PROCEEDINGS OF THE ROYAL SOCIETY B
FirstCite® e-publishing

Proc. R. Soc. B
doi:10.1098/rspb.2004.3023

Review

Host specificity of insect herbivores in tropical forests

Vojtech Novotny[1,*] **and Yves Basset**[2]

[1] *Institute of Entomology, Czech Academy of Sciences and Biological Faculty, University of South Bohemia, Branisovska 31, 370 05 Ceske Budejovice, Czech Republic*
[2] *Smithsonian Tropical Research Institute, Apartado 2072, Balboa, Ancon, Panama, Republic of Panama*

Studies of host specificity in tropical insect herbivores are evolving from a focus on insect distribution data obtained by canopy fogging and other mass collecting methods, to a focus on obtaining data on insect rearing and experimentally verified feeding patterns. We review this transition and identify persisting methodological problems. Replicated quantitative surveys of plant–herbivore food webs, based on sampling efforts of an order of magnitude greater than is customary at present, may be cost-effectively achieved by small research teams supported by local assistants. Survey designs that separate historical and ecological determinants of host specificity by studying herbivores feeding on the same plant species exposed to different environmental or experimental conditions are rare. Further, we advocate the use of host-specificity measures based on plant phylogeny. Existing data suggest that a minority of species in herbivore communities feed on a single plant species when alternative congeneric hosts are available. Thus, host plant range limits tend to coincide with those of plant genera, rather than species or suprageneric taxa. Host specificity among tropical herbivore guilds decreases in the sequence: granivores > leaf-miners > fructivores > leaf-chewers = sap-suckers > xylophages > root-feeders, thus paralleling patterns observed in temperate forests. Differences in host specificity between temperate and tropical forests are difficult to assess since data on tropical herbivores originate from recent field studies, whereas their temperate counterparts derive from regional host species lists, assembled over many years. No major increase in host specificity from temperate to tropical communities is evident. This conclusion, together with the recent downward revisions of extremely high estimates of tropical species richness, suggest that tropical ecosystems may not be as biodiverse as previously thought.

Keywords: food web; herbivore guild; host plant range; insect sampling; rainforest; species richness

1. INTRODUCTION

Plant–phytophage food webs represent more than 40% of global terrestrial biodiversity (Price 2002), most of it concentrated in tropical forests. Arguably, their diversity makes tropical forests a logical starting place for the study of host specificity, rather than the impoverished forests of northern temperate regions. Estimates of host specificity (or lack thereof) played an important role in the recent controversy surrounding global estimates of insect species richness, ranging from 30 million (Erwin 1982) to 4–6 million (Novotny *et al.* 2002*b*). Narrow insect host specificity was also invoked as the mechanism maintaining the high species richness of insects in tropical forests (Basset 1992). Further, the Janzen–Connell hypothesis assumed that specialized insect herbivores or other pests reduce recruitment near conspecific plants, thus demographically favouring rare species and maintaining high plant diversity in tropical forests (Wright 2002). Finally, host specificity of insect herbivores is also central to the study of indirect effects between different plant species, mediated by their shared herbivores (Godfray *et al.* 1999; Novotny *et al.* 2004*b*).

Janzen (1983, p.167) characterized his review of tropical food webs as 'rich in extrapolation and conjecture, held in place by very few data points'. Later, Basset (1992) remarked on the scarcity of information on the host specificity of tropical herbivores, while a recent review (Godfray *et al.* 1999) discussed possible developments in this discipline. Recently, there has been progress in the study of plant–herbivore interactions as the emphasis of tropical research has graduated from the diversity of species to that of interspecific interactions. This can be illustrated by a shift in focus in two recent monographs on tropical insects: namely, Stork *et al.* (1997) and Basset *et al.* (2003). Studies on phytophages used to be reliant on insect distribution data, obtained by canopy fogging, light and Malaise trapping and other mass collecting methods (reviewed in Basset 2001*a*). This approach is being superseded by studies that rely on observation *in situ*, experimental verification of insect feeding, and insect rearing, which are reviewed here.

2. MEASURING HOST SPECIFICITY

Herbivores are often classified as mono-, oligo- and polyphagous, or as generalists and specialists. Several meanings have been attached to these terms by different

---

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

Received 5 August 2004
Accepted 23 November 2004

authors (Symons & Beccaloni 1999), since no universal criterion that distinguishes specialists from generalists exists. They probably cannot be resurrected for any specific use; instead, they should be redefined whenever used. The terms species-, genus- and family specialist (Barone 1998) are used for herbivorous species feeding on a single plant species, genus and family. They represent a potentially useful set of host specificity definitions, used in the present review.

