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Guild-specific patterns of species richness and host specialization in plant–herbivore food webs from a tropical forest

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Summary

1. The extent to which plant–herbivore feeding interactions are specialized is key to understand the processes maintaining the diversity of both tropical forest plants and their insect herbivores. However, studies documenting the full complexity of tropical plant–herbivore food webs are lacking.

2. We describe a complex, species-rich plant–herbivore food web for lowland rain forest in Papua New Guinea, resolving 6818 feeding links between 224 plant species and 1490 herbivore species drawn from 11 distinct feeding guilds. By standardizing sampling intensity and the phylogenetic diversity of focal plants, we are able to make the first rigorous and unbiased comparisons of specificity patterns across feeding guilds.

3. Specificity was highly variable among guilds, spanning almost the full range of theoretically possible values from extreme trophic generalization to monophagy.

4. We identify guilds of herbivores that are most likely to influence the composition of tropical forest vegetation through density-dependent herbivory or apparent competition.

5. We calculate that 251 herbivore species (48 of them unique) are associated with each rain forest tree species in our study site so that the ~200 tree species coexisting in the lowland rain forest community are involved in ~50 000 trophic interactions with ~9600 herbivore species of insects. This is the first estimate of total herbivore and interaction number in a rain forest plant–herbivore food web.

6. A comprehensive classification of insect herbivores into 24 guilds is proposed, providing a framework for comparative analyses across ecosystems and geographical regions.

Key-words: apparent competition, effective specialization, herbivorous guild, Janzen-Connell hypothesis, New Guinea, rain forest, species accumulation

Introduction

Plant–herbivore food webs comprise at least 40% of global terrestrial biodiversity (Price 2002), most of it concentrated in the tropics. The organization and specialization of plant–herbivore food webs is of considerable relevance for understanding the magnitude of tropical diversity and the processes maintaining it. High plant diversity can be promoted where specialized herbivores or pathogens have density-dependent effects on plant growth and fitness, putting locally

*Correspondence author. E-mail: novotny@entu.cas.cz rare species at an advantage (Janzen 1970; Leigh *et al*. 2004; Lewinsohn & Roslin 2008). High herbivore diversity can also be promoted if plant–herbivore interactions are specialized, because finely partitioned plant resources will facilitate species coexistence (Lewinsohn & Roslin 2008). By contrast, generalist herbivores can mediate indirect interactions, such as apparent competition (Holt 1977), linking the dynamics of plant species that might not otherwise interact (Connell 1990). Furthermore, measures of herbivore specificity have also been used widely to calculate the local and global magnitude of species richness (Novotny *et al*. 2002b; Hamilton *et al*. 2010).

Despite the importance of understanding patterns of plant–herbivore interactions, comprehensive studies of tropical plant–herbivore food webs are not available, and three major gaps in knowledge inhibit a full understanding of diversity and specificity of plant–herbivore interactions: (i) previous plant–herbivore studies have focused for practical reasons on individual herbivorous taxa or guilds, which may not be representative of the specificity patterns in the entire food web. More than half of all such studies are restricted to leaf-chewing herbivores, particularly caterpillars (Novotny & Basset 2005; Lewinsohn & Roslin 2008) and equivalent information is unavailable for most other feeding guilds. (ii) Measures of food web specificity are hampered because specificity is sensitive to the phylogenetic diversity and composition of the host plants surveyed (Novotny *et al*. 2006; Weiblen *et al*. 2006). Surveys using equal sampling effort among plant species are particularly suited to comparative analyses of herbivore specialization (Novotny *et al*. 2004b). (iii) Measures of host specificity are also highly sensitive to the intensity of sampling. The ratio of specialists to generalists tends to decrease with sample size as numerous rare, marginally feeding generalists continue to accumulate in samples when all specialists have been recorded (Novotny *et al*. 2002a). Thus, careful standardization of sampling protocols and fully quantified measures of host specialization are required to generate unbiased measures of specialization.

In this article, we present the most comprehensive assessment of plant–herbivore food webs yet to be documented, involving a suite of 11 insect herbivore guilds sampled from rain forest vegetation in Papua New Guinea. Herbivore guilds (groups of species exploiting the same resources in a similar way: Simberloff & Dayan 1991) are typically defined by the combination of feeding mode and the plant part exploited, sometimes refined by distinguishing internally and externally feeding species, mobile and sessile species, and larvae and adults (Basset *et al*. 2004; Andrew & Hughes 2005; Grimbacher & Stork 2007). Current guild definitions vary greatly (e.g. Cornell & Kahn 1989; Lawton, Lewinsohn & Compton 1993), and we suggest a comprehensive guild classification 1 which should be useful for comparative studies among communities, ecosystems and geographic areas. We compare herbivore specificity across these guilds and use the food web data to infer the likely effects of different guilds on plant dynamics and diversity. Finally, we use our data to estimate the size and specificity of the regional food web of plant–herbivore interactions.

Materials and methods

CLASSIFICATION AND SAMPLING OF HERBIVOROUS GUILDS

Insect herbivores were classified into guilds according to their feeding mode (chewing, sucking), developmental stage (larva and adult), whether feeding internally or externally on the plant, and on the basis of the plant part used for feeding (leaves, flowers, fruits, and xylem and phloem tissue) (Table 1). The resulting matrix of 72 possible combinations of these four factors was reduced to 24, corresponding to individual guilds, by combining larvae with adults in hemimetabolous insects, combining external xylem chewers with phloem chewers, and excluding biologically impossible combinations (Table 1). In leaf chewers, adult and larval guilds are partially separated as they include both holometabolous (Coleoptera, Hymenoptera) and hemimetabolous (Phasmatodea, Orthoptera) taxa, while all sucking guilds are hemimetabolous. Insects feeding on xylem and phloem

Table 1. Classification of herbivorous guilds based on the feeding mode, developmental stage and feeding location of the herbivore and the plant part used

