REPORT

No tree an island: the plant–caterpillar food web of a secondary rain forest in New Guinea

Vojtech Novotny,[1]***** **Scott E. Miller,**[2] **Jan Leps,**[1] **Yves Basset,**[3] **Darren Bito,**[4] **Milan Janda,**[1] **Jiri Hulcr,**[1] **Kipiro Damas**[5] **and George D. Weiblen**[6]

[1]*Institute of Entomology, Czech Academy of Sciences and Biological Faculty, University of South Bohemia, Branisovska 31, 370 05 Ceske Budejovice, Czech Republic*
[2]*National Museum of Natural History and National Zoological Park, Smithsonian Institution, PO Box 37012, Washington, DC 20013-7012, USA*
[3]*Smithsonian Tropical Research Institute, Apartado 2072, Balboa, Ancon, Panama*
[4]*Department of Biology, University of Papua New Guinea, Port Moresby and New Guinea Binatang Research Center, PO Box 604, Madang, Papua New Guinea*
[5]*Forest Research Institute, PO Box 314, Lae, Papua New Guinea*
[6]*Department of Plant Biology, University of Minnesota, 1445 Gortner Avenue, St Paul 55108, MN, USA*
Correspondence: E-mail: novotny@entu.cas.cz

Abstract

We characterized a plant–caterpillar food web from secondary vegetation in a New Guinean rain forest that included 63 plant species (87.5% of the total basal area), 546 Lepidoptera species and 1679 trophic links between them. The strongest 14 associations involved 50% of all individual caterpillars while some links were extremely rare. A caterpillar randomly picked from the vegetation will, with $\geq$ 50% probability, (1) feed on one to three host plants (of the 63 studied), (2) feed on < 20% of local plant biomass and (3) have $\geq$ 90% of population concentrated on a single host plant species. Generalist species were quantitatively unimportant. Caterpillar assemblages on locally monotypic plant genera were distinct, while sympatric congeneric hosts shared many caterpillar species. The partitioning of the plant–caterpillar food web thus depends on the composition of the vegetation. In secondary forest the predominant plant genera were locally monotypic and supported locally isolated caterpillar assemblages.

Keywords

Ecological succession, herbivore communities, host specificity, insect–plant interactions, invasive species, Lepidoptera, Malesia, Papua New Guinea, species richness, tropical forests.

INTRODUCTION

Janzen (1983) characterized tropical food webs as 'rich in extrapolation and conjecture, held in place by very few data points'. Twenty years later, this remains a fitting description of the state of the field (Godfray *et al.* 1999; Kitching 2000; Novotny *et al.* 2003a). Considering that plants and their insect herbivores represent more than 40% of global

terrestrial biodiversity (Price 2002), knowledge of plant–herbivore food webs is relatively scarce. Studies of tropical insect herbivores have focused on host specificity (Janzen 1988, 2003; Marquis 1991; Memmott *et al.* 1994; Basset 1996; Barone 1998; Lewis *et al.* 2002; Novotny *et al.* 2002a; Janzen & Hallwachs 2003; Ødegaard 2003) but few have combined herbivore feeding preferences with local host abundance to predict forest insect population sizes

(Henneman & Memmott 2001). The scarcity of quantitative data on food webs is unfortunate, as they could be used to test hypotheses on the abundance, distribution and host specificity of herbivorous insects in tropical forests.

Light trap samples of rain forest Lepidoptera are characterized by low dominance even for the most abundant species (Robinson & Tuck 1993; Intachat *et al.* 1999) while caterpillar assemblages feeding on individual plant species include a principal dominant, which often represent half of the individuals in the assemblage (Novotny *et al.* 2002c). We suggest that the dominance patterns found in light trap samples could result from the aggregation of Lepidoptera from numerous sympatric host plant genera each hosting a largely unique caterpillar fauna. This hypothesis predicts that the dominance of the most common Lepidoptera species will be approximately half of the dominance of the most common plant genus in the forest.

Host specificity of herbivores is often characterized by the distribution of herbivore densities across a set of local plant species (Novotny *et al.* 2003a). We hypothesize that this distribution is more aggregated than suggested by the host specificity estimates alone, as the highly uneven use of plants by herbivores (Novotny & Basset 2000) is compounded by the uneven abundance of plant species in the forest.

Plants have the potential to influence one another through interactions with shared herbivores, but the importance of such indirect interactions remains unknown (Morris *et al.* 2004). The presence of herbivores feeding on several host species is required for such interactions to occur, but no study has answered the fundamental question of whether an herbivorous insect randomly picked from tropical forest vegetation is more likely to be a generalist or a specialist.

The pattern of increasing host specificity in the course of succession is well established in temperate areas (Brown & Southwood 1983). However, many tropical successions begin with pioneer trees rather than annual herbs, representing a longer-lived and more predictable resource for insects than temperate herbaceous series that may favour polyphagous species (Leps *et al.* 2001). The pattern of increasing host specificity in the course of succession therefore may not apply to tropical succession.

The aim of our study was to test the above hypotheses on the dominance structure of herbivorous communities, the distribution of herbivores among plant species, and the extent of host specificity. We used quantitative data on woody and large herbaceous plants occurring in 1 ha of forest, combined with abundance data for caterpillar species feeding on 63 plant species that together represent nearly 90% of the total basal area in a secondary vegetation at our study site.

METHODS

Study area and vegetation

The study area was located in the lowland perhumid rain forests in Madang Province, Papua New Guinea. The average annual rainfall is 3558 mm, with a moderate dry season from July to September; mean air temperature is 26.5 °C (McAlpine *et al.* 1983). Fieldwork was concentrated within a 10 × 20 km area, encompassing a mosaic of primary and secondary forests, near Baitabag, Ohu and Mis Villages (145°41–8′ E, 5°08–14′ S, *c.* 0–200 m).

Early secondary vegetation was the subject of the study, characterized by a closed canopy of trees less than 20 cm diameter at breast height (d.b.h.). This is an *c.* 5–30-year-old stage of succession giving way to primary lowland hill forest (described in Laidlaw *et al.* 2004). Succession typically starts in abandoned garden clearings after traditional swidden agriculture. Similar succession follows natural disturbance events that are common throughout the region such as tree falls and landslides (Johns 1986; Leps *et al.* 2001).

