THE ROYAL SOCIETY

Received 31 May 2002
Accepted 15 August 2002
Published online 18 October 2002

Predictably simple: assemblages of caterpillars (Lepidoptera) feeding on rainforest trees in Papua New Guinea

Vojtech Novotny[1*], Scott E. Miller[2], Yves Basset[3], Lukas Cizek[1], Pavel Drozd[4], Karolyn Darrow[2] and Jan Leps[1]

[1]*Institute of Entomology, Czech Academy of Sciences and Biological Faculty, University of South Bohemia, Branisovska 31, 370 05 Ceske Budejovice, Czech Republic*
[2]*Department of Systematic Biology, National Museum of Natural History, Smithsonian Institution, Washington, DC 20560-0105, USA*
[3]*Smithsonian Tropical Research Institute, Apartado 2072, Balboa, Ancon, Panama*
[4]*Department of Biology, University of Ostrava, 30. dubna 22, 701 03 Ostrava, Czech Republic*

Predictability in the composition of tropical assemblages of insect herbivores was studied using a sample of 35 952 caterpillars (Lepidoptera) from 534 species, feeding on 69 woody species from 45 genera and 23 families in a lowland rainforest in Papua New Guinea. Caterpillar assemblages were strongly dominated by a single species (median 48% of individuals and 49% of biomass). They were spatially and temporally constant (median normalized expected species shared (NESS) similarity between assemblages from the same host was greater than or equal to 0.85 for three sites 8–17 km apart as well as for three four-month periods of the year). Further, the median presence of species was 11 months per year. Assemblages on hosts from different families and genera were virtually disjunct (NESS similarity less than 0.05) as the caterpillars were mostly specialized to a single plant family (77% of species) and, within families, to a single genus (66% of species), while capable of feeding on multiple congeneric hosts (89% of species). The dominance of caterpillar assemblages by a small number of specialized species, which also exhibited low spatial and temporal variability, permitted robust and reliable estimates of assemblage composition and between-assemblage similarity from small samples, typically less than 300 individuals per host plant. By contrast, even considerably larger samples were insufficient for estimates of species richness. A sample of 300 individuals was typically obtained from 1050 m^2 of foliage sampled during 596 tree inspections (i.e. a particular tree sampled at a particular time) in the course of 19 sampling days (median values from 69 assemblages). These results demonstrate that, contrary to some previous suggestions, insect herbivore assemblages in tropical rainforests have a predictable structure and, as such, are amenable to study.

Keywords: insect herbivory; host specificity; Malesia; sample size; temporal and spatial variability; species richness

1. INTRODUCTION

Numerous studies, particularly those using insecticide fogging, have reported low predictability of insect assemblages from tropical forests (e.g. Allison *et al.* 1997; Mawdsley & Stork 1997; Stork *et al.* 1997; Floren & Linsenmair 1998, 2003; Wagner 1997). In these studies, spatially and temporally replicated samples from the same forest type, host-plant species or even individual host plant varied widely and unpredictably in their composition. The high variability within putatively homogeneous sets of samples suggests that the spatial and/or temporal scope of present studies is unsuitable for the analysis of arthropod assemblages and that a radical change in the sampling methods should be considered.

Ideally, studies of arthropod assemblages should focus on a well-defined resource and examine species closely associated with this resource in numerous spatial and temporal replicates. For instance, it is essential that studies of herbivorous assemblages on a particular host-plant species include only individuals feeding on this host, and sample a large number of individual plants for at least one year (Janzen 1988, 2003; Marquis 1991; Basset *et al.* 1996; Barone 1998; Novotny *et al.* 2002*a*).

Most of the information on the assemblages of herbivorous insects in the tropics was obtained by fogging and other mass collecting methods, such as those relying on light, Malaise, flight interception or sticky traps (e.g. Stork *et al.* 1997; Intachat *et al.* 1999; Basset *et al.* 2001). These studies provide data only on insect distribution, rather than their resource use. Further, they exhibit undue bias towards the study of adults, which are often the only taxonomically tractable life stage and are also easy to sample. This is unfortunate since the biology of larvae, which tend to be more sedentary and host specific than adults, is probably a key determinant of the species' distribution in many herbivore assemblages (Basset & Samuelson 1996).

It remains unclear whether the unpredictability of samples obtained from herbivorous assemblages in rainforests reflects the underlying unpredictability of the assemblages themselves or whether it is a sampling arte-

*Author for correspondence (novotny@entu.cas.cz).

fact. In particular, numerous transient species, not associated with the resource under study, can contribute to random variance in the composition of these samples, unless they are excluded by feeding experiments (Basset 1997; Novotny & Basset 2000).

The present study is an attempt at revealing regular patterns in the structure of rigorously defined assemblages of tropical herbivores, if there are any. It is based on extensive sampling and rearing of caterpillars (Lepidoptera) feeding on 69 species of woody plants in a lowland rainforest in Papua New Guinea, followed by detailed taxonomic examination of the reared adults (Basset *et al.* 2000).

2. MATERIAL AND METHODS

(a) *Study area and host plants*

The study area was located in lowland evergreen rainforest (more than 150 species of woody plants per ha; Laidlaw *et al.* 2002) 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 near Baitabag, Ohu and Mis villages (145°41–8′ E, 5°08–14′ S, *ca.* 0–200 m). At each site, an area of 5–10 km^2 of primary and secondary forests was sampled.