Feeding mode developmental stage feeding location	Chewing larva internal	Chewing larva external	Chewing adult external	Sucking larva + adult external
Leaf	**Leaf miners**	**l. leaf chewers**	**a. leaf chewers**	**Leaf suckers**
Xylem, above-ground	**Xylem chewers**	l. stem chewers	a. stem chewers	**a-g. xylem suckers**
Xylem, below-ground		**Root chewers**	Not applicable	b-g. xylem suckers
Phloem, above-ground	**Phloem chewers**	l. stem chewers	a. stem chewers	**a-g. phloem suckers**
Phloem, below-ground		**Root chewers**	Not applicable	b-g. phloem suckers
Flower	l. i. flower chewers	l. e. flower chewers	a. flower chewers	Flower suckers
Fruit	**l. i. fruit chewers**	l. e. fruit chewers	a. fruit chewers	Fruit suckers
Induced gall tissue	Chewing gallers	Not applicable	Not applicable	Sucking callers
Induced fungal infection	**Fungal chewers**	Not applicable	Not applicable	Not applicable

The combinations of parameters representing non-existing guilds are highlighted in grey. The guilds studied here are in bold.
l., larval; a., adult; i., internal; e., external; a-g., above-ground; b-g., below-ground. Larval and adult leaf chewers are distinct guilds for holometabolous taxa, but can be combined into single guild for hemimetabolous Phasmatodea and Orthoptera. 9

were placed in different guilds as the nutrition values and modes of exploitation are very different for these two vascular tissues (Raven 1983). The distinction between above-ground (stems, leaves) and below-ground (roots) location of vascular tissue is important only for externally feeding herbivores, where root feeding requires adaptation to subterranean life. Furthermore, while externally sucking insects specialize on either phloem or xylem, external chewers tend to feed on the entire vascular bundle in herbaceous plants, seedlings, young shoots and fine roots, and are unable to exploit large stems, trunks and roots. The phloem and xylem tissues were thus combined as a single resource for external chewers. Finally, herbivore-induced gall tissue, and herbivore-induced fungal infection of plant tissue constitute additional resource classes in our classification. The combination of different feeding modes, developmental stages, feeding locations and plant parts constitutes 24 guilds, of which 11 are studied here:

Fruit chewers

The study was limited to dacine fruit flies (Tephritidae: Dacinae) reared from plant species sampled as >100 fruits weighing >1 kg (Novotny *et al*. 2005). Dacine fruit flies are endemic to subtropical and tropical forests from the Indian subcontinent across to Oceania, reaching their greatest diversity in New Guinea (Drew 1987). Other taxa from this guild, not studied here, include species of Lepidoptera, Coleoptera and Diptera.

Fungal chewers

This guild includes ambrosia beetles (Curculionidae: Scolytinae and Platypodinae). Three individual trees were sampled per species. Each tree was girdled, killed by fire, and left standing dead to allow for beetle colonization. After 20 days, the tree was felled and standardized wood samples were taken for insect rearing: (i) 20–30 cm section of roots with adjacent 10 cm of the trunk base, (ii) two 50 cm sections of the trunk, (iii) branches (2–10 cm in diameter) filling 90 dm^3 volume, and (iv) twigs (diameter <2 cm) filling 90 dm^3 volume (Hulcr *et al*. 2007b). Ambrosia beetles create galleries inside the sapwood of dead or moribund hosts, where they cultivate and feed on symbiotic fungi. Ambrosia beetles form a majority of this guild, although some cerambycid beetles are probably also xylomycetophagous.

Adult leaf chewers

All externally feeding adult insects (Orthoptera, Phasmatodea and Coleoptera) were collected by hand from the foliage. The foliage area sampled was identical for all plant species and amounted to 1500 m^2 per species. In the laboratory, each insect was provided with fresh leaves of the plant species from which it was collected and kept on it until the insect fed or died. Only insects that fed were included in the analyses (Novotny *et al*. 2002a).

Larval leaf chewers

All externally feeding holometabolous larvae (Lepidoptera, Coleoptera), including leaf rollers and leaf tiers, were collected by hand from the foliage (Novotny *et al*. 2002a). The foliage area of 1500 m^2 was sampled for each plant species. Each larva was reared in the laboratory on leaves of the plant species from which it was collected. Lepidopteran species are illustrated at http://www.entu.cas.cz/png/caterpillars. The samples were dominated by Lepidoptera, while Hymenoptera were very rare (Bito & Smith 2005).

Leaf miners

Leaf miners excavate characteristic tunnels or blotches inside the leaf lamina (Hespenheide 1997). All leaf miners (Lepidoptera, Coleoptera, Diptera) were sampled by hand from the foliage area of 1500 m^2 per plant species. Twigs with leaves including miners were placed in plastic bags and reared in the laboratory to adults. The samples were dominated by small moths (particularly Gracillariidae), followed by beetles (mostly Buprestidae) and flies (mostly Agromyzidae).

Leaf suckers

This guild includes species of Heteroptera (Andrew & Hughes 2005) and the cicadellid subfamily of Typhlocybinae (Auchenorrhyncha), where the feeding mode of piercing and emptying individual mesophyll cells evolved from phloem feeding (Novotny & Wilson 1997). Only the latter group was studied here. Typhlocybine larvae were hand collected from foliage (1500 m^2 per plant species) and reared to adults on excised leaves in the laboratory. Only larvae reared to males were used in the analysis as the taxonomy of this group is based mostly on the morphology of male genitalia; females are often impossible to identify.

Phloem chewers

This guild includes true bark beetles (Curculionidae: Scolytinae) which are phloemophagous, i.e. feeding on dead host tissues, in most cases on nutrient-rich phloem. Both adults and larvae build their own tunnels as they feed and travel under the bark. Bark beetles were sampled using identical methods to those for fungal feeders (see above, Hulcr *et al*. 2007b).

Phloem suckers

This guild includes species tapping phloem vascular elements and extracting phloem sap from their host plants. They include the Sternorrhyncha, and a large part of the Auchenorrhyncha. This study is limited to larval Auchenorrhyncha, hand collected from the foliage (1500 m^2 per plant species). The larvae were reared to adults on caged saplings of the same tree species from which they were collected. The reared species represented 11 families, particularly Cicadellidae, Flatidae and Ricaniidae.