The composition of secondary forest vegetation was recorded in 25 non-contiguous quadrats, each 20 × 20 m, in August 2002. The quadrats were positioned randomly within subjectively selected areas of the early secondary forest. D.b.h. of all stems taller than 1.5 m above ground was recorded and their basal area (i.e. the area of their cross-section at 1.5 m above the ground) was used as an index of aboveground standing biomass. Plants were vouchered and identified at the Lae Herbarium (Papua New Guinea).

The vegetation from the entire 1 ha included 6848 stems from 171 species, 120 genera and 54 families (see Appendix S1 in Supplementary material for details). Their total basal area was 14.4 m². The three most abundant species, *Piper aduncum* L., *Spathodea campanulata* (L.) Kunth. and *Trichospermum pleiostigma* (F. Muell.) Kostermans represented 47.9% of the total basal area (Table 1, Fig. 1), while the rarest 79 species represented together only 1% of the basal area. The most species-rich genera were *Ficus* (27 species), *Macaranga* (six species), *Litsea* and *Syzygium* (four species each), but a majority of species (106), representing 80.6% of the basal area had no sympatric congeners. The locally monotypic genera *Piper*, *Spathodea* and *Trichospermum* had the highest basal area, followed by species-rich *Ficus* and *Macaranga*.

One peculiar feature of the vegetation we studied was the dominance of alien *Piper aduncum* and *Spathodea campanulata*, aggressive invaders of disturbed forest in many tropical areas (Heartsill-Scalley & Aide 2003). This alien-dominated vegetation is widespread throughout the lowlands of Madang Province (Hartemink 2001; Leps *et al.* 2002), although secondary vegetation in the remote interior of the New Guinea lowlands appears to be dominated by native species (Novotny *et al.*, unpublished data).

Plant species	Family	BA	N	d_{ii}
Piper aduncum L.	Piperaceae	21.4	19.8	0.86
Spathodea campanulata (L.) Kunth.	Bignoniaceae	14.3	11.1	0.94
Trichospermum pleiostigma (F. Muell.) Kost.	Malvaceae	12.3	24.5	0.91
Melanolepis multiglandulosa (Reinw. ex Bl.) Reichb. f. & Zoll.	Euphorbiaceae	4.7	0.2	0.24
Hibiscus tiliaceus L.	Malvaceae	3.9	5.7	0.79
Macaranga brachytricha A. Shaw	Euphorbiaceae	3.1	3.1	0.64
Premna obtusifolia R. Br.	Verbenaceae	3.1	7.2	0.96
Kleinhovia hospita L.	Malvaceae	3.1	4.1	0.63
Ficus pungens Reinw. ex Bl.	Moraceae	2.3	1.1	0.35
Cordyline terminalis P. Beauv.	Agavaceae	2.1	1.6	0.30
Macaranga aleuritoides F. Muell.	Euphorbiaceae	2.0	2.8	0.63
Ficus variegata Blume	Moraceae	1.5	1.7	0.47
Pterocarpus indicus Willd.	Fabaceae	1.5	3.0	0.74
Artocarpus communis J. R. et G. Forst.	Moraceae	1.4	2.9	0.99
Musa sp.	Musaceae	1.1	ns	ns
Dracaena angustifolia Roxb.	Ruscaceae	1.1	0.9	0.37
Endospermum labios Schodde	Euphorbiaceae	1.0	0.7	0.96
47 additional species sampled			8.7	9.6
107 additional species not sampled			11.4	

Table 1 Characteristics of the most abundant plant species and their caterpillars

Family: according to APG II (2003), BA: % dominance in vegetation based on basal area (plant species with $BA \geq 1\%$ are listed; total basal area was 14.4 m^2 ha^{-1}); N: % of caterpillars from the community web hosted by the plant species (the total community web included 4731 caterpillars); d_{ii}: source web isolation (see Methods); ns: not sampled.
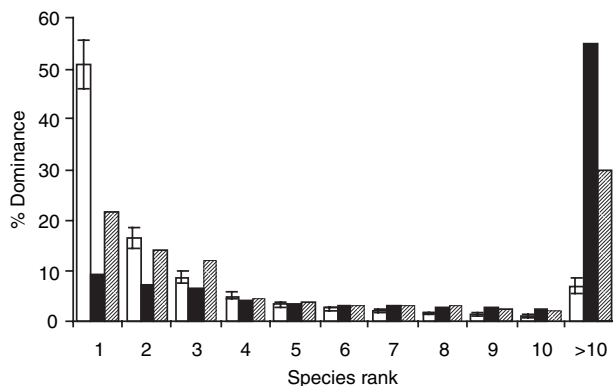

Figure 1 Dominance of plant and Lepidoptera species in source and community food webs. The proportion of individuals represented by the most abundant species (1–10) and by all remaining species combined (rank > 10) is reported for 63 source webs of caterpillars (medians with first and third quartiles; empty bars), and the community web (solid bars). Similarly, the proportion of basal area is reported for plants (hatched bars).

Caterpillars

Sixty-three plant species (see Appendix S1) were sampled for caterpillars (Lepidoptera). Plants included 16 of the 17 most common species that individually contributed > 1% of the total basal area (Table 1), as well as rarer species, selected to represent major plant lineages. Target host plants represented 43 of 120 genera and 22 of 54 families present in 1 ha. They included congeneric species (17 *Ficus* and six *Macaranga*), confamilial genera (two Moraceae, two Verbenaceae, four Malvaceae, six Euphorbiaceae and 11 Rubiaceae), as well as representatives of locally monotypic families. Our sampling of plants included the major woody growth including trees and shrubs (but not lianas which are scarce in secondary forest at our study site) as well as large herbaceous monocotyledons. The studied vegetation represented 87.5% of the total basal area in 1 ha of forest.

All externally feeding caterpillars, including leaf rollers and leaf tiers, were collected by hand from the foliage. Each tree species was sampled for the period of at least 1 year between July 1994 and December 2002. Sampling included accessible branches from the understorey and the forest canopy, which could be climbed or reached from the ground. The approximate area of foliage sampled was estimated visually. Sampling effort was equalized for all plant species and amounted to *c*. 1500 m^2 of foliage area examined per species, except for the three most abundant tree species, which were sampled with higher intensity: *Piper aduncum* and *Spathodea campanulata* 3100 m^2 and *Trichospermum pleiostigma* 1800 m^2 of foliage. Our sampling effort represented *c*. 30 person-days of fieldwork for each host species.