Sixty-nine species of trees and shrubs from 45 genera and 23 families (listed in Novotny *et al.* 2002*a*) were selected for the study of their caterpillars. These included 15 species of *Ficus* and 1 species of *Artocarpus* (Moraceae), 6 species of *Macaranga* and 9 species representing 9 other genera of Euphorbiaceae, 4 species of *Psychotria* and 12 species representing 12 other genera of Rubiaceae, 3 species of *Syzigium* (Myrtaceae) and 19 species representing 19 other families of flowering plants.

Moraceae, Euphorbiaceae and Rubiaceae, studied in detail, are important components of lowland rainforest flora in the Madang area and elsewhere in New Guinea (Oatham & Beehler 1998). The four genera represented by multiple species are among the most important in local rainforests, with a combined diversity of 475 species in New Guinea (Höft 1992).

This selection included all main lineages of flowering plants, viz. gymnosperms, monocotyledons, basal eudicots, euasterids and eurosids (APG 1998). Further, locally common plants from all main habitats within the study area, including early and late stages of forest succession as well as riverine and seashore habitats, were represented (Leps *et al.* 2001).

(b) *Insect sampling*

All externally feeding caterpillars (Lepidoptera), including leaf rollers and leaf tiers, were collected by hand from the foliage. At each sampling occasion, a collector spent one day walking throughout the study area and searching the foliage of the target tree species for caterpillars. The sampling was irregular, as it included any tree from the target species encountered during the sampling walk within the study area. Numerous trees were thus sampled at each sampling occasion, and many of the trees were sampled repeatedly on different sampling occasions. The sampling included accessible branches from the forest canopy and understorey that could be climbed or reached from the ground. This sampling reached most of the microhabitats provided to folivorous herbivores by the study trees. Particularly poorly accessible species of trees were not sampled.

The number of tree inspections, that is, a particular tree sampled at a particular time, was recorded, together with the approximate area of the foliage sampled, which was estimated visually. Each tree species was sampled continuously for a period of at least one year between July 1994 and December 2001. Sampling effort was equal for all plant species and amounted to *ca.* 1500 m^2 of foliage examined per species, while the number of tree inspections exceeded 1000 per plant species. This sampling effort represented *ca.* 1800 person-days of fieldwork.

In the laboratory, each caterpillar was provided with fresh leaves of the plant species it was collected from and reared to an adult whenever possible. Only caterpillars that fed were considered in the analyses. This amounted to *ca.* 90% of those collected, or 35 952 individuals, including 14 609 individuals successfully reared to adults.

All caterpillars were assigned to morphospecies, which were verified and refined using the adults reared from them. Altogether, the caterpillars were classified into 534 morphospecies, including 403 morphospecies successfully reared to adults. The morphospecies were verified by specialist taxonomists and identified as far as possible. The largest numbers of morphospecies were recruited from Geometridae (93 species), Noctuidae (72 species), Crambidae (72 species), Tortricidae (49 species) and Lymantriidae (45 species). The taxonomic methods and classification used are detailed in Holloway *et al.* (2001). Insect vouchers are deposited in the Smithsonian Institution (Washington), the National Agricultural Research Institute (Port Moresby) and Bishop Museum (Honolulu), plant vouchers in BISH, L, LAE and US (Holmgren *et al.* 1990).

(c) *Data analysis*

The analysis focused on the assemblages of externally feeding caterpillars on particular host-plant species. This taxonomic definition is suitable for ecological analysis as caterpillars represented more than 95% of species, individuals and biomass of all externally feeding holometabolous larvae in the studied ecosystem (Novotny *et al.* 2002*a*).

Host specificity was quantified as the proportion of individuals (P) feeding on a single most preferred host-plant species from a set of: (i) species from different families (P_f); (ii) species from different confamilial genera (P_g); and (iii) different congeneric species (P_s). Herbivore species characterized by P_f, P_g and P_s values of more than or equal to 0.9 were classified respectively as family specialists, genus specialists and monophages. Although arbitrary, we preferred this threshold to the strict definition requiring that all individuals feed on a particular plant taxon, as it is known that some individuals have anomalous host-plant preferences (Marohasy 1998). Only species for which at least 10 individuals were collected were considered in any of the classifications using the $P = 0.9$ threshold. Our data permitted analysis of host ranges including: (i) 23 plant families; (ii) 10 Euphorbiaceae and 12 Rubiaceae genera; and (iii) 15 *Ficus*, 6 *Macaranga*, 4 *Psychotria* and 3 *Syzigium* species.

The species with the highest number of individuals and highest biomass index in an assemblage were called, respectively, the principal abundance and principal biomass dominant of this assemblage. The body length multiplied by body width was used as an index of the caterpillar's biomass. Only the largest available measurement was used for each species, in order to approach the size of the last instar.

The similarity between assemblages from different hosts, sites or times of the year was characterized by Sørensen, percentual similarity and normalized expected species shared (NESS) coefficients. The Sørensen coefficient is $S\text{Ø} = 2S_C/(S_A + S_B + 2S_C)$, where S_A and S_B are, respectively, the numbers of species unique

to samples A and B, and S_C is the number of species shared by the two samples. The Sørensen coefficient ranges from zero (no common species) to one (identical species composition of both samples).

Percentual similarity is $PS = \Sigma\min(a_i, b_i)$, where a_i and b_i are the dominance values of species i (i.e. the number of individuals of species i divided by the total number of individuals in a sample) in samples A and B. PS ranges from 0 (no common species) to 1 (dominance values of all species are identical), and is an extension of the Sørensen coefficient for quantitative data (Ludwig & Reynolds 1988).