Plant–herbivore matrices from tropical forests are characterized by a large number of rare plant–herbivore interactions. For example, as many as 40–50% of trophic links can be established on single feeding individuals (Nakagawa *et al.* 2003; Novotny *et al.* 2004*a*). Thus, estimates of the number of host species used by herbivores are dependent on sample size and are unreliable even for a large sampling effort (Novotny *et al.* 2002*a*, 2004*a*). The host plant lists that indiscriminately include all host plant records become rapidly dominated by marginal hosts and errors committed by either herbivores or ecologists. A more robust definition of monophagous species, that is, species with at least 90% of individuals feeding on a single host species (Thomas 1990; Tavakilian *et al.* 1997; Novotny *et al.* 2002*a*) may be more legitimate.

Analyses of host specificity need to consider phylogenetic relationships of the host plants. Thus far, these have been approximated by supraspecific taxonomic ranks. Host range is then described as the number of host plant species and various supraspecific taxa (Symons & Beccaloni 1999). As information on plant phylogeny accumulates, this imprecise approach will become superseded by host specificity measures based on host plant phylogeny, defined by cladograms (Symons & Beccaloni 1999; Webb *et al.* 2002). New phylogenetic measures of host specificity, including the clade dispersion index (Symons & Beccaloni 1999) and the net relatedness index (Webb *et al.* 2002), quantify overall clustering of host taxa on a phylogenetic tree. Although promising, these indices have not been widely applied (Weiblen *et al.* in press). Phylogenetic constraints on host plant selection may be examined as a relationship of species turnover between herbivore communities and the phylogenetic distance of their host plant species (Novotny *et al.* 2002*b*).

Indices describing the distribution of herbivore individuals among host plant species represent an alternative approach to host specificity measurement, which ignores plant phylogeny but responds to herbivore abundance on various hosts and, as such, is relatively unaffected by rare host plant records. These include Lloyd's index (Novotny & Basset 1998) and Hurlbert's (1971) probability of interspecific encounter index (the latter was recently modified and used for food webs; e.g. Müller *et al.* 1999; Lewis *et al.* 2002; Morris *et al.* 2004). Local plant availability can also constrain host plant use, particularly in tropical forests where many genera and families are locally monotypic (e.g. Condit *et al.* 1996). Therefore, estimates of host specificity should always be considered with regard to the number of potential alternative hosts that are available.

Host specificity patterns of individuals in herbivore communities have received so little attention that even the simple but fundamental question of whether a herbivorous insect selected at random from tropical vegetation is likely to be a generalist or a specialist has yet to be answered (Novotny *et al.* 2004*b*).

Host specificity estimates depend on sound taxonomy of herbivores and plants. Modern revisions of tropical insect faunas often synonymize almost as many species as they describe (Scoble *et al.* 1995), while molecular research may reveal specialized cryptic species in what appeared to be a single generalist species (Berkov 2002). The analysis of cytochrome oxidase I ('DNA bar coding') may be particularly useful for species-level identifications in insects (Hebert *et al.* 2003).

Usually, studies of herbivores in tropical forests sample only part of the local flora—typically less than 100 species (Marquis 1991; Basset 1996; Barone 1998; Ødegaard 2000*a*; Novotny *et al.* 2002*a*). Often, the flora studied is structured according to plant phylogeny (e.g. congeneric species: Marquis 1991; allofamilial species: Basset 1996) or ecology (e.g. lianas versus trees: Ødegaard 2000*a*; early versus late successional species: Leps *et al.* 2001) and selected from locally common species. More extensive studies sampling a larger proportion of local vegetation (Janzen 1980, 2003; Tavakilian *et al.* 1997) are qualitative surveys that catalogue host–plant relationships, but do not monitor sampling effort and population densities of herbivores on individual plant species. A study that is both quantitative and comprehensive is still awaited.

The number of tropical multispecies studies of host specificity is limited (table 1). Regrettably, groundbreaking studies, rather than promoting analogous research in other ecosystems and geographical areas, tend to petrify into solitary textbook case studies. For instance, Janzen's (1980) pioneer survey of granivorous beetles from local vegetation still remains the only such comprehensive study of this herbivore guild from tropical forests.

3. HOST SPECIFICITY AND HOST PLANT TRAITS

The host specificity of herbivores feeding on a particular plant species may be regarded as a one of the latter's characteristics and analysed in the context of its other traits. Rather surprisingly, such analyses are rare, which contrasts with the attention paid to a similar variable: the number of herbivores feeding on different plant species (Lewinsohn 1991; Basset 1996; Basset & Novotny 1999; Kelly & Southwood 1999).

Temperate zone studies along successional series documented a positive relationship between plant predictability and host specificity of their herbivores, since ephemeral plants from early successional stages are colonized by polyphages (Brown & Southwood 1983). However, tropical succession often starts with pioneer trees, rather than with annual herbs. Already, these represent a permanent and predictable resource for insects with no advantage for polyphages (Leps *et al.* 2001). Polyvoltine insects in continuous tropical forests may be able to colonize even rare perennial plants. Thomas (1990) reported on rapid colonization of isolated plants in a rainforest, but further studies would need to examine plants isolated from their conspecifics by a distance larger than the 50 m used in his study. Shanahan *et al.* (2001) reported rapid colonization by fig wasps of a new volcanic island 55 km offshore.