Root chewers

Species of Chrysomelidae (particularly Eumolphinae) dominated the root feeding guild, although beetles from other families (Curculionidae, Elateridae, Scarabaeidae) were also present. Only chrysomelid beetles were sampled in this study. Vegetation within a 5-m radius around each target tree was cleared and two traps, 1 m^2 each, collecting insects emerging from the ground, were placed within a 2-m radius of each target tree and operated for 6 months (Pokon, Novotny & Samuelson 2005).

Xylem chewers

This guild includes species feeding on nutrient-poor xylem tissue. The insects were reared from eight trunk sections, each weighing 20 kg, per tree species. The sections were sawn from freshly felled trees and exposed in the forest (four in the understorey and four in the canopy) to allow their colonization by insects. After 3 weeks, each section was individually enclosed in a rearing cage and emerging insects collected for 6 months. We included in this guild all Cerambycidae beetles reared from dead wood, although some of the species may also be xylomycetophages or phloemophages.

Xylem suckers

This guild includes species tapping xylem vascular elements and extracting xylem sap. This mode of feeding on extremely energy-poor xylem sap has originated only 2–3 times in insect evolution, in all cases in Auchenorrhyncha (Novotny & Wilson 1997). This guild includes Cercopoidea and Cicadellidae: Cicadellinae, both studied here using the same methods as those for phloem suckers (see above). Subterranean Cicadoidea larvae, which we classify in another guild, were not studied here.

Non-sampled guilds and taxa

Flower-feeding guilds, chewing and sucking gallers, and sap-sucking Hemiptera other than Auchenorrhyncha represent the main gaps in our coverage of rain forest herbivores. Species richness of missing guilds was estimated using published richness estimates from other tropical forests and semi-quantitative estimates from the forests we studied (Table 2). In particular, a detailed analysis of taxonomic composition of insects on a subtropical Australian tree (Basset 1991) provided information on relative species richness of various herbivore taxa.

Herbivore guilds were each sampled from 13 to 88 plant species at three study sites, Baitabag, Ohu and Mis Villages, within a 10 × 20 km area, encompassing a mosaic of secondary and primary lowland hill forest in the Madang Province (Papua New Guinea) for at least 1 year between 1995 and 2008. This selection always included both closely related (congeneric) plant species and representatives of [2] major plant lineages (Table S4, Appendix S1).

All insects were assigned to morphospecies and later identified by specialists as far as possible (Miller, Novotny & Basset 2003). Species identifications were often verified by dissection of genitalia, and reference to type specimens. Comparisons of mitochondrial cytochrome oxidase I DNA sequence divergence with morphology were used for several thousand insect specimens to verify our species boundaries, including polymorphic species and cases of sexual dimorphism (Hulcr *et al.* 2007a; Craft *et al.* 2010).

Plant vouchers are deposited in PNG Forest Research Institute in Lae and University of Minnesota St. Paul, insect vouchers in the Bishop Museum in Honolulu, the Smithsonian Institution in Washington, PNG Agriculture Research Institute in Port Moresby, and the Natural History Museum in London.

PLANT PHYLOGENY, SPECIES COMPOSITION AND ABUNDANCE

Phylogeny for most host plant clades was estimated from 1285 base pairs of aligned chloroplast DNA encoding ribulose-1,5-bisphosphate carboxylase (rbcL) in 92 host plant species (Table S2, Appendix S1). In addition, phylogeny estimates for three locally diverse host plant clades were obtained by analyses of a gene encoding a subunit of NADH-plastoquinone oxidoreductase (ndhF) for Euphorbiaceae and the internal transcribed spacer region of nuclear ribosomal DNA (ITS) for Ficus (Moraceae) and Syzygium (Myrtaceae). Each independent estimate was grafted to the rbcL phylogeny according to the position of the clade in Soltis *et al.* (1998). Branch lengths estimated from ndhF and ITS were scaled to the relative rate of change in rbcL compared between pairs of taxa in each of the three clades (Fig. S1). A matrix of phylogenetic distances, consisting of the absolute number of nucleotide substitutions in rbcL, was calculated for all pairs of host plant species.

FOOD WEB ANALYSIS

Our data on herbivore assemblages feeding on focal plant species were standardized for food web analysis as follows: (i) trophic relationships documented by only a single feeding individual were excluded as poorly documented, (ii) only records for insect larvae successfully reared to adults, or adults tested experimentally for feeding, were retained, and (iii) each plant species was sampled with equal effort for each guild, removing biases in measures of specificity resulting from variations in host plant abundance (sample size for each guild is defined above). The standardized data matrix included 526 assemblages, i.e. particular guilds feeding on particular plant species (Table S1).

Potential for interactions among plants, mediated by shared herbivores, was measured by the host plant isolation $d_i = \sum_k D_{ki} C_{ki}$. It is a product of herbivore dominance $D_{ki} = n_{ki}/n_i$ (the abundance of herbivore k on plant i divided by the total number of herbivores feeding on i) and herbivore density $C_{ki} = n_{ki}/n_k$ (the abundance of herbivore k on plant i divided by the abundance of k in the entire food web). The host plant isolation is defined as the probability that, for an individual herbivore on plant species i, any other conspecific individual, randomly selected from the entire food web, also feeds on plant species i (Müller *et al.* 1999; Novotny *et al.* 2004b). This is also the probability that the parent of a randomly selected herbivore feeding on plant species i fed on the same host species, provided that herbivores redistribute themselves randomly across the potential range of host plants, and that there is no tendency for individuals to prefer their natal host plant.

Food web parameters were calculated for each guild on a set of nine plant species, spanning the continuum between close relatives and distantly related lineages. Each selection included: (i) four species from Eurosids 1, including two Ficus and one Artocarpus species (Moraceae), and one species from the family Euphorbiaceae, (ii) two species from Eurosids 2, and (iii) three species from Euasterids (Fig. 1, Fig. S2, Table S2). The plant species were thus matched to control for differences between guilds in the phylogenetic distribution of plant resources (Novotny *et al.* 2006).

