c approximates the species richness of an average assemblage on a single host species. We fitted this function, using ordinary least-squares linear regression of log-transformed data, to the empirical species-accumulation curves generated by amalgamating data from $x = 1, 2, 3, \dots, n$ host-plant species in a randomized sequence. Average values from 1000 random sequences were used for each such calculation.

In method 1, we fitted the power function to the data for 18 plant species, each representing a different family, and used it to estimate the number of herbivore species expected for a single representative of each of the 45 families present in the plot. Further, we used data for 9 plant species, each representing a different genus of Euphorbiaceae, to estimate the number of additional herbivore species expected due to the presence of confamilial plant genera. Only herbivore species feeding exclusively on Euphorbiaceae were considered in this analysis. The number of additional herbivore species corresponding to 1–9 confamilial genera, present in each of the 22 families in the plot (Fig. 1), was estimated on the basis of this relationship. Finally, we used data for 6 species of *Macaranga* to estimate the number of additional herbivore species expected due to the presence of congeneric plant species, following the same procedure as that for genera of Euphorbiaceae. Only those herbivore species feeding exclusively on *Macaranga* were used for the analysis. We used this relationship to estimate the number of

additional herbivore species due to the 1–11 congeneric species present in each of the 21 tree genera in the plot (Fig. 1).

We performed the same analysis for the Rubiaceae, using 13 genera from this family and 4 species of *Psychotria*, and for the Moraceae, using 2 genera from this family and 13 species of *Ficus*. These analyses produced three independent estimates of the number of herbivore species feeding on additional confamilial genera and congeneric species of plants.

Macaranga quadriglandulosa was chosen to represent *Macaranga* and Euphorbiaceae, *Psychotria micralabastra* represented *Psychotria* and Rubiaceae, and *Ficus wassa* represented *Ficus* and Moraceae in the above analyses. These species were selected because their successional optimum and habitus were representative of their respective genus (Leps *et al.* 2001).

In method 2 we fitted the power function to the data from a subset of the studied 59 plant species that exactly matched an equally sized, randomly selected subset of the 152 species from the 1-ha plot in taxonomic structure (i.e., distribution of genera among families and species among genera [cf. Fig. 1]) but not necessarily in the identity of plant species, genera, or families.

At each step of the analysis, one species was randomly selected without replacement from the 152 species recorded in the 1-ha plot. The selection continued as long as the resulting set of selected species could be matched in taxonomic structure by an analogous set of species studied for herbivores, which was selected from the 59 species available.

The selection from the 59 species studied for herbivores was random within the constraints given by the taxonomic structure of the mirrored selection from the 152 species. For instance, a family represented by a single species in the random selection from the 152 species could be matched by a randomly selected family from all 18 families studied for herbivores, whereas a family represented by 10 different genera had to be always matched by Rubiaceae, because no alternative was available among the families sampled for herbivores.

The resulting set of species selected from the 59 species studied for herbivores was used for extrapolation of species richness of herbivores on 152 plant species. The process of random plant selection and species-richness extrapolation was repeated 50 times. Only 11–24 plant species were used for each analysis because we could not match precisely the taxonomic structure of larger selections from the set of 59 plant species sampled for herbivores with randomly selected subsets of the 152 species from the 1-ha plot. The most important constraints limiting the number of species that could be used in the analysis included the low number of families with multiple genera and the genera with multiple species, sampled for herbivores.

Table 1. The most common plant species, genera, and families in the 1-ha study plot in Baitabag.

Plant species, genus, and family	Basal area (m ²)	n ^a	Herbivores ^b
Species^c			
<i>Pometia pinnata</i>	4.35	42	yes
<i>Pimelodendron amboinicum</i>	2.02	83	yes
<i>Pterocarpus indicus</i>	1.89	10	yes
<i>Neonauclea bagenii</i>	1.80	6	no
<i>Intsia bijuga</i>	1.77	2	no
others (147 species)	16.73	899	23 species
Genus			
<i>Pometia</i>	4.35	42	yes
<i>Pimelodendron</i>	2.02	83	yes
<i>Neonauclea</i>	1.91	9	yes
<i>Pterocarpus</i>	1.89	10	yes
<i>Celtis</i>	1.89	43	yes
others (92 genera)	16.50	855	15 genera
Family			
Sapindaceae	4.67	55	yes
Rubiaceae	2.93	60	yes
Euphorbiaceae	2.42	140	yes
Meliaceae	2.18	122	no
Caesalpiniaceae	2.12	14	no
others (40 families)	14.25	651	10 families

^aNumber of individual plants with diameter at breast height ≥ 5 cm.