In the laboratory, each caterpillar was provided with fresh leaves of the plant species from which it was collected and reared to an adult whenever possible. Only caterpillars that fed in captivity were considered in the analyses. This amounted to 37 288 individuals, including 14 980 individuals successfully reared to adults. All feeding caterpillars were assigned to morphospecies that were later verified and refined according to reared adults. Altogether, caterpillars were classified into 546 morphospecies, including 419 morphospecies successfully reared to adults. The adult morphospecies were identified as far as possible by taxonomic experts. Taxonomic methods are detailed in Holloway *et al.* (2001) and Miller *et al.* (2003). Insect vouchers are deposited in the Smithsonian Institution (Washington), the National Agricultural Research Institute (Port Moresby) and Bishop Museum (Honolulu).

Data analysis

Plant–caterpillar community web

Quantitative data on the composition of caterpillar assemblages feeding on individual plant species, namely source webs *sensu* Hall & Raffaelli (1993), were used to reconstruct the assemblage of caterpillars feeding on the vegetation as a whole, namely the plant–caterpillar community web. This was achieved by combining individual source webs in proportion to the relative abundance of their host plants in the local vegetation.

We reduced the size of caterpillar samples from each plant species in relative proportion to the basal area of the most abundant species, *Piper aduncum* (3.08 m^2 ha^{-1}). For example, *Melanolepis multiglandulosa* had a basal area of 0.68 m^2 ha^{-1}, which is 22% of the basal area for *P. aduncum*. As sampling effort was estimated by the area of foliage inspected, we set the sampling effort for *Melanolepis* equal to 0.22 times the total area of *P. aduncum* foliage sampled (3100 m^2), yielding 682 m^2. Caterpillar species abundance based on 1500 m^2 of *Melanolepis* foliage was reduced by a factor of 1500 m^2/682 m^2 = 2.2 and species with less than one individual in the reduced sample were excluded from the analysis. Analogous sample reduction was performed for all plant species so that the resulting community web reflected caterpillar species abundance in the vegetation as a whole. However, the community web cannot be attributed to a specific forest area as abundance was measured in different units for caterpillars and plants, individuals per unit area of foliage inspected and basal area, respectively.

Caterpillar host specificity

Host specificity of each caterpillar species k was characterized by the following parameters:

Host species number HN_k, defined as the number of caterpillar hosts from the 63 plant species sampled with equal effort (1500 m^2 of foliage). Caterpillar–plant combinations supported by only one caterpillar were excluded owing to the ambiguity of singletons. This index reflects the local resources available for herbivore species, viz. the number of distinct plant populations that can be exploited by a herbivore. It therefore treats plant species as independent resources, ignoring their phylogenetic relationships.

Host specificity HS_k, defined as the proportion of individuals feeding on the most preferred host, gathered from equal sampling effort of 1500 m^2 of foliage across 63 plant species. The HS_k values thus ranged from 1 for monophagous species to $1/n$ for species equitably distributed on all n plant species studied ($n = 63$). Species with $HS_k \geq 0.9$ were considered specialists while species with $HS_k < 0.5$ were considered generalists as no single host species supported a majority of the population.

Local host specificity HL_k, defined as the proportion of individuals feeding on the host exploited by the largest number of individuals from caterpillar k in the community web of 63 plant species. Species with $HL_k \geq 0.9$ were considered local specialists and those with $HS_k < 0.5$ local generalists.

Host plant biomass HB_k, defined as the proportion of total basal area of the vegetation represented by all hosts of the caterpillar species k.

The sensitivity of HN_k, HS_k and HL_k parameters to sample size was investigated using subsets of caterpillar species with minimum abundance thresholds (N) of five to 100 individuals per species. While the values of HS_k and HL_k were insensitive to the minimum species abundance across this range, mean HN_k increased from 3.2 hosts for caterpillar species with $N \geq 5$ to 5.5 hosts for caterpillar species with $N \geq 100$ (unpublished data). We set an arbitrary threshold of $N \geq 10$ and restricted all analyses to the 221 Lepidoptera species represented in the sample by at least 10 individuals.

Each individual caterpillar (I) in the community web was assigned the host specificity parameters of its species and the distribution of these parameters among individual caterpillars in the entire community web (HN_I, HS_I, HL_I and HB_I) was examined. This enabled us to estimate the average host specificity of a caterpillar randomly sampled from the community.

Source web interactions

Caterpillar species k on host plant i was characterized by the following parameters:

Caterpillar density C_{ki}, defined as the proportion of the total population of k in the community web feeding on i.

Caterpillar dominance D_{ki} defined as the abundance of caterpillar k on i divided by the total number of caterpillars feeding on i.

Web interaction d_{ij} defined as the probability that the parents of caterpillar k feeding on plant i fed on plant j in the previous generation (Müller *et al.* 1999):

$$d_{ij} = \sum_k D_{ki} C_{kj}$$

Web interaction is the product of caterpillar dominance on i and caterpillar density on j, summarized for all caterpillar species k. This parameter quantifies the potential for interactions between source webs from plant species i and j. The interactions between source webs can be asymmetric, so that $d_{ij} \neq d_{ji}$.

The web interaction parameter can be illustrated in a community web that includes a single caterpillar species k with 25% individuals feeding on i and the remaining 75% on j. In this case, $D_{ki} = D_{kj} = 1$ and $d_{ij} = C_{kj} = 0.75$. Assuming that the same proportions of individuals also fed on i and j in the previous generation, it is likely that 75% of the parents of caterpillars feeding presently on i fed in the previous generation on j.

Web isolation d_{ii} is the probability that the parents of caterpillar k feeding on plant i fed on the same host species in the previous generation:

$$d_{ii} = \sum_k D_{ki} C_{ki}$$

This parameter gives the proportion of conspecific caterpillars from the entire community web that fed on i, estimated across all caterpillar species k feeding on i. The number of caterpillars in a source web on host i that originated on this plant species can be determined as $d_{ii} N_i$, where N_i is the number of caterpillars in the source web and the remaining caterpillars, $(1 - d_{ii})N_i$, are of external origin.

Note that the probability that the parents of caterpillar k feeding on a particular host also fed on the same host, calculated for the entire population of k across all plant species, is $\Sigma_i(C_{ki})^2$, i.e. equal to the value of the Simpson's diversity index. Further, Hurlbert's (1971) classical probability of inter-specific encounter (PIE) index represents a related concept as $1 - \text{PIE}$ can be restated as the probability that two randomly selected individuals from caterpillar k feed on the same host plant species.