SPECIES RICHNESS AND HOST SPECIFICITY ANALYSIS

The accumulation of herbivore species with increasing number of plant species was described by the Mao Tau function, an analytical analogue of a species accumulation curve derived by amalgamation of samples in random order, implemented in the program EstimateS (Colwell 2008). The trends in herbivore species richness were extrapolated to 100 plant species, using a power function fitted either to the entire empirical species accumulation curve, or only its terminal part (excluding data for the first 5–30 plant species), depending of the goodness-of-fit for each function (Fig. S3). Insect species documented by single feeding individuals, as well as morphospecies known only from larval stages were retained in the analysis of herbivore species richness. The number of herbivore species feeding on a particular plant species (S_{chao}) was estimated using the Chao1 index (Colwell 2008).

Family specialists, feeding on plants from a single family, were identified using single representatives of 6–31 families sampled for

Table 2. Species richness in herbivorous guilds

Guild	Taxa	S_{obs} (SE)	S_{chao} (SE)	S_{est}	F	$S \times F$	Note
Adult leaf chewers	Col., Ort., Pha.	53·3 (2·5)	73·2 (3·5)		0·08	6·2	
Fruit chewers	Dip.	1·0 (1·0)	1·4 (0·2)		0·58	0·8	
Fungal chewers	Col.	12·0 (1·9)	18·0 (2·8)		0·26	4·7	
Larval leaf chewers	Lep.	23·6 (1·9)	30·8 (2·1)		0·29	8·9	
Leaf miners	Col., Dip., Lep.	2·3 (0·2)	3·6 (0·4)		0·74	2·6	
Leaf suckers	Hem.	1·1 (0·2)	1·5 (0·3)		0·78	1·1	
Phloem chewers	Col.	0·9 (0·4)	1·4 (0·6)		0·63	0·9	
Phloem suckers	Hem.	13·0 (1·3)	17·8 (2·1)		0·18	3·2	
Root chewers	Col.	9·6 (2·0)	13·5 (3·0)		0·23	3·1	
Xylem chewers	Col.	8·1 (1·1)	12·1 (1·6)		0·19	2·3	
Xylem suckers	Hem.	2·6 (0·8)	3·8 (1·3)		0·25	1·0	
Flower chewers, adult	Col.			36	0·05	1·9	[1]
Flower chewers, adult	Ort., Pha.			0	0·08	0·0	[2]
Flower chewers, larval	Lep., Col., Hym.			3	0·29	0·9	[3]
Gallers	Dip., Hem., Hym., Thy.			0·3	1·00	0·3	[4]
Phloem, xylem chewers, int.	Col.			9·0	0·40	3·6	[5]
Phloem, xylem, leaf suckers	Hem. excl. Auch.			16·1	0·40	6·5	[6]
Fruit chewers	Lep., Col.			1·2	0·58	0·7	[7]
Xylem suckers, undergr.	Auch.			2·4	0·25	0·6	[8]
Phloem suckers, undergr.	Hem.			1	0·18	0·2	[9]
Flower and fruit suckers, ext.	Hem., Thy.			1	0·40	0·4	[10]
Phloem, xylem chewers, ext.	Col., Lep.			0	0·08	0·0	[11]
Root chewers	Col. excl. Chry.			4	0·23	0·9	[12]
Total		127·5	177·0	74		50·8	

Notes: [1] The number of flower-chewing species per tree species amounted to 105% of the number of leaf-chewing species for rain forest beetles in Panama, and the *F*-value for flower chewers amounted to 64% of the value for leaf chewers (Ødegaard 2000). These ratios were applied to our data on leaf-chewing beetles to estimate *S* and *F* for flower chewers.
[2] Species composition of flower chewers largely overlaps with leaf chewers (pers. obs.). **10**
[3] Species richness was estimated from *ad hoc* field observations. *F*-values for larval leaf chewers were used.
[4] Mean number of herbivore species and their *F*-values were estimated from tropical forest studies by Cuevas-Reyes *et al*. (2003, 2004) and Ribeiro & Basset (2007).
[5] Taxa sampled in this study represented 60% of the diversity in this guild on a subtropical tree species in Australia (Basset 1991). Mean *F*-values for phloem and xylem chewers were used.
[6] The taxa sampled in this study represented 59% of the diversity in this guild on a subtropical tree species in Australia (Basset 1991). Mean *F*-values for phloem, xylem and leaf suckers were used.
[7] Data from 135 plant species sampled in the study area (R. Ctvrtecka, pers. comm.) were used to estimate species richness. *F*-values for fruit-chewing Tephritidae were used.
[8] Underground species represented 39% of all xylem suckers sampled as adults in the study area (Novotny & Basset 1999). *F*-values for above-ground xylem feeders were used.
[9] Species richness was estimated from *ad hoc* field observations. *F*-values for above-ground phloem feeders were used.
[10] Species richness was estimated from *ad hoc* field observations. Hemiptera species feeding on fruits overlap with those feeding on leaf chewers. Mean *F*-values for phloem, xylem and leaf suckers were used.
[11] Species composition largely overlaps with leaf chewers (pers. obs.).
[12] Species richness estimated from *ad hoc* field observations (R. Pokon, unpubl. data). *F*-values for root-chewing Chrysomelidae were used.
S_{obs}, mean (± SE) number of herbivorous species observed per plant species; S_{chao}, mean (± SE) number of herbivorous species per plant species estimated by Chao1 index; S_{est}, number of herbivore species per plant species, estimated for herbivorous guilds and taxa not included in the present study; *F*, effective specialization. The product of herbivore species richness and effective specialization ($S \times F$) denotes the number of unique herbivorous species feeding on particular plant species in the studied rain forest community ($S_{chao} \times F$ and $S_{est} \times F$ for respectively the guilds studied and not studied here). Insect orders (Coleoptera, Diptera, Hemiptera, Hymenoptera, Lepidoptera, Orthoptera, Phasmatodea, Thysanoptera) are abbreviated using first three letters; Auch, Auchenorrhyncha; Chry, Chrysomelidae.

each guild (listed in Table S2). Host specificity was assessed only for species sampled as ≥10 individuals. This is a compromise between the need to avoid artificial inflation of host specificity estimates due to insufficient opportunity to detect rare hosts, and the need to retain as many species in the analysis as possible (Novotny *et al*. 2002a).