NESS(m) (Grassle & Smith 1976) is a similarity index ranging in value from 0 (no common species) to 1 (samples are random samples from the same assemblage). The number of common species is calculated for random draws of a particular size (number of individuals, specified by the parameter m) from two different samples and compared with the number of common species resulting from random draws from the same sample. The index becomes more sensitive to rare species with increasing m. NESS(1) and NESS(50) were calculated in this study (note that NESS(1) is the Morisita index).

Spatial variability in assemblage composition was assessed by comparing assemblages feeding on the same host at different sites, viz. assemblages from 25 hosts compared between Baitabag and Mis (8 km apart), 19 hosts between Mis and Ohu (10 km apart) and 30 hosts between Baitabag and Ohu (17 km apart). Similarly, temporal variability was assessed by comparing 29–32 assemblages feeding on the same host during three consecutive four-month periods of the year, when the host tree was continuously sampled. The remaining hosts were not sampled with sufficient intensity (more than, or equal to, 100 individuals per sample) at more than one site or during more than one four-month period.

The effects of sample size on species richness and assemblage similarity were studied by amalgamation of subsamples, representing 1–3 months of sampling, in randomized sequences, and calculating these parameters for each sample size. One hundred random sequences were generated for each calculation.

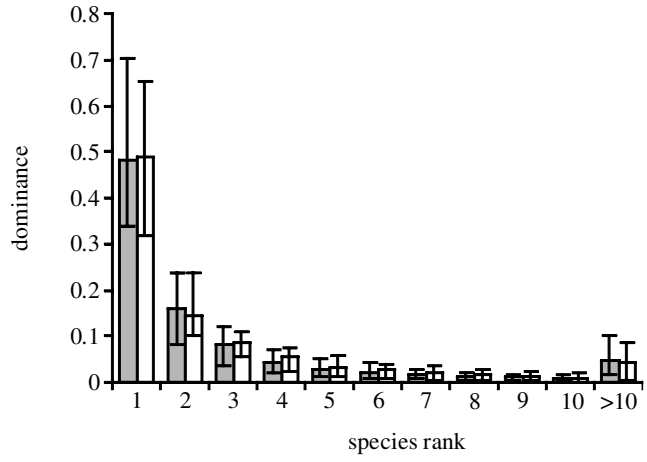

Figure 1. Dominance in herbivore assemblages. Medians with first and third quartiles, calculated from 69 assemblages, are reported for the percentage of individuals (shaded bars) and biomass (empty bars) represented by the first, second, … tenth most abundant species in an assemblage, and by all remaining species combined (rank greater than 10).

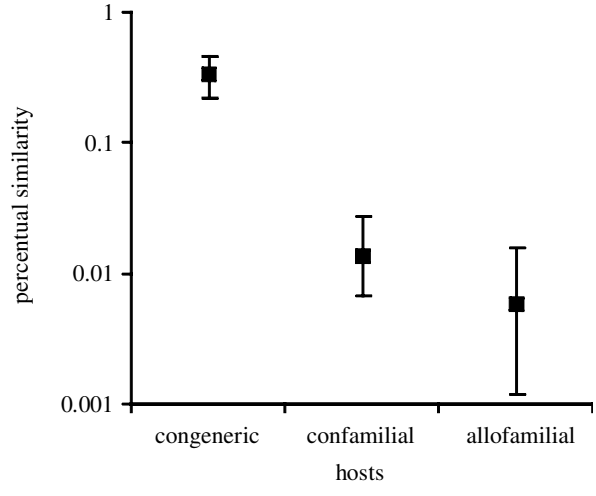

Figure 2. Percentual similarity for pair-wise comparisons between assemblages feeding on congeneric hosts, confamilial hosts from different genera and hosts from different families. Median with first and third quartiles is given for 129 congeneric, 219 confamilial and 1998 allofamilial pair-wise comparisons obtained from a complete similarity matrix including the 69 hosts studied.

3. RESULTS

(a) *Species richness and dominance structure*

Species richness ranged from 8 to 70 (median 23) species and abundance from 17 to 1196 (median 428) individuals per host plant. The total species richness was not sampled, as species accumulation curves on individual host plants did not show any asymptote. Species accumulation curves for combined samples from all congeneric hosts, all confamilial hosts and all hosts studied also did not approach an asymptote. The total of 534 species collected from 69 plant species is, thus, an underestimation of overall diversity.

Each assemblage was strongly dominated by a single or few species, in terms of both abundance and biomass (figure 1). The single most abundant species represented 9–99% (median 48%) of individuals and 15–99% (median 49%) of biomass in the assemblage. By contrast, 135 species (25% of the total) were collected as single individuals, and combined they represented only 0.4% of all individuals in the samples. Dominance structures based on abundance and biomass were almost identical (figure 1), despite 21 assemblages out of the 69 studied having different principal dominants depending on whether abundance or biomass was considered.

(b) *Host specificity*

Seventy-seven per cent of the 212 species analysed were family specialists, while 66% of the 90 species were genus specialists and 11% of the 91 species were monophagous. The complete matrix of pair-wise comparisons between assemblages from the 69 hosts studied included 129 comparisons between congeneric hosts, 219 comparisons between confamilial hosts from different genera and 1998 comparisons between hosts from different families. The median PS of two assemblages feeding on congeneric hosts was 0.34, on hosts from different confamilial genera it was 0.01 and on hosts from different families it was 0.006 (figure 2).