Tree species from mature forests invest more in anti-herbivore defences than early successional species (Coley & Barone 1996). This is particularly so in mature leaves, which also suffer lower herbivore damage in late, rather than early, successional trees. Although these important patterns in anti-herbivore defence were observed 20 years ago (Coley 1983), it remains unclear how they are associated with host specificity patterns in herbivore communities from early and late successional trees. Young and mature leaves in tropical trees are so different, physically and chemically, that they represent distinct resources for insect herbivores. Further, there seem to be two anti-herbivore strategies, 'defence' and 'escape', employed by tropical trees to defend their young leaves (Kursar & Coley 2003). It is probable that herbivores respond by different levels of host specificity. In particular, the escape strategy may select for polyphagy in herbivores, but no data are available to confirm this assumption.

Plant growth form determines host specificity of herbivores in temperate areas (Ward *et al.* 1995), but most studies from the tropics concentrate only on shrubs and trees. Comparative studies of herbivores from other growth forms (e.g. herbaceous or epiphyte species) would be more difficult but also more rewarding, as demonstrated for example by a recent study of lianas (Ødegaard 2000*a*). Herbivore host specificity probably differs among plant lineages (cf. an example from temperate plants in Frenzel & Brandl 2001). Tropical woody vegetation provides an excellent, albeit neglected, opportunity for the analysis of the host specificity patterns in all major plant lineages, using plant species from the same growth form.

In addition to plant traits effecting 'bottom–up' influences on host specificity via secondary metabolites and other anti-herbivore defences, predators and parasitoids associated with each plant species may exercise 'top–down' control. Specialized herbivores appear to be less susceptible to predators in tropical forests (Dyer 1995), but tend to suffer higher parasitism rates (Gentry & Dyer 2002).

Interpreting differences in herbivorous communities feeding on different plant species is always difficult as they differ in multiple traits. Therefore, it is surprising how few studies have attempted to separate historical and ecological factors by comparative analyses of herbivore communities feeding on the same, or at least closely related, plant species exposed to well-defined differences in their environment or different experimental treatments. This approach has been used to study herbivore communities and their response to disturbance caused by selective logging (Basset *et al.* 2001), stratification between young and mature (Basset 2001*b*) and differences between living and dead (Ødegaard 2004) trees. However, the comparative approach has much greater potential, for example, for the studies of herbivore communities along successional, altitudinal or other environmental gradients (Novotny *et al.* in press). Replicated studies of herbivores feeding on identical or related plant species in various geographical areas can provide useful insights into the process of assembly of herbivore communities from regional species pools. Regrettably, a pioneering study on the cosmopolitan bracken fern (Lawton *et al.* 1993) has not been followed by similar studies concentrating on other widely distributed plant species or genera. Species-rich pan-tropical genera, such as *Ficus*, *Piper* or *Psychotria*, are promising candidates for such studies (Dyer & Palmer 2004).

4. HOST SPECIFICITY IN HERBIVOROUS GUILDS AND COMMUNITIES

Only a small proportion (27%) of species in herbivore communities feed on a single plant species when alternative congeneric hosts are available (table 1). By contrast, the proportions of species feeding on a single plant genus (48%) and family (58%) are higher and not statistically different from one another. Thus, limits of host plant range tend to coincide with those of plant genera, rather than those of families or higher taxonomic ranks. However, this analysis employed taxonomic ranks as a substitute for plant phylogeny and also ignored numerous methodological discrepancies among individual datasets and is therefore preliminary.

In theory, host specificity comparisons between different herbivore taxa and guilds are straightforward since all herbivores may be sampled simultaneously from identical study plants and sites. However, while some studies include herbivores from several insect orders (table 1), studies of more than one guild on the same hosts are lacking from tropical forests, probably because each guild requires a specific sampling method.

Concealed herbivore guilds are more specialized than those that feed externally on temperate vegetation (Mattson *et al.* 1988). In tropical forests, the average percentage of family specialists decreases among guilds in the sequence: granivores (99%) > leaf-miners (96%) > fructivores (83%) > leaf-chewers (56%) = sap-suckers (56%) > xylophages (24%) > root-feeders (10%) (see table 1). The proportion of genus specialists (but not species specialists) follows the same pattern. With the exception of xylophages, which feed on dead plant material, all endophytic guilds are thus more specialized than the external feeders. These conclusions remain tentative since replicated studies produced inconsistent host specificity estimates in several guilds: xylophagous beetles, leaf-chewing beetles, granivorous beetles and leaf-chewing Orthoptera (table 1). Some of these differences may have been caused by different methods of study, but they emphasize the need for replicated studies.

Although it is believed that larval host plant ranges are more restricted than those of adults, rigorous larval–adult comparisons are rare. This is a notable problem in herbivorous beetles where larvae and adults often belong to different guilds. The species richness (Basset 2001*a*) and host specificity (Ødegaard 2000*b*) of leaf-chewing beetles were studied extensively in tropical forests. However, adults predominate in this guild, while their root-feeding, xylophagous and granivorous larvae are mostly ignored.