^bTaxa sampled for herbivores.

^cPlant species were ranked on the basis of basal area.

Results

Tree Flora

The 1-ha plot in Baitabag contained 1042 plants with a dbh of ≥ 5 cm, including 453 plants with a dbh of ≥ 10 cm. Their basal area was 28.6 m²/ha (26.4 m²/ha for plants with a dbh of ≥ 10 cm), and they represented 152 species (112 species with a dbh of ≥ 10 cm) from 97 genera and 45 families. Botanical results are described by Laidlaw et al. (2003).

Sapindaceae, Rubiaceae, and Euphorbiaceae ranked highest in basal area (Table 1). The most species-rich family was Moraceae (19 spp.), followed by Meliaceae and Rubiaceae (both 15 spp.). Rubiaceae and Euphorbiaceae had the highest number of genera (10 and 7, respectively; Fig. 1). Twenty families were locally monotypic. *Ficus* (12 spp.) was the most species-rich genus in the plot, whereas each of 20 other genera was represented by 2–6 species, and the remaining 76 genera were locally monotypic (Fig. 1). The most abundant species, *Pometia pinnata*, *Pimelodendron amboinicum*, and *Pterocarpus indicus*, constituted 29% of the total basal area and 13% of all plants in the plot (Table 1). In contrast, the rarest 40 species (26%) were each represented by only one individual.

Twenty-six species (17%), 20 genera (21%), and 13 families (29%) occurring in the 1-ha plot were also sampled

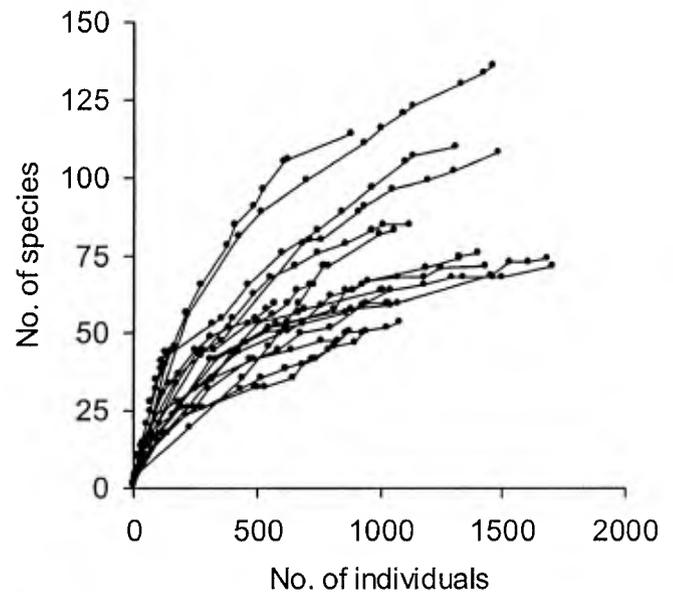


Figure 2. Species-accumulation curves for herbivores feeding on 18 plant species, each representing a different family. Each curve was created by amalgamation of 1-month samples in the order they were collected during 1 year.

for their herbivores. Forty-seven plant species (31%) from the plot belonged to genera included in the insect study. The herbivore study also included a majority of the plant species, genera, and families most abundant in the plot (Table 1).

Assemblage of Insect Herbivores

The sampling of leaf-chewing assemblages on 59 plant species produced 58,483 feeding individuals belonging to 940 species: 452 Lepidoptera, 379 Coleoptera, and 109 orthopteroid species. Their host-plant associations represented 4619 herbivore-host plant combinations. The number of leaf-chewing species feeding on a plant species ranged from 31 to 132. After 1 year of sampling, the species-accumulation curves for individual plants did not approach an asymptote, indicating that the total species richness of their herbivore assemblages had not been sampled (Fig. 2).