The similarity in herbivore species feeding on plant species *i* and *j* was quantified by Jaccard's similarity $J_{ij} = a/(a + b + c)$, where *a* is the number of herbivore species shared by plant species *i* and *j*, and *b* and *c* are species limited to respectively *i* and *j*. J_{ij} can be also interpreted as a host specificity index as it equals the probability that a herbivore species from the combined pool of species feeding on *i* and *j* feeds on both these plant species.

The effective specialization, i.e. the proportion of herbivorous species feeding on a particular host plant that was unique to that plant, was estimated as $F = S_p/T_{ph}$, i.e. as the ratio of the total number of herbivorous species found on all hosts studied (S_p), divided by the number of trophic interactions involving these hosts (T_{ph}) (May 1990). The effective specialization was estimated for herbivore species sampled as ≥10 individuals on a set of 12–88 plant species for each guild, matched as far as possible in their taxonomic structure to an

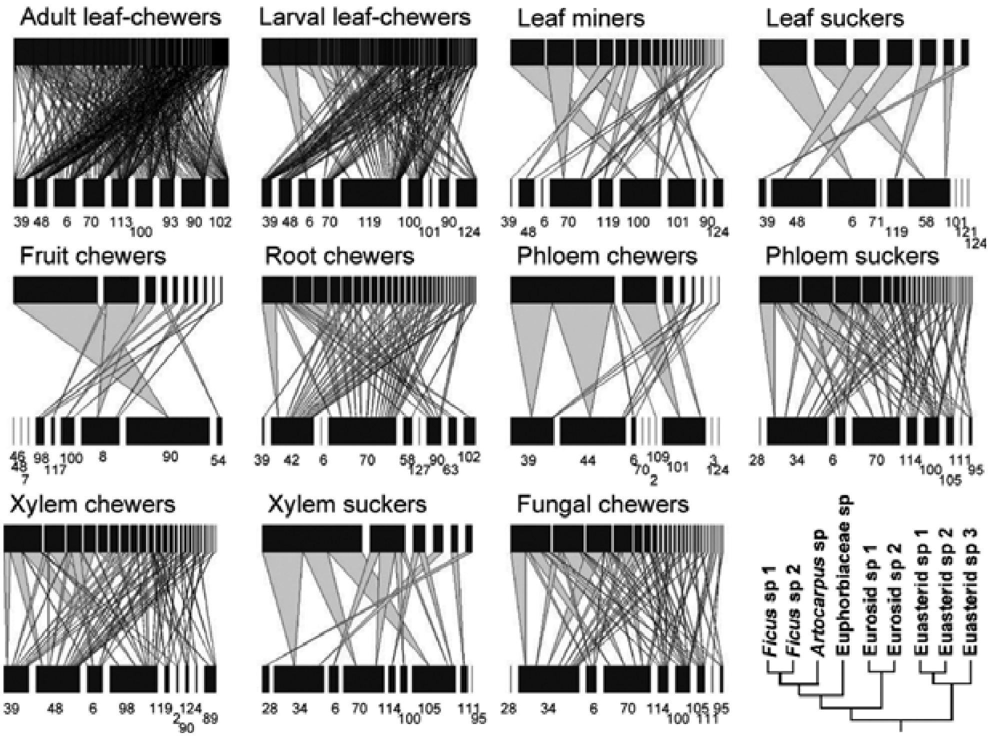

Fig. 1. Quantitative plant–herbivore food webs for insect guilds feeding on phylogenetically standardized sets of nine plant species and phylogenetic relationships among these plant species. For each web, the lower bars represent the frequency with which each host plant is consumed by herbivores, and upper bars represent herbivore abundance. The width of the links between trophic levels is proportional to the frequency of each interaction. Herbivores from each guild were sampled with equal effort on all plant species. Guild definitions are given in Table 1. Numbers refer to plant species in Table S2. Herbivore species included in the food webs

equally sized set of plant species randomly drawn from the local vegetation. In particular, we tried to match the proportion of phylogenetically isolated species, with no co-occurring congeneric species, in the set of plants used for effective specialization estimates with that found in subsets of 10–100 plant species, randomly drawn without replacement from plant data obtained by surveying 1 ha forest plots in Baitabag and Wanang. This proportion decreased from 86% in sets of 10 plant species randomly drawn from local vegetation to 57% in sets of 100 plant species (Fig. 2).

The number of herbivore species in the plant–herbivore food web was estimated as a product of the estimated number of herbivores feeding per plant species (S_{chao}), their local effective specialization (F), and local plant species richness (S_{plant}), i.e. as $S_{\mathrm{chao}} \times F \times S_{\mathrm{plant}}$. The number of trophic interactions was estimated as $S_{\mathrm{chao}} \times S_{\mathrm{plant}}$.

Results

Quantitative plant–herbivore food webs were constructed for 11 herbivorous guilds (Table 1) using information on 6818 distinct trophic links between 224 plant and 1490 herbivore species, supported by experimentally verified feeding or rearing of 203 222 individuals (Table S1). Our data set includes members of all major herbivorous orders (Lepidoptera, Coleoptera, Hemiptera, Diptera, Orthoptera and Phasmatodea) feeding on all principal vegetative plant tissues and organs, plus fruits.