Trends in the diversity of species along environmental gradients (e.g. latitudinal or altitudinal) are popular themes for study, whereas analogous trends in the diversity of interactions, including plant–herbivore trophic links, are not (Ollerton & Cranmer 2002). Although there is extensive literature comparing species richness in herbivorous communities at different

Table 1. Host specificity of insect herbivores in tropical forest communities.
(Wherever possible, data for feeding guilds and insect orders (Coleoptera, Diptera, Hemiptera, Lepidoptera, Orthoptera and Phasmatodea, abbreviated by the first letter of their name) are separated. All analyses are based on larval (L) or adult (A) feeding, noted in the L/A column. Host specificity is estimated as the percentage of herbivore species feeding on a single host within a set of three or more plant species that are congeneric (Spp), from different confamilial genera (Gen), and from different families (Fam). Only datasets that included 10 or more herbivore species are considered. Results from multiple datasets originating from the same study are averaged. As far as possible, (A) confamilial genera and different families were each represented by only one plant species (compliance noted by 1 in the A column), (B) only herbivore species with 10 or more feeding records from the analysed set of plants were included (1 in the B column), and (C) all study plants were sampled with equal sampling effort (1 in the C column).)

guild	order	L/A	Fam	Gen	Spp	forest type	country	A–B–C	source
fruit-eating	D	L	83	—	—	lowland perhumid	Papua New Guinea	1–1–0	Novotny *et al.* (in press)
leaf-chewing	C	A	81	64	57	lowland humid seasonal	Panama	0–0–1	Ødegaard (2000*a*)[a]
leaf-chewing	C	LA	22	—	—	lowland perhumid	Guyana	0–0–1	Basset & Charles (2000)
leaf-chewing	CLO	LA	85	48	26	lowland humid seasonal	Panama	0–0–0	Barone (1998)
leaf-chewing	L	L	61	36	6	lowland dry seasonal	Costa Rica	0–0–0	Janzen (2003)
leaf-chewing	C	A	28	14	0	lowland perhumid	Papua New Guinea	1–1–1	Novotny *et al.* (2002*a*)
leaf-chewing	C	A	—	—	26	lowland perhumid	Costa Rica	1–0–0	Marquis (1991)
leaf-chewing	C	LA	—	—	0	lowland perhumid	Costa Rica	1–1–0	Thomas (1990)
leaf-chewing	CLOP	LA	54	—	—	montane perhumid	Papua New Guinea	1–0–1	Basset (1996)
leaf-chewing	L	L	52	37	5	lowland perhumid	Papua New Guinea	1–1–1	Novotny *et al.* (2002*a*)
leaf-chewing	L	L	—	—	21	montane perhumid	Papua New Guinea	1–1–1	Novotny *et al.* (in press)
leaf-chewing	L	L	91	—	60	cerrado savannah/ woodland	Brazil	1–0–1	Diniz & Morais (1997)
leaf-chewing	L	L	—	—	56	lowland perhumid	Costa Rica	1–1–0	Thomas (1990)
leaf-chewing	L	L	—	—	11	lowland perhumid	Costa Rica	1–0–0	Marquis (1991)
leaf-chewing	L	L	—	—	24	lowland and montane	Costa Rica	1–1–0	Janzen & Hallwachs (2004)[b]
leaf-chewing	L	L	73	23	42	lowland perhumid	Costa Rica	1–1–1	Gentry & Dyer (2002)[a]
leaf-chewing	C	A	62	—	—	lowland humid seasonal	Panama	1–1–0	Y. Basset *et al.*[a]
leaf-chewing	OP	LA	0	0	0	lowland perhumid	Papua New Guinea	1–1–1	Novotny *et al.* (2002*a*)
leaf-chewing	O	LA	65	42	—	lowland perhumid	Costa Rica	0–0–0	Rowell (1978)
leaf-mining	CL	L	92	—	—	lowland perhumid	Papua New Guinea	1–1–1	Novotny *et al.*[a]
leaf-mining	CDL	L	100	87	—	lowland humid seasonal	Belize	1–1–0	Lewis *et al.* (2002)[a]
root-feeding	C	L	10	—	10	lowland perhumid	Papua New Guinea	1–1–1	Pokon *et al.* (in press)[a]
sap-sucking	H	LA	—	67	—	lowland dry	Costa Rica	0–0–0	Wood (1984)
sap-sucking	H	LA	—	83	—	lower montane	Costa Rica	0–0–0	Wood (1984)
sap-sucking	H	LA	—	54	—	lowland wet	Costa Rica	0–0–0	Wood (1984)
sap-sucking	H	LA	—	48	—	premontane	Costa Rica	0–0–0	Wood (1984)
sap-sucking	H	LA	63	—	50	lowland humid seasonal	Panama	0–0–0	Loye (1992)