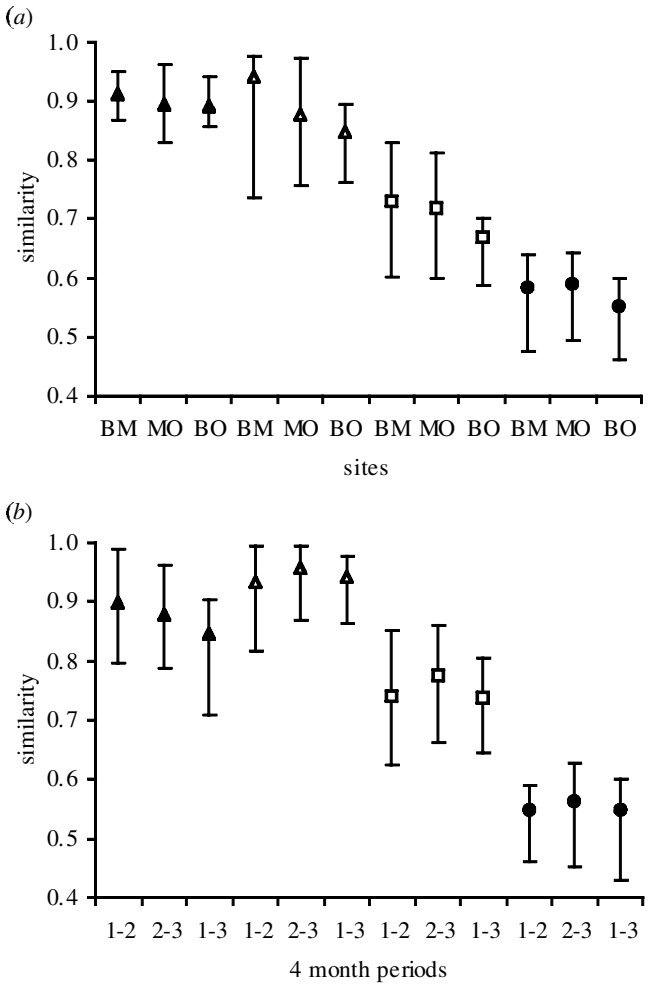

Figure 3. Similarity between assemblages feeding on the same hosts at different sites (*a*) and during different four-month periods of the year (*b*). Median with first and third quartiles is reported for NESS(50) (filled triangles), NESS(1) (open triangles), percentual similarity (open squares) and Sørensen similarity (dots) between assemblages from Baitabag and Mis (BM; 8 km apart; 25 assemblages analysed), Mis and Ohu (MO; 10 km apart; 19 assemblages analysed) and Baitabag and Ohu (BO; 17 km apart; 30 assemblages analysed) and between assemblages from the first, second and third four-month periods of the year (29–32 assemblages analysed).

Assemblages on congeneric plants often shared their principal dominant, while 43 out of 45 assemblages on plants from different genera and families had a unique principal dominant. There were 52 family specialists among the 57 species that were the principal abundance dominant in at least one of the 70 assemblages. This was a slightly higher proportion (91%) than the 72% of family specialists found among the remaining 155 species (χ^2-test: $p < 0.01$).

(c) *Spatial and temporal variability*

Assemblage composition was spatially constant over distances less than 20 km. The median similarity between assemblages from the same host at different sites 8–17 km apart ranged from 0.89 to 0.91 for NESS(50), from 0.85 to 0.94 for NESS(1), from 0.67 to 0.73 for PS and from 0.55 to 0.59 for Sørensen similarity (figure 3*a*).

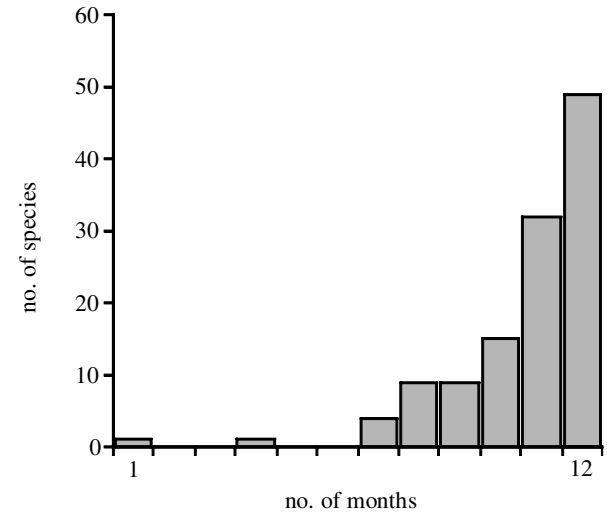

Figure 4. Seasonality of Lepidoptera species. The number of months from one year of continuous sampling when caterpillars were present is reported for all Lepidoptera species where at least 50 individuals were collected.

Caterpillar assemblages were also constant throughout the year. The median similarity between assemblages from the same host sampled during different four-month periods of the year ranged from 0.85 to 0.90 for NESS(50), from 0.93 to 0.96 for NESS(1), from 0.74 to 0.78 for PS and from 0.55 to 0.56 for Sørensen similarity (figure 3*b*). Further, caterpillars from a majority of the 120 species for which a sufficient sample (at least 50 individuals collected during one year of continuous sampling) was available were present during most of the year (median presence was 11 months per year; figure 4).