The species richness of herbivores and their host specificity on phylogenetically standardized sets of nine tree species varied widely among guilds (Fig. 1). The average host plant isolation d_{ii} ranged from 0·3 to 1·0 among guilds, i.e. spanned almost the entire range of values from 0 (indicating extreme generalization) to 1 (indicating extreme specialization)

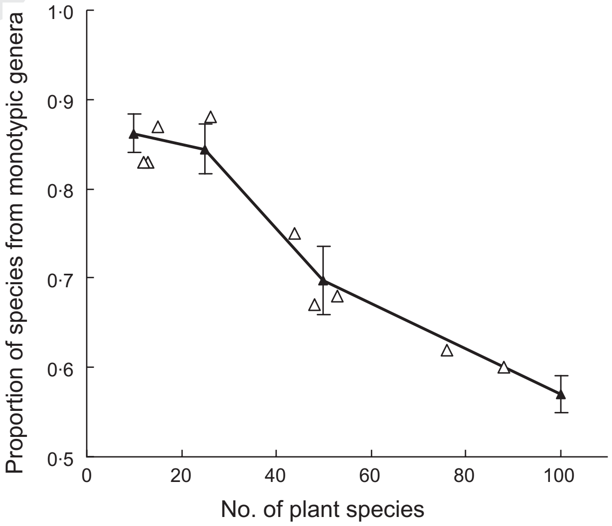

Fig. 2. Representation of species from monotypic genera in rain forest vegetation. The proportion of plant species with no congeners (mean ± SE) is shown for groups of 10–100 plant species randomly drawn from local rain forest vegetation in our study area. Markers indicate the composition of sets of plant species, one for each herbivore guild, used to estimate the effective specialization (F) of their herbivores.

(Fig. 3a). For the seven herbivore guilds with mean $d_{ii} < 0{\cdot}6$, herbivores recorded as feeding on a particular plant species were species and individuals feeding partly or mostly on other plant species. In the remaining four guilds with mean $d_{ii} > 0{\cdot}8$ the herbivore assemblages on particular plant species were largely isolated from one another. The average number of species (s) from the set of nine focal tree species used as hosts by herbivore species was close to 1 for virtually monophagous guilds of leaf suckers, leaf miners, fruit chewers and larval leaf chewers. By contrast, herbivorous species from xylem-chewing, adult leaf-chewing and fungal-chewing guilds had on average $> 2{\cdot}25$ host species, i.e. they were feeding on more than a quarter of plant species considered in this analysis (Fig. 3b).

Jaccard's similarity (J_{ij}) between herbivore assemblages decreased with the phylogenetic distance of their host plant species (D_{ij}) in seven of the 11 guilds. Plant phylogeny explained only a small proportion of variation in the similarity of their herbivore assemblages (from 1 to 43%, mean 14%), even in the seven guilds where the relationship was significant (Fig. 4a). In larval feeding guilds, this relationship was generated particularly by a marked change from high J_{ij} values for herbivores feeding on pairs of congeneric plant species to much lower values on confamilial plant species from different genera, followed by much smaller further reduction in J_{ij} from confamilial to allofamilial pairs of plant species (Fig. 4b).

Specificity estimated as the proportion of herbivore species feeding on a single plant family varied widely, from 0 to 100%, among the studied guilds (Fig. 5a). In the herbivorous assemblage composed from all 11 studied guilds feeding on a single plant species 33% of species were specialized on a single plant family. As plant diversity increases, specialized herbivore guilds accumulate species more rapidly than generalist guilds (Fig. 5b). For instance, adult leaf chewers represented 42% of all herbivore species feeding on a single plant species but only 29% of species feeding on 100 plant species, while more specialized larval leaf chewers increased their share of species from 19% on a single plant species to 30% on 100 plant species (Fig. 5b). The relative importance of small but highly specialized guilds increased with plant diversity even more, for instance from 3 to 12% for leaf suckers and from 1 to 4% for leaf miners. Thus, as the number of tree species increased from one to 100 species, the proportion of associated herbivore species specialized to a single plant family increased from 33 to 50%.

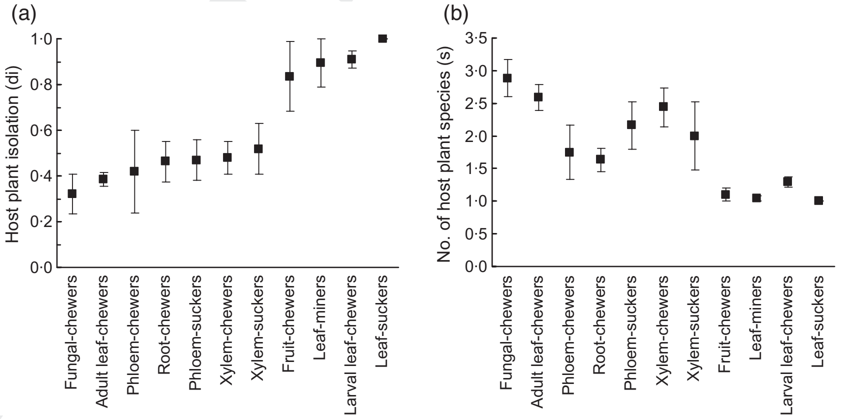

Fig. 3. Specialization and species richness in plant–herbivore food webs comprising different guilds feeding on phylogenetically standardized sets of nine plant species. (a) The mean (±SE) host plant isolation d_i, (b) the mean (±SE) number of host plant species per herbivore species *s*.

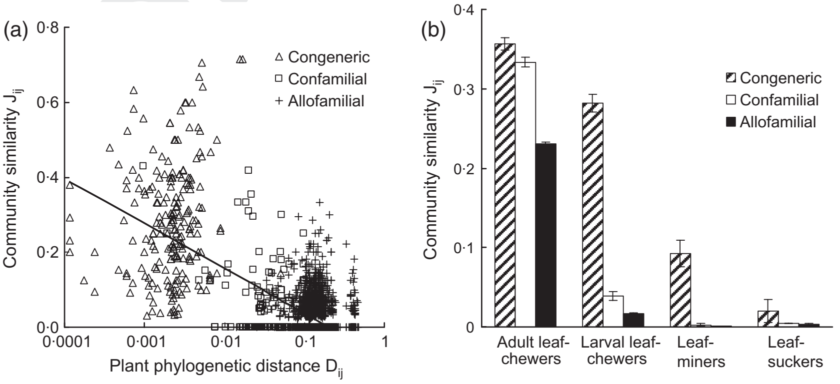

Fig. 4. Plant phylogenetic distance and similarity of their herbivore assemblages from folivorous guilds. (a) Relationship between phylogenetic distance of plants (D_{ij}) and Jaccard's similarity (J_{ij}) of their larval leaf-chewing herbivores (Pearson $r = -0{\cdot}425$, $P < 0{\cdot}05$, Mantel test); pairs composed of congeneric, confamilial and allofamilial plant species are distinguished by different markers. Other significant (Appendix S1 $< 0{\cdot}05$, Mantel test) relationships include phloem chewers ($r = -0{\cdot}654$), fungal chewers ($r = -0{\cdot}307$), leaf suckers ($r = -0{\cdot}425$), leaf miners ($r = -0{\cdot}236$), adult leaf chewers ($r = -0{\cdot}218$) and fruit chewers ($r = -0{\cdot}104$); (b) the mean (±SE) similarity of herbivores from folivorous guilds, feeding on plants from the same genus, different genera of the same family and different families.