The relationships among parameters describing source webs from different plant species were explored by the independent contrasts method implemented in Compare 4.4 (Martins 2001). This approach takes into account the non-independence of plant species due to their phylogenetic relationships. A community phylogeny, estimated using morphological and molecular data (Novotny *et al.* 2002b; APG II 2003; G. Weiblen, unpubl. data), was inferred for the 63 studied species.

RESULTS

Community structure

The sampling of 1500 m^2 of foliage from each of 63 plant species produced feeding records for 37 288 caterpillars totalling 546 species. These included 1679 different caterpillar–plant combinations and 1007 supported by > 1 feeding record. The latter were used to construct a caterpillar community web weighted by the differential abundance of host species. Owing to reduced samples for rare host plants, the community web included only 281 of the 1007 trophic links represented by > 1 feeding record for a total of 4731 individuals and 163 caterpillar species. The 14 most important trophic links, involving $> 50\%$ of feeding records in the community web, included 14 caterpillar species and eight plant species (Table 2). These trophic links typically involved local specialists (12 of 14 caterpillar species) and locally common hosts. The three most abundant plant species were involved in seven of 14 links.

A large proportion of trophic links occurred at extremely low frequency in secondary forest. For example, consider *Mussaenda scratchleyi* Wernh., the least common plant species in vegetation census quadrats that we also sampled for caterpillars. This plant was represented in our 1 ha vegetation census as a single individual with a basal area of 0.4 cm^2 and *c.* 1 m^2 of foliage. At the same time, 44 caterpillar species, including 18 represented by a single individual, were found by sampling 1500 m^2 of *M. scratchleyi* foliage across the larger study area.

Interspecific variation in basal area, from 0.04 to 3.1 m^2, exceeded variation in caterpillar density, ranging from 11 to 807 individuals per 1000 m^2 of foliage. The basal area of the host thus explained a large part of variability in the caterpillar abundance per host species ($R^2 = 0.80$, $N = 62$, independent contrasts). The three most common plant species hosted the three largest source webs, representing 58% of all feeding records included in the community web (Table 1).

Source webs on individual plant species were strongly dominated by single caterpillar species, with a mean (standard error) dominance of $D_i = 0.48$ (0.03). The community web was dominated by *Herpetogramma* sp. near *licarsisalis* (Walker) (Fig. 3 in Novotny *et al.* 2003b), representing 9% of all caterpillars (Fig. 1). Despite this low dominance of the most abundant species, half of all individuals in the community web still recruited from only the 12 most abundant Lepidoptera species (Table 2).

Table 2 Characteristics of the most abundant Lepidoptera and the most important trophic links in the community web

Lepidoptera species	Family	N_k	HS_k	HL_k	HN_k	HB_k	Host plant	L
Herpetogramma nr. *licarsisalis* (Walker)	Crambidae	**454**	1.00	1.00	1	0.21	*Piper aduncum*	**454**
Orthospila sp. A nr. *orissusalis* (Walker)	Crambidae	**356**	0.73	0.95	6	0.17	*Trichospermum pleiostigma*	**340**
Hyblaea sp. nr. *puera* (Cramer)	Hyblaeidae	**327**	0.98	0.95	2	0.17	*Spathodea campanulata*	**310**
Haritalodes multilinealis (Guenee)	Crambidae	**206**	0.50	0.82	17	0.26	*Hibiscus tiliaceus*	**170**
Orthospila sp. C nr. *orissusalis* (Walker)	Crambidae	**166**	0.87	0.97	4	0.20	*Trichospermum pleiostigma*	**161**
'Giaura' *leucophaea* Hampson	Nolidae	**159**	0.96	0.98	3	0.19	*Trichospermum pleiostigma*	**156**
Glyphodes pseudocaesalis Kenrick	Crambidae	**139**	1.00	1.00	1	0.01	*Artocarpus communis*	**139**
Homona mermerodes Meyrick	Tortricidae	**138**	0.26	0.34	22	0.65	*Cordyline terminalis*	47
Adoxophyes templana complex*	Tortricidae	**121**	0.25	0.41	23	0.65	*Piper aduncum*	50
Acherontia lachesis (Fabricius)	Sphingidae	**115**	0.99	1.00	2	0.14	*Spathodea campanulata*	**115**
Adoxophyes thoracica Diakonoff	Tortricidae	**111**	0.30	0.86	19	0.32	*Piper aduncum*	96
Striglina cinnamomea (Rothschild)	Thyrididae	**107**	1.00	1.00	1	0.12	*Trichospermum pleiostigma*	**107**
Europlema semibrunnea (Pag.)	Uraniidae	90	1.00	1.00	1	0.03	*Premna obtusifolia*	90
Ozola indefensa Warren	Geometridae	88	1.00	1.00	1	0.03	*Premna obtusifolia*	88
Earias uniplaga Bethune-Baker	Nolidae	86	1.00	1.00	1	0.12	*Trichospermum pleiostigma*	86
Dichomeris sp. [sp. code XXXX068]	Gelechiidae	80	0.62	0.94	6	0.06	*Macaranga brachytricha*	75

N_k: the number of individual caterpillars in the community web (the most abundant species, which together represent 50% of individuals in the community web, are in bold); HS_k: host specificity; HL_k: local host specificity; HN_k: number of host plant species; HB_k: host plant biomass; Host plant: the most preferred host species; L: the number of individual caterpillars feeding on the most preferred host plant species (the most important trophic links, which together involve 50% of individuals in the community web, are in bold). See Methods for details on HS_k HL_k HN_k and HB_k. *Adoxophyes templana* complex probably represents two species, but we cannot distinguish all individuals. An example of this moth is illustrated in Appendix 1.

Host specificity of caterpillars

The 221 species of Lepidoptera collected in sufficient numbers for host specificity analysis used between one and 27 host species of the 63 sampled. There were 74 monophagous species with $HS_k = HL_k = 1$. The majority of the remaining species, 101 of 147, exhibited higher local specificity in the community web, compared with host specificity estimates based on equal sampling effort among plant species ($HL_k > HS_k$; Fig. 2). This difference between HL_k and HS_k was significant (Wilcoxon sign rank test, $P < 0.001$, $N = 147$). Populations of most species were strongly concentrated on a single host, as indicated by the median (1–3 quartile) local host specificity $HL_k = 0.96$ (0.62–1.00). Likewise, eight of the 12 most abundant Lepidoptera species were local specialists ($HL_k \geq 0.9$; Table 2).