(*Continued.*)

Table 1. (*Continued*.)

guild	order	L/A	Fam	Gen	Spp	forest type	country	A–B–C	source
sap-sucking	H	L	48	80	64	lowland humid seasonal	Panama	1–1–0	Y. Basset *et al.*[a]
seed-eating	C	L	99	91	76	lowland deciduous	Costa Rica	0–0–0	Janzen (1980)
seed-eating	C	L	—	—	30	various lowland	Brazil	1–0–0	Hopkins (1983)
seed-eating	CL	L	—	—	13	lowland perhumid	Malaysia	1–1–0	Nakagawa *et al.* (2003)
wood-boring	C	L	39	18	7	lowland seasonal	French Guiana	0–0–0	Tavakilian *et al.* (1997)
wood-boring	C	L	8	20	9	lowland perhumid	Papua New Guinea	1–1–1	L. Cizek[a]
wood-boring	C	L	—	60	—	lowland seasonal	French Guiana	1–1–1	Berkov & Tavakilian (1999)
average			58	48	27				

[a] Calculated from unpublished data provided by the author(s).
[b] Average from the datasets for herbivores feeding on *Ficus*, *Inga*, *Psychotria* and *Piper*.
The average proportion of species specialists (Spp) is significantly different from the average proportion of genus specialists (Gen) and family specialists (Fam) (ANOVA, $p<0.05$, Tukey comparisons), while there is no difference between the proportion of genus- and family specialists ($p>0.05$).

altitudes (Brehm *et al.* 2003), host specificity comparisons between lowland and montane tropical forests are few (table 1) since lowland forests remain the most popular topic for study (Basset 2001*a*). Steep altitudinal gradients in temperature, rainfall and the abundance of ants (important as predators and mutualists of herbivores) across small geographical distances provide yet unexplored opportunities for the study of host specificity determinants in the tropics.

Whether there is a latitudinal gradient in host specificity between temperate and tropical forests is surprisingly hard to assess given a methodological dichotomy between tropical and temperate research. Almost all information on the host plants of tropical herbivores comes from local community studies on selected plant species (table 1), while even incomplete regional host plant lists are available for only a few taxa (e.g. Fiedler 1995; Flowers & Janzen 1997). By contrast, regional host plant lists for temperate herbivores, detailed particularly for Great Britain and central Europe, have been compiled for over two centuries, while quantitative community studies that include feeding experiments and rearing of larvae (e.g. Futuyma & Gould 1979) are rare. Incongruent methodology represents a serious problem as both host specificity estimates based on community and regional data have their own sets of biases (Ward 1988).

Given that reliable regional host species lists are unlikely to be forthcoming for tropical habitats, there is a need for renewed effort in collecting quantitative host specificity data for herbivorous insects from temperate vegetation. Ideally, such studies should produce quantitative food webs (Godfray *et al.* 1999) that measure the abundance or biomass of both plant and herbivore species as well as the intensity of their trophic interactions. It is important that food web studies are replicated as any tropical/temperate trends are only likely to emerge by analysing what may appear as unnecessary ‘superabundance’ of datasets.

There is no marked difference in host specificity between tropical and temperate butterflies (Fiedler 1995, 1998), although particular lineages may be less (Lycaenidae: Polyommatini; Fiedler 1995) or more specialized (Papilionidae: Scriber 1988) in the tropics than in temperate regions. Bark beetles (Coleoptera: Curculionidae: Scolytinae; Beaver 1979) and treehoppers (Hemiptera: Membracidae; Wood 1984) appear to be less specialized in the tropics than in temperate regions, while a community study of temperate caterpillars (Futuyma & Gould 1979) shows lower host specificity than analogous data from the tropics (Barone 1998; Novotny *et al.* 2002*a*). The limited evidence available indicates that there may be no major increase in host specificity from temperate to tropical herbivore communities. This conclusion, and the recent downward revisions of extremely high estimates of tropical species richness (Basset *et al.* 1996; Ødegaard 2000*b*; Novotny *et al.* 2002*b*), suggests that tropical ecosystems, although different from those temperate in many respects, may not be as species rich as thought previously.

Empirical study of host specificity patterns is only the first step towards the ultimate goal of explaining host plant use by evolutionary and ecological factors. The evolutionary dynamics of host plant selection range from cospeciation between plants and herbivores, through sequential speciation of herbivores following the evolution of their hosts, to multiple colonizations of unrelated plants with similar chemical or other traits (e.g. Becerra 1997; Weiblen 2004). These evolutionary processes generate regional species pools of herbivores that serve as sources for local communities. The composition of communities may be tested against an estimate derived from a random selection from the regional species pool. This approach, already applied to plants (Webb 2000), could be useful in the study of herbivorous communities.