(d) *Sampling issues*

The estimates of similarity between samples from different sites and hosts were only weakly dependent on sample size. This is illustrated using three similarity indices for samples of caterpillars feeding on *Macaranga quadriglandulosa* at two different sites (figure 5*a*). All indices stabilized at a sample size of *ca.* 150 individuals per study site, unlike the species richness in the samples, which continued increasing at all sample sizes. Similarity estimates for assemblages feeding on different hosts were also independent of sample size for samples of more than 300 individuals per host, as illustrated by a comparison between *M. quadriglandulosa* and *M. aleuritoides* (figure 5*b*; numerous other comparisons, not shown here, gave similar results).

The median (first to third quartile) sampling effort needed to collect 300 individuals from a particular host species was 1050 (610–1484) m^2 of foliage sampled, 596 (414–1248) tree inspections and 19 (11–31) person-days of sampling. Our sampling obtained 300 or more individuals from 54 (77%) of the studied assemblages.

4. DISCUSSION

(a) *Species richness and dominance structure*

Our results indicate that total local census of caterpillar species feeding on a particular host is all but impossible in tropical ecosystems (see also Price *et al.* 1995). The rate

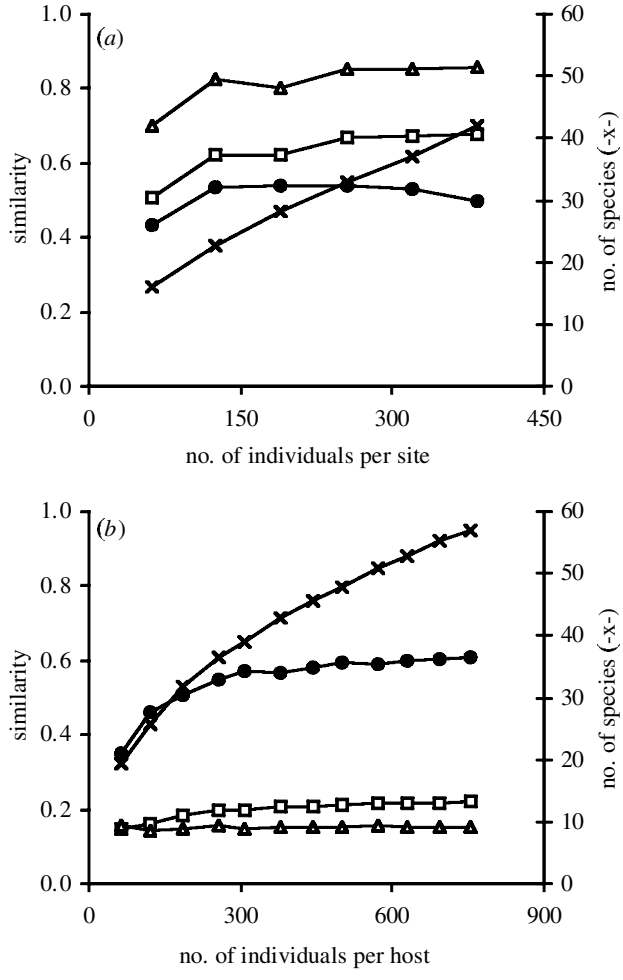

Figure 5. Similarity between assemblages on *Macaranga quadriglandulosa* from two study sites, Mis and Ohu, (*a*) and similarity between assemblages on *M. quadriglandulosa* and *M. aleuritoides* (*b*). Samples, each representing 1–3 months of sampling, were randomly amalgamated; 100 replicates were performed for each sample size. The number of species in the combined samples (crosses) and their NESS(1) (triangles), percentual similarity (squares) and Sørensen similarity (dots) are reported for various sample sizes (the average number of individuals per study site or host).

of discovery of new species remained high and constant at all sample sizes, even after substantial sampling effort. Since only feeding caterpillars were considered, the apparently endless increase in the number of species cannot be attributed to a constant influx of tourist species. Although the proportion of very rare species collected as single individuals was lower than is typical for studies that do not eliminate tourists by feeding experiments (Novotny & Basset 2000), rare species still represented an important part of each assemblage. Their densities were low, possibly because their core populations were feeding on other hosts or were distributed over large areas. In such cases, even locally restricted sampling on a single plant species would sample from a large regional pool of herbivore species. This possibility is supported by low regional to local ratios of species diversity, reported for some insect taxa (Gaston *et al.* 1996; Orr & Haeuser 1996; Bartlett *et al.* 1999) and trees (Foster & Hubbell 1990; Kochummen *et al.* 1992) from the tropics. Dominance of assemblages by a few species is a pattern that is also typical for caterpillar assemblages from temperate trees (Barbosa *et al.* 2000).

(b) *Host specificity*

The Lepidoptera assemblages included, primarily, species that fed on several closely related hosts representing only a small percentage of the locally available plant species and biomass (see also Novotny *et al.* 2002*b*). Similar host specificity was found in two neotropical forests, where family specialists represented 61% of Saturniidae (Janzen 2003) and 85% of leaf chewers, mostly Lepidoptera (Barone 1998). Comparative data from temperate forest assemblages are surprisingly rare. Futuyma & Gould (1979) observed that 12% of the caterpillars they found in their study of caterpillars on broad-leaf woody plants in a North American forest were family specialists. Leps *et al.* (1998, and personal communication) used published information on host ranges for the species feeding on woody plants in a local assemblage in Central Europe surveyed by light trapping and found that 18% of them were family specialists.