More than half of the individual caterpillars in the community web recruited from species feeding on one to three host plant species (modal $HN_I = 1$ and median $HN_I = 3$; Fig. 3a). Thirty-one per cent of caterpillars in the community web recruited from locally monophagous species ($HL_k = 1$) and 37% recruited from other local specialist species ($1 > HL_k \geq 0.9$); in other words, more than half of the individual caterpillars (68%) had $\geq 90\%$ of population concentrated on a single host plant species. An additional 20% of caterpillars belonged to less specialized species that still recruited at least half of their individuals
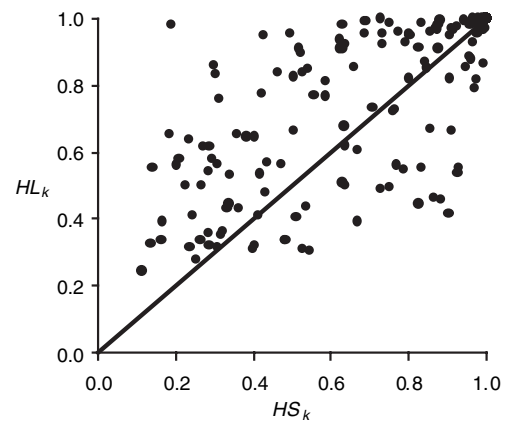

Figure 2 Relationship between caterpillar host specificity (HS_k) and local host specificity in the community web (HL_k). Only the 221 Lepidoptera species with ≥ 10 individuals were analysed. The line indicates $HS_k = HL_k$. See Methods for the explanation of HS_k and HL_k.

from a single plant species ($0.9 > HL_k \geq 0.5$). Only the remaining 12% of individuals belonged to local generalists with no single major host species ($HL_k < 0.5$; Fig. 3b). While more than half of all caterpillars (69%) fed on plants representing in combination only $\leq 20\%$ of the total basal area, 8% of caterpillars were generalists with host ranges encompassing $> 50\%$ of the vegetation (Fig. 3c).
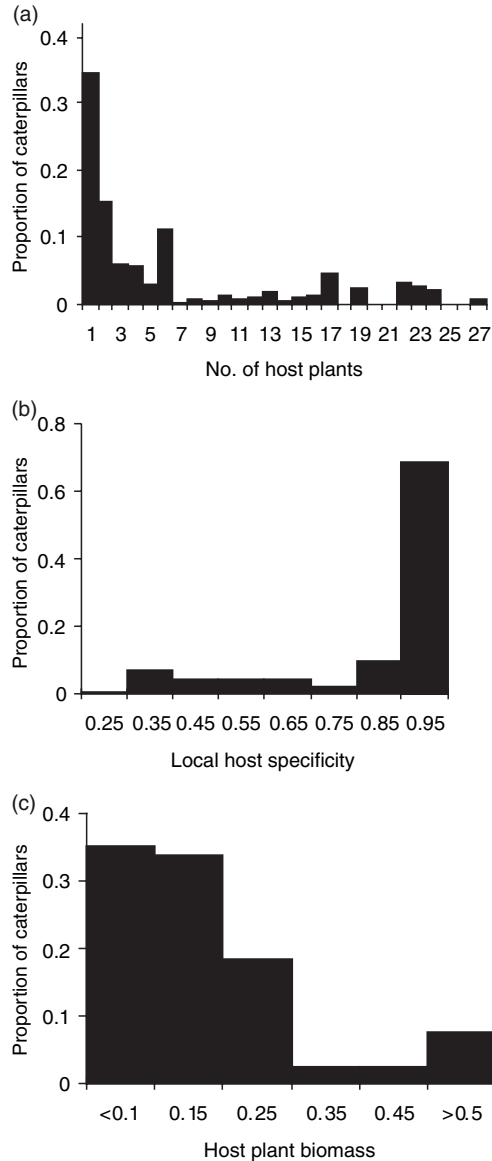
Figure 3 The distribution of the number of host plants (HN_I, Fig. 3a), local host specificity (HL_I, Fig. 3b) and host plant biomass (HB_I, Fig. 3c) values among individual caterpillars in the community web ($N = 4731$ individuals). See Methods for the explanation of HN_I, HL_I and HB_I.

Only two of the 12 most important species in the community web, *Homona mermerodes* Meyrick and *Adoxophyes templana* species complex, were true local generalists as they had no single major host plant species ($HL_k < 0.5$), fed on > 20 hosts, and included more than 50% of plant basal area in their host range (Table 2). Some other species with broad host range were present, but locally concentrated mostly on a single host plant species. For example, *Adoxophyes thoracica* Diakonoff fed on 19 plant species but 86% of its population fed on *Piper aduncum. Haritalodes multilinealis* (Guenee) fed on

17 plant species but 82% of its population fed on *Hibiscus tiliaceus* L. Generalist species, among the rare species in the community web, were few. For instance, we reared only 11 species listed as generalized major pests (Holloway *et al.* 2001), such as *Achaea janata* L. and *Spodoptera litura* (F.).

Interactions among source webs

The great majority of interactions between pairs of source webs were weak, as there were only 75 interactions with $d_{ij} > 0.1$ of 3906 possible pairings of different source webs ($i \neq j$). These interactions included 45 of 302 interactions between source webs from congeneric plant species and 30 of 3604 interactions between source webs from non-congeneric plant species.

Web isolation d_{ii} exhibited a bimodal distribution among plant species as 13 source webs were almost completely driven by caterpillars from surrounding vegetation ($d_{ii} < 0.1$), while 14 source webs were almost completely isolated ($d_{ii} > 0.9$). The remaining 36 webs assumed an intermediate position (Fig. 4).

The isolation of the 17 source webs supported by plant species from locally monotypic families (average $d_{ii} = 0.71$) and the 23 source webs supported by plant species from locally monotypic genera (average $d_{ii} = 0.73$) was dramatically higher than the isolation of the 23 source webs supported by plant species with at least one sympatric congener (average $d_{ii} = 0.24$; $P < 0.01$, ANOVA, Tukey comparisons; Fig. 4).