Herbivorous assemblages were dominated by 21 families, each represented by ≥ 10 species (the number of species from each family is given in parentheses): Lepidoptera-Geometridae (68), Crambidae (62), Noctuidae (54), Lymantriidae (41), Tortricidae (38), Uraniidae (22), Sphingidae (19), Choreutidae (18), Limacodidae (17), Psychidae (15), Lycaenidae (14), Thyrididae (10); Coleoptera-Chrysomelidae (126), Cerambycidae (112), Curculionidae (78), Elateridae (17), Brentidae (13); Orthoptera-Tettigoniidae (65), Acrididae (10); Phasmatodea-Heteronemiidae (12), and Phasmatidae (11).

Table 2. Equations ($y = cx^k$) describing the number of additional species of herbivorous insects (y) resulting from the addition of the x th plant species.

<i>Plant and herbivore taxa</i>	<i>k</i>	<i>c</i>	<i>n^a</i>	<i>R^{2b}</i>	<i>Equation number</i>
Plant families, all herbivores	-0.518	74.1	18	0.99	1
Euphorbiaceae genera, all herbivores	-0.295	18.5	9	0.92	2
Rubiaceae genera, all herbivores	-0.325	22.9	13	0.93	3
Moraceae genera, all herbivores	-0.325	25.6	2	—	4
<i>Macaranga</i> species, all herbivores	-0.613	13.9	6	0.99	5
<i>Psychotria</i> species, all herbivores	-0.322	7.6	4	0.99	6
<i>Ficus</i> species, all herbivores	-0.592	27.0	13	0.99	7
Plant families, Lepidoptera	-0.378	28.3	18	0.96	8
Plant families, Coleoptera	-0.563	28.2	18	0.99	9
Plant families, Orthopteroids	-0.802	18.3	18	0.99	10

^aTotal number of plants studied ($x = 1, 2, 3, \dots, n$).

^bVariance explained.

Species Richness of Insect Herbivores

The power function ($y = cx^k$) was a good descriptor of the relationship between herbivore and host-plant species diversity in all data sets analyzed, with $R^2 > 0.9$ in all cases (Table 2). The residuals did not show a systematic departure from the predicted values (the quadratic term of second-order polynomial regression of residuals on predicted values was not significant, $p > 0.1$, in any of the data sets in Table 2).

The increase, for instance, in the number of herbivore species accompanying the expansion of sampling from 1 to 18 plant species from different families was described by the equation

$$y = 74.1x^{-0.518} (R^2 = 0.99), \tag{1}$$

which predicts that, on average, 74 herbivore species will occur on the first plant species sampled and 52 additional species on the second plant species, through to 17 new herbivore species obtained when the last (18th) plant species is included (Table 2; Fig. 3). We verified the accuracy of this extrapolation by using a randomly selected subset of 9 plant species (half of the original data set) to estimate the number of herbivore species expected in the entire set of 18 plant species from different families. We generated 50 random subsets of 9 plant species by sampling without replacement from the full set of 18 species each time we fitted a separate regression to each subset and used it to extrapolate species richness on 18 plant

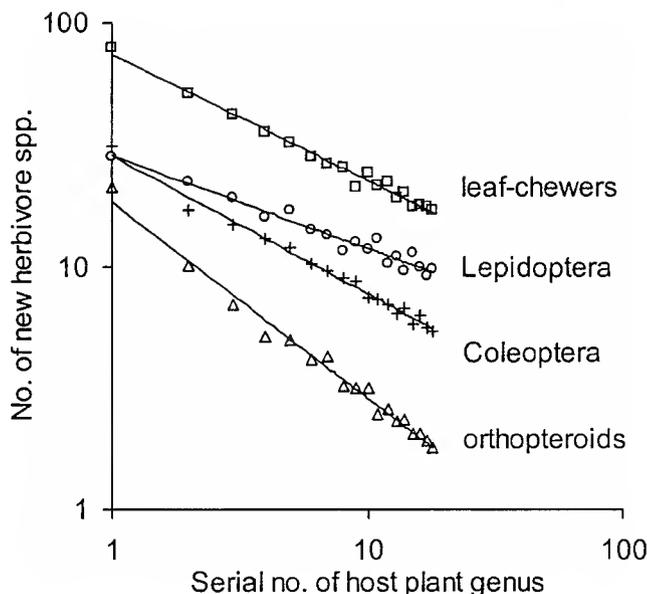


Figure 3. Number of new herbivore species obtained by sampling a new plant species. The average number of new herbivore species collected from first, second, . . . , eighteenth plant species, each from a different plant family, is depicted for all leaf-chewers, Lepidoptera, Coleoptera, and orthopteroids and fitted by power functions (lines; Eqs. 1 and 8–10 from Table 2).