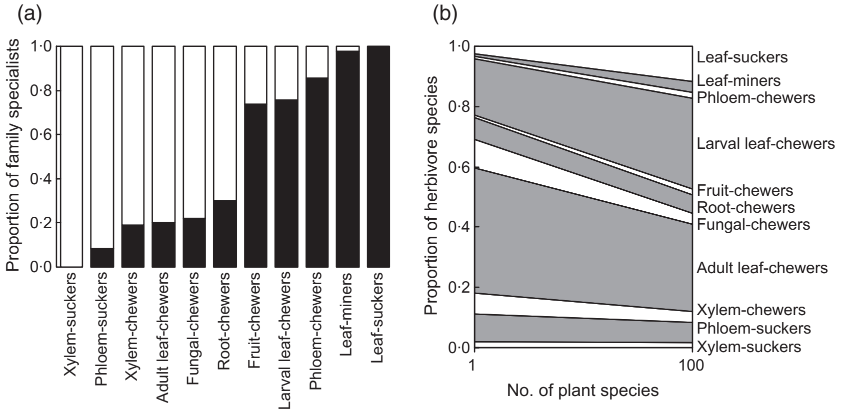

Fig. 5. Host specificity and guild composition of insect herbivores on rain forest plants. (a) Proportion of herbivore species feeding on a single plant family, estimated for herbivore species sampled as ≥10 individuals; (b) the relative species richness of different guilds estimated for 1 and 100 plant species.

On average, we calculate that 251 herbivorous species feed on each plant species, including 128 species recorded empirically, 49 species extrapolated as unrecorded in our data set due to incomplete sampling, and 74 species from the herbivorous guilds which we did not study (Table 2). We estimate that our sampling thus recorded 72% of species from the focal guilds, and 51% of all herbivorous species.

The effective specialization of herbivorous species exhibited similarly large differences among guilds as other host specificity measures as it ranged from 0·08 in adult leaf chewers to > 0·7 in leaf miners and leaf suckers (Table 2). The number of species effectively specialized, i.e. unique to a particular plant species in the studied ecosystem, ranged from 8·9 in larval leaf chewers to ~1·0 in fruit chewers, phloem chewers, xylem suckers and leaf suckers. We estimate that there are 51 herbivore species effectively specialized to a particular plant species in the studied ecosystem, including 35 species from the 11 guilds sampled here and 16 species extrapolated for the remaining guilds based on data from other studies and rain forests (Table 2).

The size of plant–herbivore food web on 200 plant species, an approximate species diversity of woody plants coexisting in 1 ha of lowland forest within the study area, was estimated at ~9600 species of herbivores, involved in ~50 000 plant–herbivore interactions. According to these estimates, our study of 1490 herbivore species and 6818 trophic links thus documented 16% of species and 14% of trophic links in the local ecosystem.

Discussion

PLANT PHYLOGENY AND HERBIVORE DIVERSITY

Our previous estimate of species diversity of larval and adult leaf chewers at 1567–2559 species feeding on 152 plant species (Novotny *et al*. 2004a) is further refined and expanded here to provide the first assessment of dimensions for the entire plant–herbivore food web in tropical rain forest. This estimate is tentative as we documented only < 20% of the estimated herbivore species and trophic links. Methods of sampling and taxonomic analysis need to be improved if we want to describe and understand food webs comprising ~50 000 trophic interactions. The understanding of these food webs will be possible only with the help of experimental manipulation as even a small perturbation, such as removal of a single species, can have complex consequences, which are difficult to predict (Morris, Lewis & Godfray 2004). Despite the recent progress in molecular methods facilitating large-scale biotic inventories (Janzen *et al*. 2009), adequate surveys of entire plant–herbivore food webs in tropical forests remain elusive.

We found that the phylogenetic relationships of host plants was a weak predictor of similarity of associated herbivore assemblages, as was also documented for leaf chewers by Ødegaard, Diserud & Ostbye (2005). This is probably because secondary chemistry and anti-herbivore defence syndromes tend to be poorly correlated with plant phylogeny (Becerra 1997; Agrawal & Fishbein 2006). The relationship between plant phylogeny and herbivore similarity was generated by congeneric plants sharing many herbivore species, particularly in host specific guilds, where allogeneric plants share only few herbivore species, no matter whether they belong to the same family, order, or only a higher clade. The closely related plant species are thus particularly important in shaping plant–herbivore interactions in tropical forests as they reduce overall levels of specialization in plant–herbivore food webs. Such species are also a major component of rain forest vegetation. For instance, there were respectively 49 and 56% of tree species and 49 and 52% of individuals with d.b.h. ≥5 cm co-occurring with one or more congeneric species in our Baitabag and Wanang 1 ha plots. Furthermore, there were 58 ± 5% of tree species with d.b.h. > 10 cm co-occurring with at least one congeneric species in 12 forest plots 20–50 ha in size, situated in tropical forests of Asia, Africa and America, and these species represented 53 ± 6% of all individual trees in the studied plots (CTFS 2008).

Host specificity estimates depend on the plant diversity from which they are derived; there is no herbivore specificity *per se*. It is likely that studies limited to only a fraction of local diversity, i.e. tens rather than hundreds of plant species, underestimate host specificity of herbivores. Herbivore assemblages from single plant species are dominated by the generalist guild of adult leaf chewers, which are relatively well known taxonomically. However, the poorly known leaf suckers and leaf miners, where $>90\%$ of the species recorded were new to science (V. Novotny and S. Miller, unpubl. data), are more specialized and thus become increasingly prominent components of overall herbivore diversity as a greater diversity of plant species is considered.