Web isolation d_{ii} was positively correlated with basal area among congeneric species both in *Macaranga* ($r = 0.964$, $P < 0.01$, $N = 5$, independent contrasts) and *Ficus* ($r = 0.692$, $P < 0.01$, $N = 16$, independent contrasts), while this correlation was not significant when all plant species were included in the analysis ($r = 0.221$, $P > 0.05$, $N = 62$, independent contrasts).

The number of caterpillars of external origin with respect to their source webs was estimated for the entire community web as $\Sigma_i(1 - d_{ii})N_i = 891$, or 19% of the total. The largest numbers of external caterpillars were hosted by two common plant species supporting large caterpillar assemblages: *Piper aduncum* (131 caterpillars) and *Trichospermum pleiostigma* (103 caterpillars).

DISCUSSION

Methodological issues

Plant-herbivore food webs are typically based on quantitative surveys of plants, herbivores, and trophic links within a specific study area. Vegetation is inventoried in representative plots and herbivores are collected from the vegetation with sampling effort proportional to host plant species abundance
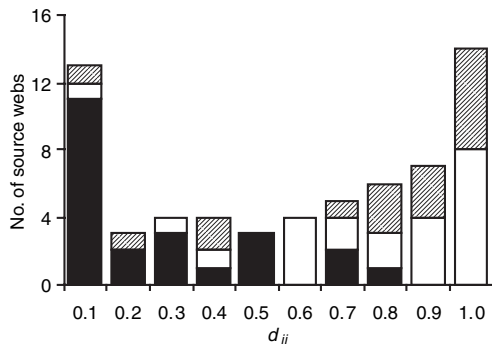
Figure 4 The distribution of web isolation (d_{ii}) values among caterpillar source webs. Solid bars – plants with ≥ 1 congeneric species, empty bars indicate plants from monotypic genera but with ≥ 1 species sampled from a confamilial genus, hatched bars indicate plants from monotypic families. See Methods for the explanation of d_{ii}.

(Henneman & Memmott 2001; Lewis *et al*. 2002). We sampled both rare and common plant species with equal effort from a large but only partially surveyed area. The advantage of this approach is that it provides information on herbivores feeding on rare plant species, while the principal disadvantage is that our reconstructed food web does not refer to any specific forest patch. Our sampling method is best suited for the study of host specificity and by distributing the sampling effort equitably among plant species it is also efficient in capturing local species diversity of herbivores. In contrast, sampling plant species in proportion to their abundance is the preferred method for the construction of quantitative food webs.

Our sampling of herbivores was limited to 63 host species in a community of at least 171 plant species but it covered the majority of plant biomass. The number of local caterpillar hosts was therefore underestimated, while the proportion of local biomass used by caterpillars was not. Further, stem basal area is not an accurate index of plant biomass (Chave *et al*. 2003). Ideally, plant abundance should be measured in the same units as herbivore abundance, namely per unit of foliage. However, such measurements are particularly difficult in forest vegetation (Breda 2003).

Another important limitation of our study is that it was restricted to secondary vegetation dominated by two alien species and we will not know the generality of our conclusions until the approach is replicated in other tropical forests. Comparable, comprehensive studies of primary forest will be significantly more difficult owing to the inaccessibility of the high canopy.

Community web structure

We previously reported that caterpillar assemblages feeding on a particular plant species typically include a principal dominant, which is specialized to a single plant genus and

represents approximately half of all individuals occurring on the plant species (Novotny *et al*. 2002c). These results led us to speculate that the dominance of the most abundant caterpillar species in a community web could be approximately half the dominance of the most abundant plant genus. This prediction was confirmed by our examination of the community web. The dominance structure of the vegetation we studied is similar to that of other tropical forests where the most abundant plant genera typically represent < 20% of the entire biomass (Boom 1986; Wright *et al*. 1997; Weiblen 1998; Chave *et al*. 2003; Laidlaw *et al*. 2004). The dominance of the most common Lepidoptera in these forests is therefore expected to be < 10%.

The community web was dominated by a small number of particularly strong trophic links because the source webs on individual plants were dominated by a small number of often specialized caterpillar species and the vegetation was dominated by a small number of plants. Most importantly, a complex web that included at least 1679 plant–caterpillar trophic links could be reduced to a mere 14 links including half of all caterpillars. Similar dominance structure was found in a plant–caterpillar food web from Hawaii (Henneman & Memmott 2001) as well as in tropical caterpillar–parasitoid webs (Memmott *et al*. 1994; Lewis *et al*. 2002). The dominant components of these food webs can therefore be investigated by relatively limited sampling, as discussed in Novotny *et al*. (2002c).

Extensive sampling of caterpillars on rare plant species demonstrated that in addition to a small number of particularly important trophic links, there were numerous links that occurred at very low frequency. Recording all local plant–caterpillar interactions in any tropical forest ecosystem thus appears to be exceedingly difficult (Price *et al*. 1995; Novotny & Basset 2000; Janzen 2003) and a complete inventory of plant–herbivore webs requires exhaustive sampling effort even in simple temperate ecosystems (Martinez *et al*. 1999). However, even these weak links can be important for food web dynamics (Berlow 1999).

Host specificity and source web isolation

Many commonly used host specificity indices, including HS_k, describe the distribution of herbivores among host plants in a highly hypothetical community web where all plant species have equitable abundance. As we have shown, the distribution of herbivores among host species may be more aggregated than suggested by these indices because actual plant communities are characterized by uneven abundance of host species.

Our study provided a rare opportunity to evaluate the dominance of generalists in herbivorous communities as we sampled a large fraction of local plant biomass. We found

that generalists were quantitatively less important than specialists, even in a community web where insect populations are aggregated across multiple host species. Janzen (1988, 2003) and Barone (1998) reported a similar pattern for caterpillar assemblages in Neotropical forests. Interestingly, generalists were quantitatively less important despite the dominance of alien plants in the studied vegetation, as the most abundant caterpillars colonizing the two alien species did not recruit from generalists. For example, *Hyblaea* sp. near *puera* (Cramer) colonized exotic *Spathodea* from a single native host, *Premna obtusifolia* R. Br., and the alien supported 95% of the *Hyblaea* population (Table 2). The potential for native herbivores to colonize alien hosts has long been recognized in agricultural situations and plantation forestry (Szent-Ivany 1961).