Low overlap among caterpillar assemblages from allogeneric and allofamilial hosts generated a highly fragmented structure of the local compound assemblage from diverse rainforest vegetation. For instance, a 1 ha plot from our Baitabag site included 1042 plants with stem diameters at breast height of at least 5 cm from 152 species, 94 genera and 45 families (Laidlaw *et al.* 2002). On average, an individual plant shared this plot with 20 plants from the same species, 66 plants from a different species of the same genus, 31 plants from a different genus of the same family and 924 plants from a different family. Most of the plant's neighbours were, thus, potential hosts of caterpillar assemblages very different from its own.

(c) *Spatial and temporal variability*

Adult Lepidoptera can often disperse hundreds of metres or more during their lifetime (e.g. Scott 1975; Mallet 1986). Such dispersal ability, in combination with a generation time two to three orders of magnitude shorter than that of their woody hosts, leads to the expectation of low species turnover in caterpillar assemblages feeding on a particular host over distances of several to several tens of kilometres. This expectation was confirmed by our study, as indicated by NESS similarity values approaching unity. The low values of the Sørensen index are a sampling artefact, which can be expected when comparing assemblages with numerous rare species. Unfortunately, data on species turnover over larger scales, from tens to hundreds of kilometres, are not available for tropical caterpillars.

Seasonality of tropical herbivore assemblages tends to be correlated with the seasonality of rainfall (Wolda 1988; Janzen 1993; Novotny & Basset 1998). This relationship also applies to the assemblages studied here, as a humid climate with only a moderate two-month dry season (Novotny & Basset 1998) coincided with the year-round presence of caterpillars of most of the species and high constancy of their assemblages throughout the year.

(d) *Sampling issues*

An important corollary of caterpillar assemblages being strongly dominated by a small number of aseasonal and spatially constant species is that their basic structure and

between-assemblage similarity relationships can be reliably assessed from samples of limited size, usually less than 300 individuals per assemblage.

The insensitivity of PS and NESS(1) indices to sample size follows directly from the constant representation of dominant species in the samples, as these indices are determined primarily by common species. By contrast, the independence of the Sørensen index, which is based solely on the presence and absence of species, from sample size was unexpected.

Replicated samples from different sites and sampling periods provided consistent data on the composition of and similarity relationships among caterpillar assemblages. This is in marked contrast to the frequent failure of tropical insect studies, particularly those using insecticide fogging and light-trap sampling techniques, to find repeated patterns in replicated samples, even those obtained from the same tree species or site and/or during the same period of time (Orr & Haeuser 1996; Allison *et al.* 1997; Mawdsley & Stork 1997; Floren & Linsenmair 1998, 2003). Such discrepancy can be attributed to different sampling strategies. While fogging, light-, Malaise- and similar trapping methods sample a large part of the entire insect fauna from a small area, and often also over a short period of time (Basset *et al.* 1997), our sampling included only species exploiting a precisely defined resource, viz. the foliage of a particular tree species, over an area of several square kilometres throughout one year. The latter approach permitted repeated sampling from the foliage of hundreds of conspecific trees, which may be necessary for a reliable description of low-density assemblages of insect herbivores, such as rainforest caterpillars, which occur as only a few individuals on the majority of individual trees.

It has to be stressed that our recommendation of 300 individuals as a sufficient sample size needs to be considered within the context of our particular sampling strategy. It is likely that the same number of individuals obtained by thorough sampling of a few individual trees, such as in studies using canopy cranes, would not be equally representative (Basset *et al.* 2003).

The median sampling effort of 19 person-days necessary to sample one caterpillar assemblage indicates that caterpillar assemblages from the 152 species of woody plants found within 1 ha of our study area (see § 4b) could be sampled during *ca.* 3000 person-days of fieldwork. This is a conservative estimate because our study avoided trees that were particularly difficult to sample. According to our experience, an additional *ca.* 9000 person-days, of laboratory work by parataxonomists or technicians (Basset *et al.* 2000) will be required for caterpillar rearing, mounting of adults, databasing and project management. Such an undertaking, although not trivial, is quite feasible, as it requires a team of 10 people working for 5 years. The total taxonomic effort is harder to estimate than the field sampling because it has included over 25 collaborators in many institutions throughout the world. The taxonomic effort required is also highly dependent on the availability of reference collections, literature and expertise. The taxonomic effort for this project has taken a little more than one person-day per species, including extensive dissection of genitalia and comparisons to type specimens.

(e) *Compound assemblages*

Tropical forest Lepidoptera are known from either samples of caterpillar assemblages feeding on a limited selection of host plants (e.g. Marquis 1991; Basset *et al.* 1996; Barone 1998) or light-trap samples of adults from entire forest vegetation (e.g. Robinson & Tuck 1993; Intachat *et al.* 1999); the integration of both approaches is rare (but see Janzen 1988, 2003).

Our results suggest that each plant genus has a unique caterpillar fauna, including a principal dominant that represents approximately half the individuals in the assemblage. As the most abundant plant genera in rainforests typically represent less than 15% of the entire biomass (e.g. Weiblen 1998; Chave *et al.* 2002; Laidlaw *et al.* 2002), the dominance of the most common species in the compound assemblage of Lepidoptera is expected to be less than 10%. This is in agreement with rainforest light-trap samples, which are characterized by low dominance, often less than 5% even for the most abundant species (Robinson & Tuck 1993; Intachat *et al.* 1999).