5. CONCLUSIONS

The present review describes the rather unsatisfactory state of current research where the lack of empirical data prevents us from making pan-tropical generalizations on host specificity patterns and their response to the key environmental variables. Rich empirical data are also essential as a source of inspiration for new hypotheses (LaFrankie 1996). As already argued by Godfray *et al.* (1999), there is a serious need for comprehensive quantitative surveys of plant–herbivore food webs in tropical forests that include a sampling effort which is 1–2 orders of magnitude greater than has been customary to date (Novotny *et al.* 2002*c*). Such surveys require a transition from solitary researchers to teams of researchers where ecologists work in synergy with taxonomists, and are supported by local field assistants and parataxonomists (Basset *et al.* 2004).

We thank Héctor Barrios, Lukas Cizek, Lee Dyer, Owen Lewis, Frode Ødegaard and Rapo Pokon for providing their unpublished data. Scott Miller, Lee Dyer and Neil Springate commented on the manuscript. Funding from US National Science Foundation (DEB-02-11591), Czech Academy of Sciences (A6007106, Z5007907), Czech Ministry of Education (ME646), Czech Grant Agency (206/04/0725, 206/03/H034) and Darwin Initiative for the Survival of Species (162/10/030) contributed to our research on host specificity.

REFERENCES

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

Basset, Y. 1992 Host specificity of arboreal and free-living insect herbivores in rain forests. *Biol. J. Linn. Soc.* **47**, 115–133.

Basset, Y. 1996 Local communities of arboreal herbivores in Papua New Guinea: predictors of insect variables. *Ecology* **77**, 1909–1916.

Basset, Y. 2001*a* Invertebrates in the canopy of tropical rain forests—how much do we really know? *Plant Ecol.* **153**, 87–107.

Basset, Y. 2001*b* Communities of insect herbivores foraging on saplings versus mature trees of *Pourouma bicolor* (Cecropiaceae) in Panama. *Oecologia* **129**, 253–260.

Basset, Y. & Charles, E. 2000 An annotated list of insect herbivores foraging on the seedlings of five forest trees in Guyana. *Anais da Sociedade Entomológica do Brasil* **29**, 433–452.

Basset, Y. & Novotny, V. 1999 Species richness of insect herbivore communities on *Ficus* in Papua New Guinea. *Biol. J. Linn. Soc.* **67**, 477–499.

Basset, Y., Samuelson, G. A., Allison, A. & Miller, S. E. 1996 How many species of host-specific insect feed on a species of tropical tree? *Biol. J. Linn. Soc.* **59**, 201–216.

Basset, Y., Charles, E., Hammond, D. S. & Brown, V. K. 2001 Short-term effects of canopy openness on insect herbivores in a rain forest in Guyana. *J. Appl. Ecol.* **38**, 1045–1058.

Basset, Y., Novotny, V., Miller, S. E. & Kitching, R. (eds) 2003 *Arthropods of tropical forests: spatio-temporal dynamics and resource use in the canopy.* Cambridge, UK: Cambridge University Press.

Basset, Y., Novotny, V., Miller, S. E., Weiblen, G. D., Missa, O. & Stewart, A. J. A. 2004 Conservation and biological monitoring of tropical forests: the role of parataxonomists. *J. Appl. Ecol.* **41**, 163–174.

Beaver, R. A. 1979 Host specificity of temperate and tropical animals. *Nature* **281**, 139–141.

Becerra, J. X. 1997 Insects on plants: macroevolutionary chemical trends in host use. *Science* **276**, 253–256.

Berkov, A. 2002 The impact of redefined species limits in *Palame* (Coleoptera: Cerambycidae: Lamiinae: Acanthocinini) on assessments of host, seasonal, and stratum specificity. *Biol. J. Linn. Soc.* **76**, 195–209.

Berkov, A. & Tavakilian, G. 1999 Host utilization of the Brazil nut family (Lecythidaceae) by sympatric wood-boring species of *Palame* (Coleoptera, Cerambycidae, Lamiinae, Acanthocinini). *Biol. J. Linn. Soc.* **67**, 181–198.

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.

Brehm, G., Sussenbach, D. & Fiedler, K. 2003 Unique elevational diversity patterns of geometrid moths in an Andean montane rainforest. *Ecography* **26**, 456–466.

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

Coley, P. D. & Barone, J. A. 1996 Herbivory and plant defenses in tropical forests. *Annu. Rev. Ecol. Syst.* **27**, 305–335.

Condit, R., Hubbell, S. P. & Foster, R. B. 1996 Changes in tree species abundance in a neotropical forest: impact of climate change. *J. Trop. Ecol.* **12**, 231–256.

Diniz, I. R. & Morais, H. C. 1997 Lepidoptera caterpillar fauna of cerrado host plants. *Biodivers. Conserv.* **6**, 817–836.

Dyer, L. A. 1995 Tasty generalists and nasty specialists—antipredator mechanisms in tropical lepidopteran larvae. *Ecology* **76**, 1483–1496.