The high host specificity of caterpillars in the early successional vegetation we studied contrasts with widespread polyphagy in herbivore communities that colonize pioneer vegetation in temperate areas (Brown & Southwood 1983; Novotny 1994). While temperate succession typically starts with ephemeral, often annual herbaceous species, tropical succession tends to be dominated by woody plants from the outset (Leps *et al.* 2001). Even short-lived pioneer trees represent a relatively permanent resource for insect herbivores that can be readily colonized by specialists, as suggested by our results and by the high levels of leaf damage they experience (Coley 1983).

While source webs on plants from locally monotypic genera were relatively isolated, congeneric plant species supported more interconnected source webs, sharing numerous species of caterpillars. The overall fragmentation of the community web can thus be inferred from the taxonomic composition of the vegetation. The vegetation we studied was dominated by locally monotypic plant genera, thus hosting relatively isolated caterpillar assemblages. Vegetation co-dominated by several congeneric species, such as *Macaranga* secondary forest described by Nykvist (1996), or *Ficus*-dominated stands we encountered in New Guinea (G. Weiblen *et al.*, unpublished data), could support a community web composed mostly of mutually interacting source webs and Lepidoptera feeding on numerous plant species. For instance, the *Ficus*–caterpillar interactions studied here were dominated by a *Ficus*-specialist, *Choreutis* sp. cf. *anthorma* (Meyrick), representing 19% of all *Ficus*-feeding caterpillars and attacking 16 of 17 *Ficus* species.

We have argued that the lack of quantitative data on tropical food webs leaves important questions about resources available to rain forest herbivores unanswered. The present study provides some tentative results for one particular ecosystem. It suggests that a caterpillar, randomly picked from secondary rain forest vegetation in New Guinea will, with ≥ 50% probability, (1) feed on one to three host plants, (2) feed on < 20% of local plant biomass, (3) feed on one of the most abundant plant species in the vegetation, (4) have at least 90% of population concentrated on a single host plant and (5) belong to a species with at least 2% dominance in the community.

SUPPLEMENTARY MATERIAL

The following material is available from http://www.blackwellpublishing.com/products/journals/suppmat/ELE/ELE666/ELE666sm.htm

Appendix S1 Plant data from 1 ha area of secondary forest vegetation.

REFERENCES

APG II (2003). An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG II. *Bot. J. Linn. Soc.*, 141, 399–436.

Barone, J.A. (1998). Host-specificity of folivorous insects in a moist tropical forest. *J. Anim. Ecol.*, 67, 400–409.

Basset, Y. (1996). Local communities of arboreal herbivores in Papua New Guinea: predictors of insect variables. *Ecology*, 77, 1906–1919.

Berlow, E.L. (1999). Strong effects of weak interactions in ecological communities. *Nature*, 398, 330–334.

Boom, B.M. (1986). A forest inventory in Amazonian Bolivia. *Biotropica*, 18, 287–294.

Breda, N.J.J. (2003). Ground-based measurements of leaf area index: a review of methods, instruments and current controversies. *J. Exp. Bot.*, 54, 2403–2417.

Brown, V.K. & Southwood, T.R.E. (1983). Trophic diversity, niche breadth and generation times of exopterygote insects in a secondary succession. *Oecologia*, 56, 220–225.

Chave, J., Condit, R., Lao, S., Caspersen, J.P., Foster, R.B. & Hubbell, S.P. (2003). Spatial and temporal variation of biomass in a tropical forest: results from a large census plot in Panama. *J. Ecol.*, 91, 240–252.

Coley, P.D (1983). Herbivory and defensive characteristics of tree species in a lowland tropical forest. *Ecol. Monogr.*, 53, 209–233.

Godfray, H.C.J., Lewis, O.T. & Memmott, J. (1999). Studying insect diversity in the tropics. *Philos. Trans. R. Soc. Lond. Biol. Sci.*, 354, 1811–1824.

Hall, S.J. & Raffaelli, D.G. (1993). Food webs: theory and reality. *Adv. Ecol. Res.*, 24, 187–239.

Hartemink, A.E. (2001). Biomass and nutrient accumulation of *Piper aduncum* and *Imperata cylindrica* fallows in the humid lowlands of Papua New Guinea. *For. Ecol. Manage.*, 144, 19–32.

Heartsill-Scalley, T. & Aide, T.M. (2003). Riparian vegetation and stream condition in a tropical agriculture-secondary forest mosaic. *Ecol. Appl.*, 13, 225–234.

Henneman, M.L. & Memmott, J. (2001). Infiltration of a Hawaiian community by introduced biological control agents. *Science*, 293, 1314–1316.

Holloway, J.D., Kibby, G., Peggie, D., Carter, D.J. & Miller, S.E. (2001). *Families of Malesian Moths and Butterflies. Fauna Malesia Handbook 3*. Brill, Leiden.

Hurlbert, S.H. (1971). The nonconcept of species diversity: a critique and alternative parameters. *Ecology*, 52, 577–586.

Intachat, J., Holloway, J.D. & Speight, M.R. (1999). The impact of logging on geometroid moth populations and their diversity in lowland forests of Peninsular Malaysia. *J. Trop. Forest Sci.*, 11, 61–78.

Janzen, D.H. (1983). Food webs: who eats what, why, how, and with what effects in a tropical forest? In: *Tropical Rain Forest Ecosystems* (ed. Golley, F.B.I.). Elsevier Scientific Publishing, Amsterdam, pp. 167–182.

Janzen, D.H. (1988). Ecological characterization of a Costa Rican dry forest caterpillar fauna. *Biotropica*, 20, 120–135.

Janzen, D.H. (2003). How polyphagous are Costa Rican dry forest saturniid caterpillars? In: *Arthropods of Tropical Forests: Spatio-Temporal Dynamics and Resource Use in the Canopy* (eds Basset, Y., Novotny, V., Miller, S.E. & Kitching, R.). Cambridge University Press, Cambridge, pp. 369–379.

Janzen, D.H. & Hallwachs, W. (2003). Caterpillar rearing voucher databases for the Area de Conservación in northwestern Costa Rica. [WWW document]. URL: http://janzen.sas.upenn.edu/caterpillars/database.htm.

Johns, R.J. (1986). The instability of the tropical ecosystem in New Guinea. *Blumea*, 31, 341–361.

Kitching, R.L. (2000). *Food Webs and Container Habitats: The Natural History and Ecology of Phytotelmata*. Cambridge University Press, New York.