species. These extrapolations provided the average (95% confidence interval) estimate of species richness at 511 (495–527) species, whereas the observed value was 520 species.

According to extrapolation from Eq. 1 (Table 2), there were 855 herbivore species feeding on 45 hosts, each representing a different family (Table 3). The aggregate number of additional herbivore species feeding on only 52 hosts representing confamilial tree genera was estimated at 700–938 (Table 3), based on Eqs. 2–4 (Table 2) and data on herbivores from three different plant families. The aggregate number of herbivore species feeding only on the other 55 hosts from these genera was estimated at 290–766 (Table 3), based on Eqs. 5–7 (Table 2) and data on herbivores from three plant genera. The total number of herbivore species feeding on plants from the 1-ha plot

Table 3. Estimated number of herbivore species feeding on different families, confamilial genera, and congeneric species of plants from 1 ha of the forest.*

	<i>Euphorbiaceae</i>	<i>Rubiaceae</i>	<i>Moraceae</i>
Families	855	855	855
Confamilial genera	700	865	938
Congeneric species	385	290	766
Total	1940	2010	2559

*Estimates were calculated from data on herbivores feeding on three plant families with equations from Table 2.

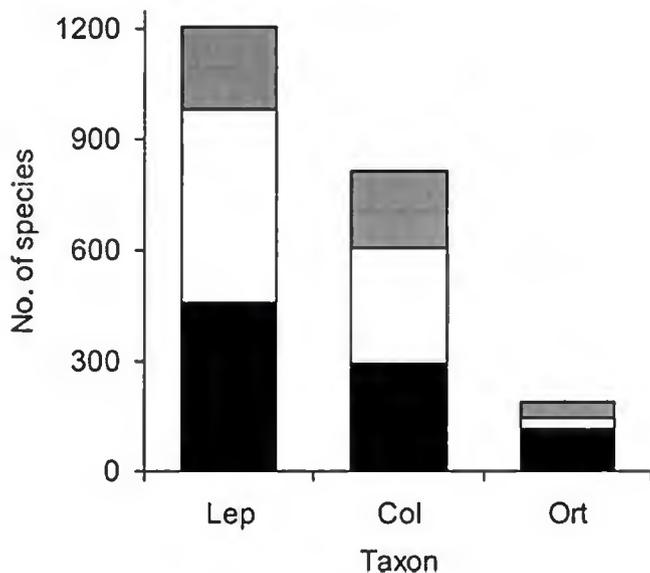


Figure 4. Number of species from Lepidoptera (Lep), Coleoptera (Col), and orthopteroids (Ort) supported by 45 host species from different plant families (black), 52 hosts representing different additional genera from these families (white), and other 55 hosts from these genera (gray).

was thus estimated by method 1 at 1940–2559 (Table 3). Separate analyses performed for Lepidoptera, Coleoptera, and orthopteroids confirmed that most of the herbivore diversity was generated by plant diversity at the familial and generic levels in all these insect taxa (Fig. 4).

Fifty estimates obtained with method 2 ranged from 1335 to 2030 species. They were normally distributed (Kolmogorov-Smirnov test, $p > 0.15$), with an average (95% confidence interval) of 1567 (1332–1802) species. These estimates were not mutually independent, however, because the same hosts were used for numerous estimates.