Dyer, L. A. & Palmer, A. D. N. (eds) 2004 *Piper: a model genus for studies of phytochemistry, ecology, and evolution.* New York: Kluwer Academic/Plenum Publishers.

Erwin, T. L. 1982 Tropical forests: their richness in Coleoptera and other arthropod species. *Coleopt. Bull.* **36**, 74–75.

Fiedler, K. 1995 Lycaenid butterflies and plants: host–plant relationships, tropical versus temperate. *Ecotopica* **1**, 51–58.

Fiedler, K. 1998 Diet breadth and host plant diversity of tropical- vs. temperate-zone herbivores: south-east Asian and west Palaearctic butterflies as a case study. *Ecol. Entomol.* **23**, 285–297.

Flowers, R. W. & Janzen, D. H. 1997 Feeding records of Costa Rican leaf beetles (Coleoptera: Chrysomelidae). *Florida Entomol.* **80**, 334–366.

Frenzel, M. & Brandl, R. 2001 Hosts as habitats: faunal similarity of phytophagous insects between host plants. *Ecol. Entomol.* **26**, 594–601.

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

Gentry, G. L. & Dyer, L. A. 2002 On the conditional nature of neotropical caterpillar defenses against their natural enemies. *Ecology* **83**, 3108–3119.

Godfray, H. C. J., Lewis, O. T. & Memmott, J. 1999 Studying insect diversity in the tropics. *Phil. Trans. R. Soc. B* **354**, 1811–1824.

Hebert, P. D. N., Ratsingham, S. & Dewaard, J. R. 2003 Barcoding animal life: cytochrome *c* oxidase subunit 1 divergences among closely related species. *Proc. R. Soc. B* **270**(Suppl.), S96–S99.

Hopkins, M. J. G. 1983 Unusual diversities of seed beetles (Coleoptera: Bruchidae) on *Parkia* (Leguminosae: Mimosoideae) in Brazil. *Biol. J. Linn. Soc.* **19**, 329–338.

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

Janzen, D. H. 1980 Specificity of seed-attacking beetles in a Costa Rican deciduous forest. *J. Ecol.* **68**, 929–952.

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. F. B. I. Golley), pp. 167–182. Amsterdam: Elsevier.

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, UK: Cambridge University Press.

Janzen, D. H. & Hallwachs, W. 2004 Caterpillar rearing voucher databases for the Area de Conservación in northwestern Costa Rica. Published at http://janzen.sas.upenn.edu/caterpillars/database.htm.

Kelly, C. K. & Southwood, T. R. E. 1999 Species richness and resource availability: a phylogenetic analysis on insects associated with trees. *Proc. Natl Acad. Sci. USA* **96**, 8013–8016.

Kursar, T. A. & Coley, P. D. 2003 Convergence in defense syndromes of young leaves in tropical rainforests. *Biochem. Syst. Ecol.* **31**, 929–949.

LaFrankie, J. V. 1996 The contribution of large-scale forest dynamic plots to theoretical community ecology. In *Biodiversity and the dynamics of ecosystems,* vol. 1 (ed. I. M. Turner, C. H. Diong, S. S. L. Lim & P. K. L. Ng), pp. 63–79. Singapore: National University of Singapore.

Lawton, J. H., Lewinsohn, T. M. & Compton, S. G. 1993 Patterns of diversity for insect herbivores on bracken. In *Species diversity in ecological communities. Historical and geographical perspectives* (ed. R. E. Ricklefs & D. Schluter), pp. 178–184. Chicago, IL: University of Chicago Press.

Leps, J., Novotny, V. & Basset, Y. 2001 Effect of habitat and successional optimum of host plants on the composition of their herbivorous communities: leaf-chewing insects on shrubs and trees in New Guinea. *J. Ecol.* **89**, 186–199.

Lewinsohn, T. M. 1991 Insects in flower heads of Asteraceae in southeast Brazil: a case study on tropical species richness. 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. 525–559. New York: Wiley.

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

Loye, J. E. 1992 Ecological diversity and host plant relationships of treehoppers in a lowland tropical rainforest (Homoptera: Membracidae and Nicomiidae). In *Insects of Panama and MesoAmerica* (ed. D. Quintero & A. Aiello), pp. 280–289. Oxford, UK: Oxford University Press.

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. New York: Wiley.

Mattson, W. J., Lawrence, R. K., Haack, R. A., Herms, D. A. & Charles, P.-J. 1988 Defensive strategies of woody plants against different insect-feeding guilds in relation to plant ecological strategies and intimacy of association with insects. In *Mechanisms of woody plant defenses against insects: search for pattern* (ed. W. J. Mattson, J. Levieux & C. Bernard-Dagan), pp. 1–38. New York: Springer.

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.

Nakagawa, M. *et al.* 2003 Resource use of insect seed predators during general flowering and seeding events in a Bornean dipterocarp rain forest. *Bull. Entomol. Res.* **93**, 455–466.

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., 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.