5. CONCLUSIONS

Our data on 69 assemblages made it possible to identify certain traits that appear to be constant for caterpillar assemblages feeding on rainforest trees, at least in lowland rainforests in the Madang area of New Guinea, and possibly elsewhere. The following assemblage characteristics are typical, i.e. apply to at least 75% of the assemblages studied: the assemblage is dominated by a single species, which represents more than one-third of the individuals and biomass of the entire assemblage and is present as larvae during at least 10 months of the year; and it remains identical over distances of at least 20 km. The dominant species is specialized to a single plant family and genus but feeds on several congeneric species, where available. The overlap of the assemblage with others feeding on plant species present within a neighbouring 1 ha of rainforest is low, with an average PS of less than 0.10. A sample of less than 300 caterpillars from this assemblage is sufficient to reveal the identity of the main assemblage dominants, as well as its similarity relationships with assemblages on other host species or at other sites.

We thank parataxonomists J. Auga, W. Boen, C. Dal, S. Hiuk, B. Isua, M. Kasbal, R. Kutil, M. Manumbor and K. Molem for assistance. Numerous collectors, acknowledged elsewhere, assisted with insect collections. Numerous colleagues provided taxonomic help, particularly J. D. Holloway, J. Brown, M. Horak, K. Tuck, M. Shaffer, E. G. Munroe and J. Y. Miller. The Bishop Museum (Honolulu) and Natural History Museum (London) provided critical facilities for the taxonomic work. W. Takeuchi commented on the manuscript. The project was funded by the US National Science Foundation (DEB-94-07297, DEB-96-28840 and DEB-97-07928), Czech Academy of Sciences (A6007106, Z5007907), Czech Ministry of Education (ES 041), Czech Grant Agency (206/99/1115), International Centre of Insect Physiology and Ecology (Nairobi) and the Otto Kinne Foundation.

REFERENCES

Allison, A., Samuelson, G. A. & Miller, S. E. 1997 Patterns of beetle species diversity in *Castanopsis acuminatissima* trees studied with canopy fogging in mid-montane New Guinea

rain forest. In *Canopy arthropods* (ed. N. E. Stork, J. A. Adis & R. K. Didham), pp. 222–234. London: Chapman & Hall.

APG 1998 An ordinal classification for the families of flowering plants. *Ann. Miss. Bot. Gard.* **85**, 531–553.

Barbosa, P., Segarra, A. & Gross, P. 2000 Structure of two macrolepidopteran assemblages on *Salix nigra* (Marsh) and *Acer negundo* L.: abundance, diversity, richness, and persistence of scarce species. *Ecol. Entomol.* **25**, 374–379.

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

Bartlett, R., Pickering, J., Gauld, I. & Windsor, D. 1999 Estimating global biodiversity: tropical beetles and wasps send different signals. *Ecol. Entomol.* **24**, 118–121.

Basset, Y. 1997 Species-abundance and body size relationships in insect herbivores associated with New Guinea forest trees, with particular reference to insect host-specificity. In *Canopy arthropods* (ed. N. E. Stork, J. A. Adis & R. K. Didham), pp. 237–264. London: Chapman & Hall.

Basset, Y. & Samuelson, G. A. 1996 Ecological characteristics of an arboreal community of Chrysomelidae in Papua New Guinea. In *Chrysomelidae biology*, vol. 2 (ed. P. H. A. Jolivet & M. L. Cox), pp. 1–7. Amsterdam: SPB Academic Publishing.

Basset, Y., Samuelson, G. A. & Miller, S. E. 1996 Similarities and contrasts in the local insect faunas associated with ten forest tree species of New Guinea. *Pacific Sci.* **50**, 157–183.

Basset, Y., Aberlenc, H.-P., Springate, N. D. & Delvare, G. 1997 A review of methods for sampling arthropods in tree canopies. In *Canopy arthropods* (ed. N. E. Stork, J. A. Adis & R. K. Didham), pp. 27–52. London: Chapman & Hall.

Basset, Y., Novotny, V., Miller, S. E. & Pyle, R. 2000 Quantifying biodiversity: experience with parataxonomists and digital photography in Papua New Guinea and Guyana. *BioScience* **50**, 899–908.

Basset, Y. (and 10 others) 2001 Stratification and diel activity of arthropods in a lowland rainforest in Gabon. *Biol. J. Linn. Soc.* **72**, 585–607.

Basset, Y., Novotny, V., Miller, S. E. & Kitching, R. 2003 Methodological advances and limitations in canopy entomology. In *Arthropods of tropical forests: spatio-temporal dynamics and resource use in the canopy* (ed. Y. Basset, V. Novotny, S. E. Miller & R. Kitching), pp. 7–16. Cambridge University Press. (In the press.)

Chave, J., Condit, R., Lao, S., Caspersen, J. P., Foster, R. B. & Hubbell, S. P. 2002 Spatial and temporal variation of biomass in a tropical forest: results from a large census plot in Panama. *J. Ecol.* (Submitted.)

Floren, A. & Linsenmair, K. E. 1998 Non-equilibrium communities of Coleoptera in trees in a lowland rain forest of Borneo. *Ecotropica* **4**, 55–67.

Floren, A. & Linsenmair, K. E. 2003 How do beetle assemblages respond to anthropogenic disturbance? In *Arthropods of tropical forests: spatio-temporal dynamics and resource use in the canopy* (ed. Y. Basset, V. Novotny, S. E. Miller & R. Kitching), pp. 190–197. Cambridge University Press. (In the press.)