Differences between Herbivore Taxa and the Plant-Herbivore Ratio

The three main herbivore groups, the Lepidoptera, Coleoptera, and orthopteroids, were each characterized by a different value of k in the $y = cx^k$ relationship (Fig. 3; Eqs. 8–10 in Table 2). In particular, the orthopteroids had a low k , which indicates a relatively large overlap among the assemblages from different plants and, accordingly, only a slow increase in the number of species with increasing diversity of plants, whereas a high k for the Lepidoptera reflected higher host specificity. Accordingly, the share of the Lepidoptera species in the compound herbivorous assemblage from diverse vegetation increased and that of the orthopteroid species decreased in comparison to assemblages from single host species. An average herbivore assemblage from a single host, calculated from

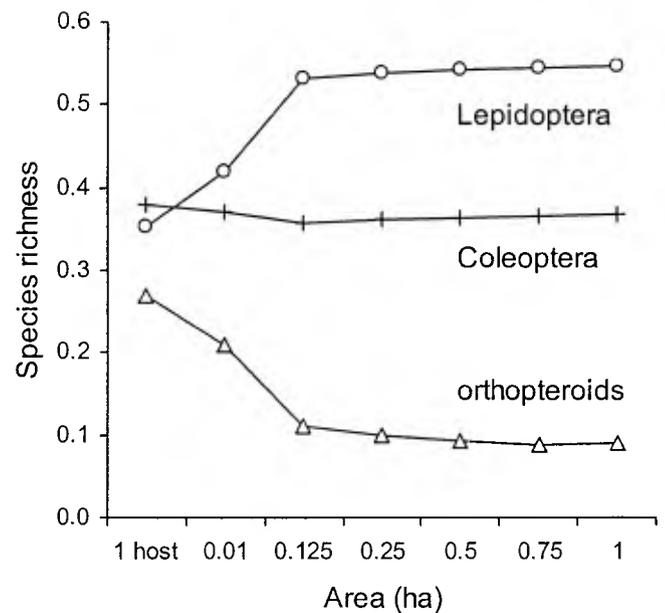


Figure 5. Relative species richness (the proportion of species) of Lepidoptera, Coleoptera, and orthopteroids in herbivorous assemblages on a single host and in assemblages estimated for plants from 0.01–1 ha of the forest vegetation. Number of herbivores on 1 host was calculated as an average from data for 18 hosts, each from a different family; number of herbivores on diverse vegetation was estimated by method 1 (see Methods).

18 assemblages from different plant families, was likely composed of 38% Coleoptera, 36% Lepidoptera, and 26% orthopteroid species, whereas a compound assemblage from 1 ha would have 54% Lepidoptera, 37% Coleoptera, and only 9% orthopteroid species.

Species richness of these herbivore taxa was also estimated for vegetation from areas of 0.01, 0.125, 0.25, 0.5, and 0.75 ha with method 1. The relative species richness of the Lepidoptera, Coleoptera, and orthopteroids remained constant from 0.25 to 1 ha (Fig. 5). Likewise, the total herbivore and plant species richness increased in parallel from 0.25 to 1 ha so that the plant-herbivore species ratio changed only slightly from 15 to 14 (Fig. 6).

Discussion

Assemblages of Insect Herbivores

Herbivorous insects were not sampled exhaustively on any of the 59 plant species studied, as evidenced by their nonasymptotic species-accumulation curves. A complete census of locally feeding herbivores appears to be all but impossible for any single plant species in a highly diverse tropical ecosystem (Price et al. 1995). Continuous

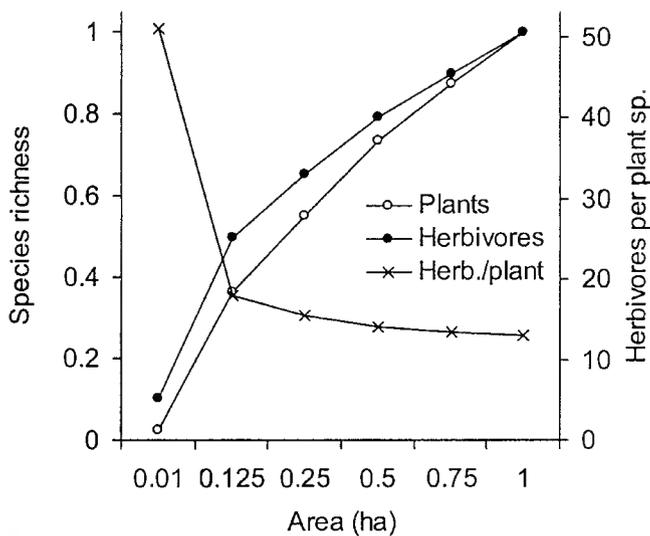


Figure 6. Species-area curves for plants and leaf-chewing herbivores. Species richness of plants and herbivores is expressed as the proportion of the species richness from 1 ha (i.e., 152 plant and 2170 herbivore species). Number of herbivores was estimated by method 1 (see Methods); means from estimates based on three different families were used. Number of herbivore species per plant species is also represented.