Laidlaw, M.J., Kitching, R.L., Damas, K. & Kiapranis, R. (2004). Structure and floristics of lowland rainforest plots in northern Papua New Guinea. *Biotropica*, in press.

Leps, J., Novotny, V. & Basset, Y. (2001). Habitat and successional status of plants in relation to the communities of their leaf-chewing herbivores in Papua New Guinea. *J. Ecol.*, 89, 186–199.

Leps, J., Novotny, V., Cizek, L., Molem, K., Isua, B., Boen, W. *et al.* (2002). Successful invasion of the neotropical species *Piper aduncum* in rain forests in Papua New Guinea. *Appl. Vegetat. Sci.*, 5, 255–267.

Lewis, O.T., Memmott, J., Lasalle, J., Lyal, C.H.C., Whiteford, C. & Godfray, H.C.J. (2002). Structure of a diverse tropical forest insect–parasitoid community. *J. Anim. Ecol.*, 71, 855–873.

Marquis, R.J. (1991). Herbivore fauna of *Piper* (Piperaceae) in a Costa Rican wet forest: diversity, specificity and impact. In: *Plant–Animal Interactions: Evolutionary Ecology in Tropical and Temperate Regions* (eds Price, P.W., Lewinsohn, T.M., Fernandes, G.W. & Benson, W.W.). John Wiley and Sons, London, pp. 179–208.

Martinez, N.D., Hawkins, B.A., Dawah, H.A. & Feifarek, B.P. (1999). Effects of sampling effort on characterization of food-web structure. *Ecology*, 80, 1044–1055.

Martins, E.P. (2001). *COMPARE, Version 4.4. Computer Programs for the Statistical Analysis of Comparative Data*. Department of Biology, Indiana University, Bloomington, IN.

McAlpine, J.R., Keig, R. & Falls, R. (1983). *Climate of Papua New Guinea*. CSIRO and Australian National University Press, Canberra.

Memmott, J., Godfray, H.C.J. & Gauld, I.D. (1994). The structure of a tropical host-parasitoid community. *J. Anim. Ecol.*, 63, 521–540.

Miller, S.E., Novotny, V. & Basset, Y. (2003). Studies on New Guinea moths. 1. Introduction (Lepidoptera). *Proc. Entomol. Soc. Wash.*, 105, 1034–1042.

Morris, R.J., Lewis, O.T. & Godfray, H.C.J. (2004). Experimental evidence for apparent competition in a tropical forest web. *Nature*, 428, 310–313.

Müller, C.B., Adriaanse, I.C.T., Belshaw, R. & Godfray, H.C.J. (1999). The structure of an aphid-parasitoid community. *J. Anim. Ecol.*, 68, 346–370.

Novotny, V. (1994). Association of polyphagy in leafhoppers (Auchenorrhyncha, Hemiptera) with unpredictable environments. *Oikos*, 70, 223–231.

Novotny, V. & Basset, Y. (2000). Ecological characteristics of rare species in communities of tropical insect herbivores: pondering the mystery of singletons. *Oikos*, 89, 564–572.

Novotny, V., Basset, Y., Miller, S.E., Drozd, P. & Cizek, L. (2002a). Host specialisation of leaf chewing in a New Guinea rainforest. *J. Anim. Ecol.*, 71, 400–412.

Novotny, V., Basset, Y., Miller, S.E., Weiblen, G.D., Bremer, B., Cizek, L. *et al.* (2002b). Low host specificity of herbivorous insects in a tropical forest. *Nature*, 416, 841–844.

Novotny, V., Miller, S.E., Basset, Y., Cizek, L., Drozd, P., Darrow, K. *et al.* (2002c). Predictably simple: communities of caterpillars (Lepidoptera) feeding on rainforest trees in Papua New Guinea. *Proc. R. Soc. Lond. Biol. Sci.*, 269, 2337–2344.

Novotny, V., Basset, Y. & Kitching, R. (2003a). Herbivore communities and their food resources. In: *Arthropods of Tropical Forests: Spatio-Temporal Dynamics and Resource Use in the Canopy* (eds Basset, Y., Novotny, V., Miller, S.E. & Kitching, R.). Cambridge University Press, Cambridge, pp. 40–53.

Novotny, V., Miller, S.E., Cizek, L, Leps, J., Janda, M., Basset, Y. *et al.* (2003b). Colonizing aliens: caterpillars (Lepidoptera) feeding on *Piper aduncum* and *P. umbellatum* in rainforests of Papua New Guinea. *Ecol. Entomol.*, 28, 704–716.

Nykvist, N. (1996). Regrowth of secondary vegetation after the 'Borneo fire' of 1982–1983. *J. Trop. Ecol.*, 12, 307–312.

Ødegaard, F. (2003). Taxonomic composition and host specificity of phytophagous beetles in a dry forest in Panama. In: *Arthropods of Tropical Forests. Spatio-Temporal Dynamics and Resource Use in the Canopy* (eds Basset, Y., Novotny, V., Miller, S.E. & Kitching, R.L.). Cambridge University Press, Cambridge, pp. 220–236.

Price, P.W. (2002). Resource-driven terrestrial interaction webs. *Ecol. Res.*, 17, 241–247.

Price, P.W., Diniz, I.R., Morais, H.C. & Marques, E.S.A. (1995). The abundance of insect herbivore species in the tropics: the high local richness of rare species. *Biotropica*, 27, 468–478.

Robinson, G.S. & Tuck, K.R. (1993). Diversity and faunistics of small moths (Microlepidoptera) in Bornean rainforest. *Ecol. Entomol.*, 18, 385–393.

Szent-Ivany, J.J.H. (1961). The zoo-geographical factor in economic entomology on Pacific Islands with special reference to New Guinea. *Verh. XI Int. Kong. Ent.*, 1, 534–537.

Weiblen, G.D. (1998). Composition and structure of a one hectare forest plot in the Crater Mountain Wildlife Management Area, Papua New Guinea. *Science in New Guinea*, 24, 23–32.

Wright, D.D., Jessen, J.H., Burke, P. & Silva Garza, H.G. (1997). Tree and liana enumeration and diversity on a one-hectare plot in Papua New Guinea. *Biotropica*, 29, 250–260.

Appendix 1 *Orthospila* sp. A, near *O. orissusalis* (Walker) (Lepidoptera: Crambidae), male wings (a) and genitalia (b).