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

Novotny, V., Basset, Y., Miller, S. E., Kitching, R., Laidlaw, M., Drozd, P. & Cizek, L. 2004*a* How many insect species feed on woody plants from one hectare of a lowland rainforest? *Conserv. Biol.* **18**, 227–237.

Novotny, V., Miller, S. E., Basset, Y., Cizek, L., Kaupa, B., Kua, J. & Weiblen, G. D. In press. An altitudinal comparison of caterpillar (Lepidoptera) assemblages on *Ficus* trees in Papua New Guinea. *J. Biogeogr.*

Novotny, V., Miller, S. E., Leps, J., Bito, D., Janda, M., Hulcr, J., Basset, Y., Damas, K. & Weiblen, G. D. 2004*b* No tree an island: the plant–caterpillar food web of secondary rainforest in New Guinea. *Ecol. Lett.* **7**, 1090–1100.

Novotny, V., Clarke, A. T., Drew, R. A. I., Balagawi, S. & Clifford, B. 2005 Host specialization and species richness of fruit flies (Diptera: Tephritidae) in a New Guinea rainforest. *J. Trop. Ecol.* **21**, 67–77.

Ødegaard, F. 2000*a* The relative importance of trees versus lianas as hosts for phytophagous beetles (Coleoptera) in tropical forests. *J. Biogeogr.* **27**, 283–296.

Ødegaard, F. 2000*b* How many species of arthropods? Ervin's estimate revised. *Biol. J. Linn. Soc.* **71**, 583–597.

Ødegaard, F. 2004 Species richness of phytophagous beetles in the tropical tree *Brosimum utile* (Moraceae): the effects of sampling strategy and the problem of tourists. *Ecol. Entomol.* **29**, 76–88.

Ollerton, J. & Cranmer, L. 2002 Latitudinal trends in plant–pollinator interactions: are tropical plants more specialised? *Oikos* **98**, 340–350.

Pokon, R., Novotny, V. & Samuelson, G. A. In press. Host specialization and species richness of root feeding chrysomelid larvae (Chrysomelidae, Coleoptera) in a New Guinea rainforest. *J. Trop. Ecol.*

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

Rowell, H. F. 1978 Food plant specificity in neotropical rainforest acridids. *Entomol. Exp. Appl.* **24**, 651–662.

Scoble, M. J., Gaston, K. J. & Crook, A. 1995 Using taxonomic data to estimate species richness in Geometridae. *J. Lep. Soc.* **49**, 136–147.

Scriber, J. M. 1988 Tale of the tiger: Beringial biogeography, binomial classification, and breakfast choices in the *Papilio glaucus* complex of butterflies. In *Chemical mediation of coevolution* (ed. K. C. Spencer), pp. 241–301. New York: Academic Press.

Shanahan, M., Harrison, R. D., Yamuna, R., Bowen, W. & Thornton, I. W. B. 2001 Colonization of an island volcano, Long Island, Papua New Guinea, and an emergent island, Motmot, in its caldera lake. V. Colonization by figs (*Ficus* spp.), their dispersers and pollinators. *J. Biogeogr.* **28**, 1365–1377.

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

Symons, F. B. & Beccaloni, G. W. 1999 Phylogenetic indices for measuring the diet breadths of phytophagous insects. *Oecologia* **119**, 427–434.

Tavakilian, G., Berkov, A., Meurer-Grimes, B. & Mori, S. 1997 Neotropical tree species and their faunas of xylophagous longicorns (Coleoptera: Cerambycidae) in French Guiana. *Bot. Rev.* **63**, 303–355.

Thomas, C. D. 1990 Herbivore diets, herbivore colonization, and the escape hypothesis. *Ecology* **71**, 610–615.

Ward, L. K. 1988 The validity and interpretation of insect foodplant records. *Br. J. Entomol. Nat. Hist.* **1**, 153–161.

Ward, L. K., Hackshaw, A. & Clarke, R. T. 1995 Foodplant families of British insects and mites: the influence of life form and plant family. *Biol. J. Linn. Soc.* **55**, 109–127.

Webb, C. O. 2000 Exploring the phylogenetic structure of ecological communities: an example for rain forest trees. *Am. Nat.* **156**, 145–155.

Webb, C. O., Ackerly, D. D., McPeek, M. A. & Donoghue, M. J. 2002 Phylogenies and community ecology. *Annu. Rev. Ecol. Syst.* **33**, 475–505.

Weiblen, G. D. 2004 Correlated evolution in fig pollination. *Syst. Biol.* **53**, 1–12.

Weiblen, G. D., Webb, C. O., Novotny, V., Basset, Y. & Miller, S. E. In press. Phylogenetic dispersion of host use in a tropical insect herbivore community. *Ecology.*

Wood, T. K. 1984 Life history patterns of tropical membracids (Homoptera: Membracidae). *Sociobiology* **8**, 299–344.

Wright, S. J. 2002 Plant diversity in tropical forests: a review of mechanisms of species coexistence. *Oecologia* **130**, 1–14.