sampling tends to uncover additional species continually, many of them feeding on the target tree species only marginally and, accordingly, occurring at extremely low population densities on that species (Novotny & Basset 2000). High spatial diversity within the vegetation makes this “mass effect” (Shmida & Wilson 1985) particularly important in rainforests. For instance, an average 100-m² subplot of the Baitabag plot contained 10.8 plant individuals from 9.1 species; that is, almost none of any two adjacent trees were conspecific. Such spatial heterogeneity provides ample opportunity for colonization of each tree by polyphagous herbivores from neighboring trees (Basset 1999).

The nonasymptotic increase in species with sampling effort suggests that no particular magnitude of species richness could properly be used to characterize a community per se, without reference to a particular sample size or sampled area (cf. Gotelli & Colwell 2001). The local species richness of herbivores thus depends not only on the species richness of plants but also on the abundance of individual plant species. The latter factor was not included in the present analysis because herbivore diversity supported by each host was assessed on the basis of equal sample size, corresponding to 1500 m² of foliage for each tree species studied. This sample size, set by logistic constraints, is arbitrary but probably high enough to include all regular members of the herbivorous assemblages studied (Novotny et al. 2002a).

A more sophisticated estimate should combine species-accumulation curves, describing an increase in species richness of herbivores with foliage area for each plant species, with data on the foliage area of plant species in the studied area of forest. Unfortunately, such data were not available.

Local Species Richness of Insect Herbivores

Our estimate of the number of leaf-chewing species feeding on plants from a 1-ha area of the forest is necessarily only approximate, and its accuracy is compromised by several methodological problems. The vegetation survey was incomplete, not including lianas, epiphytes, and plant species with a dbh of <5 cm. Liana species in particular may have a rich herbivore fauna (Ødegaard 2000a). Further, we used 1-ha plots because they have become standard units for quantitative vegetation analysis in tropical rainforests, despite the fact that they do not represent an adequate sample of the local flora (e.g., Condit 1997; Oatham & Beehler 1998). Our sampling probably also missed some of the herbivore species limited to poorly accessible parts of the forest canopy, which may be an important bias (Basset et al. 2001). A further caveat to our study is that conclusions are valid only for the leaf-chewing taxa and stages we studied: larval Lepidoptera, mostly adult Coleoptera, and both immature and adult Orthoptera and Phasmatodea.

We probably underestimated the host specificity of the taxa studied only in the adult stage because immature individuals tend to be more host-specific than adults.

Species-richness estimates made by methods 1 and 2 were close to each other, which is not surprising because both methods are theoretically equally sound and both were based on the same data set. This also means that both estimates may be biased by limitations of available data, particularly those on the overlap among herbivore assemblages on congeneric plant species and confamilial plant genera. In both cases, the extrapolation was based on data sets from only three families from the 45 present, which may not be representative of other taxa. The estimates based on data from Moraceae were particularly susceptible to error because they were based on the study of only two confamilial genera. However, the three families used for extrapolation were prominent in the vegetation because they included 20 from the 97 genera and 42 from the 152 species present in the 1-ha plot. Further, the dominant position of *Ficus* and paucity of species from other genera are characteristic of the family Moraceae not only in our study design but also in New Guinean flora (Höft 1992).

The estimates of herbivore species richness supported by congeneric host species and confamilial host genera were obtained by the analysis of three different plant families and were thus mutually independent. The highest estimate was 160% of the lowest one; we consider this

variation acceptable, given the exploratory and rather preliminary nature of insect species-richness estimates in tropical forests, including those in the present study.