Foster, R. B. & Hubbell, S. P. 1990 The floristic composition of the Barro Colorado Island forest. In *Four neotropical forests* (ed. A. H. Gentry), pp. 85–98. New Haven, CT: Yale University Press.

Futuyma, D. J. & Gould, F. 1979 Associations of plants and insects in a deciduous forest. *Ecol. Monogr.* **49**, 33–50.

Gaston, K. J., Gauld, I. D. & Hanson, P. 1996 The size and composition of the hymenopteran fauna of Costa Rica. *J. Biogeogr.* **23**, 105–113.

Grassle, J. F. & Smith, W. 1976 A similarity measure sensitive to the contribution of rare species and its use in investigation of variation in marine benthic communities. *Oecologia* **25**, 13–22.

Höft, R. 1992 *Plants of New Guinea and the Solomon Islands. Dictionary of the genera and families of flowering plants and ferns*, handbook no. 13. Wau, Papua New Guinea: Wau Ecology Institute.

Holloway, J. D., Kibby, G., Peggie, D., Carter, D. J. & Miller, S. E. 2001 *Families of Malesian moths and butterflies*. Fauna Malesia handbook, vol. 3. Leiden, The Netherlands: Brill.

Holmgren, P. K., Holmgren, N. H. & Barnett, L. C. (eds) 1990 *Index herbariorum. Part I: the herbaria of the world*. New York Botanical Garden.

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. Tropical Forest Sci.* **11**, 61–78.

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

Janzen, D. H. 1993 Caterpillar seasonality in a Costa Rican dry forest. In *Caterpillars, ecological and evolutionary constraints on foraging* (ed. N. E. Stamp & T. M. Casey), pp. 448–477. New York: Chapman & Hall.

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* (ed. Y. Basset, V. Novotny, S. E. Miller & R. Kitching), pp. 369–379. Cambridge University Press. (In the press.)

Kochummen, K. M., LaFrankie Jr, J. V. & Manokaran, N. 1992 Diversity of trees and shrubs in Malaya at regional and local level. *Malay. Nat. J.* **45**, 545–554.

Laidlaw, M. J., Kitching, R. L., Damas, K. & Kiapranis, R. 2002 Structure and floristics of lowland rainforest plots in northern Papua New Guinea. *Biotropica*. (In the press.)

Leps, J., Spitzer, K. & Jaros, J. 1998 Food plants, species composition and variability of the moth community in undisturbed forest. *Oikos* **81**, 1–11.

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.

Ludwig, J. A. & Reynolds, J. F. 1988 *Statistical ecology: a primer of methods and computing*. New York: Wiley.

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

Mallet, J. 1986 Dispersal and gene flow in a butterfly with home range behavior: *Heliconius erato* (Lepidoptera: Nymphalidae). *Oecologia* **68**, 210–217.

Marohasy, J. 1998 The design and interpretation of host-specificity tests for weed biological control with particular reference to insect behaviour. *Biocontrol News Inform.* **19**, 13N–20N.

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* (ed. P. W. Price, T. M. Lewinsohn, G. W. Fernandes & W. W. Benson), pp. 179–208. London: Wiley.

Mawdsley, N. A. & Stork, N. E. 1997 Host-specificity and the effective specialization of tropical canopy beetles. In *Canopy arthropods* (ed. N. E. Stork, J. Adis & R. K. Didham), pp. 104–130. London: Chapman & Hall.

Novotny, V. & Basset, Y. 1998 Seasonality of sap-sucking insects (Auchenorrhyncha, Hemiptera) feeding on *Ficus* (Moraceae) in a lowland rain forest in New Guinea. *Oecologia* **115**, 514–522.

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.

2002*a* Host specialisation of leaf chewing insects 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. & Drozd, P. 2002*b* Low host specificity of herbivorous insects in a tropical forest. *Nature* **416**, 841–844.

Oatham, M. & Beehler, B. M. 1998 Richness, taxonomic composition and species patchiness in three lowland forest tree plots in Papua New Guinea. In *Forest biodiversity research, monitoring and modeling: conceptual background and Old World case studies* (ed. F. Dallmeier & J. A. Comiskey), pp. 613–631. Paris and New York: UNESCO and Parthenon Publishing Group.

Orr, A. G. & Haeuser, C. L. 1996 Temporal and spatial patterns of butterfly diversity in a lowland tropical rainforest. In *Tropical rainforest research—current issues* (ed. D. S. Edwards, W. E. Booth & S. C. Choy), pp. 125–138. Dordrecht, The Netherlands: Kluwer.

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.

Scott, J. A. 1975 Flight patterns among eleven species of diurnal Lepidoptera. *Ecology* **56**, 1367–1377.

Stork, N. E., Adis, J. A. & Didham, R. K. (eds) 1997 *Canopy arthropods*. London: Chapman & Hall.

Wagner, T. 1997 The beetle fauna of different tree species in forests of Rwanda and East Zaire. In *Canopy arthropods* (ed. N. E. Stork, J. A. Adis & R. K. Didham), pp. 169–183. London: Chapman & Hall.

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

Wolda, H. 1988 Insect seasonality: why? *A. Rev. Ecol. Syst.* **19**, 1–18.

As this paper exceeds the maximum length normally permitted, the authors have agreed to contribute to production costs.