Effective specialization is used to extrapolate herbivore diversity on local as well as global vegetation (Novotny *et al.* 2002b). The phylogenetic diversity of vegetation depends on geographical scale; for instance, the proportion of species from monotypic genera decreases from 42% in local rain forest vegetation studied here to 6% in the flora of New Guinea (Höft 1992). The effective specialization of a particular guild on a plant community will thus be different from that on a regional flora. The sets of plants and their herbivores used to estimate effective specialization should match the phylogenetic diversity of the target vegetation.

PATTERNS OF HOST SPECIFICITY

We documented a wide range of host specificity patterns among herbivorous guilds: host specificity measures spanned almost the full range of theoretically possible values from extreme trophic generalization to monophagy. These results demonstrate the importance of taxonomically and ecologically comprehensive studies, as no single guild can be designated as ecologically representative of all herbivores. Likewise, individual taxonomic lineages can differ in their host specificity within the same guild. In our study, taxonomically restricted sampling may be a problem particularly in fruit, xylem and root chewers, limited respectively to fruit flies, cerambycid beetles and chrysomelid beetles.

Our results also imply that the ecological roles of herbivores in tropical forests can be quite diverse. The guilds with low d_i values are unlikely to have density-dependent effects on their host plants because low specificity will limit the effects that changes in the abundance of any particular host species will have on its herbivores. However, inter-assemblage trophic connections for such herbivores may lead to indirect interactions among plant species, such as apparent competition.

The fitness consequences of herbivory from different guilds will also influence the dynamics of plant–herbivore interactions. Fungal, phloem and xylem chewers feeding on dead or dying plant tissues are unlikely to have significant impacts on the population dynamics of their host plants, and the impacts of fruit chewers studied here is similarly limited (Drew 1987). The guilds most likely to have density-dependent effects on plant fitness are the highly specialized leaf suckers, leaf miners, and larval leaf chewers, while the guilds of adult leaf chewers, root chewers, phloem and xylem suckers have the potential to mediate apparent competition among plant species. The evidence for such direct and indirect interactions is currently limited. Plant recruitment is often density-dependent for locally common rain forest trees (Leigh *et al.* 2004), but the role of insect herbivores in generating such patterns, either by inflicting damage to plant biomass or by transmitting pathogens, is poorly documented (Hammond & Brown 1996; Wyatt & Silman 2004). However, the evidence from better-studied temperate systems suggests that such effects may be widespread (Connell 1990; Chaneton & Bonsall 2000). In particular, viruses transmitted by sap-sucking insects are an important mortality factor in many well studied plant species, particularly crops, while they remain virtually unknown in tropical forests (Nault & Ammar 1989). Interactions such as apparent competition are of particular relevance in species-rich tropical forests where individuals of any given pair of plant species are unlikely to grow in close proximity. Mobile natural enemies such as herbivores are therefore able to link the dynamics of plants that are unlikely to compete directly for resources (Connell 1990).

The analysis of host plant isolation and web isolation separated fruit chewers, leaf miners, larval leaf chewers, and leaf suckers from the remaining seven guilds. These four guilds are highly specialized, with very little exchange of conspecific individuals among different plant species, leading potentially to highly compartmentalized food webs (Prado & Lewinsohn 2004). They are all larval guilds feeding either on leaves or fruits, i.e. the chemically most diverse plant parts. The guilds feeding on xylem and phloem, as well as adult feeders were much less specialized, in agreement with results from previous studies (Beaver 1979; Janzen 1980; Mattson *et al*. 1988; Dyer 1995; Tavakilian *et al*. 1997; Lewinsohn & Roslin 2008).

DEFINING HERBIVORE GUILDS

Each herbivore guild uses a distinct resource which can be defined as a particular plant organ, or plant tissue. We opted for a combined approach based primarily on plant organs (leaves, flowers, fruits, stems and roots), but recognizing phloem and xylem as nutritionally and chemically distinct tissues within stems and roots (Raven 1983). This classification could be refined for particular studies. For instance, a broadly defined fruit-chewing guild can be further divided into guilds feeding on seeds as opposed to the rest of the fruit tissues, on fleshy vs. dry fruit, and attacking fruits before or after dispersal. These categories can be further split, for example Johnson (1981) recognized three guilds of bruchid beetles feeding on pods of Fabaceae. Such detailed systems become unsuitable for broad comparisons of entire food webs where they would include a large number of guilds.

Herbivore feeding mode is often used for guild definition as it partly determines the plant resource used. For instance, phloem and xylem sap can only be used by sucking insects, while herbivores sucking contents of individual cells avoid cell walls and other structural elements encountered by chewers. The separation of larval and adult guilds is more contentious, as larvae and adults can consume identical resources. Particularly in external chewers, combining larval and adult stages could simplify the classification and reduce the number of guilds to 19. We propose to keep larvae and adults separate mainly because of different ecological significance of their respective trophic interactions; larvae often feed on a single individual plant for their entire life span and use this plant to build their entire body biomass, while adults tend to feed on many individual plants, if not species. The distinction made between internal and external feeders for guild definition is appropriate as it has important consequences for life-history, host specificity, predation and parasitism of herbivores (Mattson *et al.* 1988; Hespenheide 1997). Our guild classification attempts to provide a simple yet comprehensive system of guilds, suitable for broad comparisons using data from different sites and studies.

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Supporting Information

Additional supporting information may be found in the online version of this article.

Appendix S1. List of plant species sampled for herbivores with GenBank accession numbers for their molecular data.

Fig. S1. Phylogenetic relationships among the studied plant species.

Fig. S2. Distribution of phylogenetic distances among the plant species used for phylogenetically standardized comparison of plant–herbivore food webs.

Fig. S3. Species accumulation of insect herbivores on rain forest plants.

Table S1. Basic description of plant–herbivore food webs used for the analysis.

Table S2. Plant species sampled for each herbivorous guild.

Table S3. Herbivore species included in the food web analysis.

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