Further, any approach based on taxonomic rank is potentially misleading because the level at which supraspecific taxa are recognized is a convention (Stevens 1998). New approaches based on intertaxon distances calculated from higher-level molecular phylogenies may help resolve this inadequacy in the future (Kitching et al. 2003).

An approach similar to ours was adopted by Ødegaard (2003), who sampled herbivorous beetles from 50 species of trees and lianas in a rainforest in Panama and then extrapolated the results to 500 plant species present locally. His estimate for 150 plant species was approximately 1250 species of herbivorous beetles, including species feeding on flowers and wood. Because leaf-chewing beetles represent 46% of all species effectively specialized (*sensu* May 1990) to an average plant species, the estimate for leaf-chewing beetles on 150 plant species in Panama is 571 species—not far from the 788 species of leaf-chewing beetles estimated for 152 plant species by method 1 in our study.

Janzen (1988) relied on mass light-trapping of adults and collecting of caterpillars from diverse vegetation of a dry forest in Costa Rica rather than extrapolation. He found 3140 species of Lepidoptera in an ecosystem with 725 species of vascular plants. No plant species was attacked by more than 20 species of caterpillars. Our study found, on average, 29 caterpillar species per plant species, but our data were too limited for prediction of species richness over the entire local vegetation.

We are not aware of any other study quantifying herbivore diversity supported by different levels of taxonomic diversity of the vegetation—by single representatives of all plant families, confamilial genera, and congeneric species present in the study area. The crucial role of the familial and generic diversity of plants and the lesser role of congeneric plant species in supporting herbivorous diversity reflect a low host specificity of herbivores with regard to congeneric hosts (Novotny et al. 2002a).

Extrapolation to Other Taxa and beyond the Local Scale

The extrapolation methods we applied are suited only to estimates of local species richness because they take no account of beta diversity. It is always tempting to extrapolate such data, even to an estimate of the global species richness of all biota, but there are problems associated with long-range extrapolations (Stork 1988; Basset et al. 1996; Ødegaard 2000b; Gotelli & Colwell 2001; Novotny et al. 2002b). One frequently used approach is extrapolation based on taxon-to-taxon (e.g., plant-to-insect) ratios of species richness (Erwin 1982; May 1990; Gaston 1992). It relies on the often relatively accurate estimates of local and regional species richness of one taxon and its locally

estimated ratio to another taxon, which is then assumed to remain constant on a regional scale, thus allowing for calculation of its regional species richness. This approach is based on an assumption that the beta-diversity of both taxa remains approximately the same.

Our data confirm this assumption for taxon-to-taxon ratios involving Lepidoptera, Coleoptera, and orthopteroids, as well as for a plant-to-herbivore species ratio, but only on a limited spatial scale from 0.25 to 1 ha. The generality of this result requires further confirmation. We showed that herbivore diversity is associated particularly with the diversity of vegetation on familial and generic levels. The species-to-genus and species-to-family ratios tend to change with spatial scale (Gotelli & Colwell 2001), which may also affect plant-to-herbivore species ratios.

Our tentative estimate of local species richness of rainforest leaf-chewing insects feeding on a single plant species and on plants from a 1-ha area of a lowland forest is in broad agreement with similarly low estimates for other tropical host trees (Janzen 1988; Marquis 1991; Basset 1996; Barone 1998) and to a community-wide estimate for herbivorous beetles from a Neotropical forest (Ødegaard 2003). In contrast, mass collecting methods, particularly insecticide fogging and light-trapping, yield samples that often include very large numbers of herbivorous species. For instance, Floren and Linsenmair (1998) obtained 1063 herbivorous beetles by fogging 19 trees from three species in Borneo; Missa (personal communication) collected 1168 species of weevils from 1 km² of a rainforest in New Guinea; and Barlow and Woiwod (1990) obtained 1520 species of macrolepidoptera and pyralids by light-trapping at a single site in Sulawesi. These data are difficult to compare with ours because they include herbivores other than externally feeding leaf-chewers and, more important, numerous tourist species. Reconciling these two methodological approaches through more detailed study of the role of species in communities and better comprehensive sampling programs remains an important step toward understanding the organization of insect communities in tropical rainforests and toward resolving the current debate over the magnitude of biodiversity on large geographical scales (Erwin 1982; Stork 1988; Basset et al. 1996).

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