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Herbivore assemblages and their food resources

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ABSTRACT

Ultimately, all communities are limited by the resources available to them, but the process of matching the supply and demand sides in rainforest ecosystems is rarely straightforward. When live plants or animals are exploited as resources, the pattern of their use is a particularly complex result of the interplay between adaptations on the part of predators or parasites and the counter-adaptations of their potential prey or host species. This phylogenetical component is further modified by often equally complex patterns of resource availability in space and time, resulting from contemporaneous ecological processes. Rainforest canopies contain an exceptionally rich array of organic resources for an equally diverse number of consumers, thereby constituting a very attractive as well as difficult field for study. We review briefly the main methodological approaches, results and remaining challenges in this field of study, focussing primarily on ecological aspects of the plant–herbivore, host–parasitoid and prey–predator interactions and their importance in shaping invertebrate assemblages in the rainforest canopies of three continents.

INTRODUCTION

The canopies of tropical rainforests provide a vast array of different food resources to arthropods. Since forest canopies are the principal site of energy assimilation by primary production (e.g. Lowman & Nadkarni, 1995), they are particularly attractive to phytophagous arthropods (mostly insects and mites). One can further argue that plant resources and the arthropods that feed on them in the canopy can be more conveniently studied than any other arthropod-resource system in this habitat, perhaps with the exception of fungi and fungal-feeders. For example, leaf-chewing species can be collected alive and tested on a variety of potential food plants (e.g. Basset & Novotny, 1999; Novotny *et al.*, 1999b). Without doubts, there are problems associated with determining the diet of larvae and adults, respectively, but these problems (see below) are common to most arthropod taxa.

This chapter discusses the plant resources available to insect herbivores in the canopy of tropical forests. As the authors are most familiar with this category of herbivores, we will refrain from referring explicitly to phytophagous mites, although some of the items discussed here may also apply to this group. Ecological information about phytophagous mites in tropical canopies is rather scarce and mostly originates from Australia (e.g. Walter *et al.*, 1994, 1998; Walter & O'Dowd, 1995; Walter & Behan-Pelletier, 1999).

We will first concentrate on the different types of canopy resource available and their characteristics. We discuss briefly resource patchiness by considering its spatial and temporal availability within the canopy. A number of problems are associated with the study of insect herbivores in tropical canopies. For example, our knowledge of insect/plant use in the canopy is greatly constrained by two main factors: plant phylogeny and the spatial distribution of the herbivores themselves. We will then discuss more particularly the constraints on the ecological specialization of insect herbivores and review patterns of host specificity, as they are currently understood. We conclude by providing some suggestions on how our current knowledge of insect–plant interactions in the canopy of tropical forests may be improved.

TYPE AND AVAILABILITY OF RESOURCES IN THE CANOPY

The main plant resources used by insect herbivores in canopies and their characteristics are summarized in Table 5.1. These may be classified according to the plant parts (tissues) and plant life-forms available to insects in the canopy. Sap is understood here as a liquid carried by vascular tissues, such as in the phloem and xylem vessels. The sap in mesophyll tissues represents the contents

Table 5.1. *The main plant resources used by insect herbivores and their availability in the canopy of tropical forests*

Plant part	Spatial availability	Temporal availability	Insect taxa[a]	References
Leaves				
Trees	High but depends on the relative palatability and toughness of mature and young foliage	Restricted for young foliage; depends on tree phenology and successional status	Some Orthoptera, Lepidoptera, Phasmida, Chrysomelidae some Curculionidae, *Atta*, etc.	Coley, 1983; Basset, 1996; Basset & Novotny, 1999; Ødegaard, 2000a
Lianas	High, same as above	As above but higher than for trees because of often rapid growth	As above	Benson *et al.*, 1976; Ødegaard, 2000a
Vascular epiphytes	Patchy, depends on support trees	Probably restricted as mature leaves of many species are tough	Lepidoptera, Curculionidae, etc.	Brévignon, 1990, 1992; Frank, 1999
Nonvascular plants	As above?	Probably not as restricted as above	Lithosiinae, Tingidae	Drake & Ruhoff, 1965
Sap[b]				
Trees	High	High, but may vary in quality because of translocation events	Homoptera, some Heteroptera Thysanoptera[c], *Atta*, etc.	Novotny, 1993; Novotny & Leps, 1997; Basset, 1991d
Lianas	High	High, may be of high quality compared with that of trees	As above, in particular Membracidae	Blüthgen *et al.*, 2000a
Vascular epiphytes	Patchy	Relatively high?	As above	Blüthgen *et al.*, 2000a
Flowers				
Trees	Patchy	Patchy	Apidae, Agaonidae Curculionidae, Chrysomelidae, Lepidoptera	Roubik, 1989; Compton & Hawkins, 1992 Basset & Samuelson, 1996
Lianas	Patchy	Patchy	As above	Ødegaard, 2000a
Vascular epiphytes	Probably low?	Probably low?	As above	Singer & Cocucci, 1999
Seeds/fruits				
Trees	Patchy	Patchy to low, depends on supra-annual phenology	Lepidoptera, Bruchinae, Curculionidae, some Diptera, etc.	Janzen, 1971a; Hopkins, 1983; DeVries *et al.*, 1997
Lianas	Patchy	As above?	As above	Ødegaard, 2000a
Vascular epiphytes	Probably low?	Probably low?	As above	–
Stems[d]				
Trees	High for dead wood of small branches	May depend on stochastic events such as treefall, wind break, etc.	Cerambycidae, Curculionidae, Scolytinae, etc.	Tavakilian *et al.*, 1997; Jordal & Kirkendall, 1998
Lianas	High for soft tendrils	High for soft tendrils	As above, plus Baridinae and Chlamisinae for tendrils	Ødegaard, 2000a
Vascular epiphytes	Low	Low	As for trees, above	–

[a]Refers to known examples of taxa feeding on these resources, with particular reference to canopy studies in the tropics.

[b]Phloem and xylem sap (see text).

[c]Most feed on mesophyll tissues (see text).

[d]Including live and dead bark, cambium and inner wood.

of mesophyll cells, which are exploited by various taxa (most Thysanoptera and Typhlocybinae: Novotny & Wilson, 1997). In essence, it is identical to the leaf resources exploited by leaf-chewing species, with the exception of the selective avoidance of certain parts of the leaf (e.g. lactifers). Indeed, factors affecting the local species richness of leaf chewers and mesophyll-feeders appear similar on certain host plants, such as *Ficus* spp. (Basset & Novotny, 1999). For the sake of simplicity, we also consider the 'stem' resource as including bark, cambium and heartwood.

The main differences among the plant resources provided by temperate and tropical forests are the much higher occurrence of lianas and vascular epiphytes in the latter (e.g. Gentry & Dobson, 1987; Nieder *et al.*, 2001). This has important consequences for many arthropod species, including insect herbivores, leading to an enhanced local species richness (Stuntz *et al.*, 1999; Ødegaard, 2000a; Chs. 17 and 21). Liana abundance and biomass in tropical forests increase on nutrient-rich soils and with forest disturbance (Laurance *et al.*, 2001). Thus, the magnitude of these effects may be optimal in dry forests exposed to disturbance, as within the crane perimeter studied by Ødegaard (2000a) in Panama. In addition, it is very possible that the proportion of dead suspended wood in the canopy of tropical forests may also be higher than that in temperate forests. For example, in Central Amazonian forests, the biomass of dead wood on the forest floor varies from 1.8 to 33.0 ton (dry weight) ha^{-1}. There are a further 1.1 to 7.6 ton ha^{-1} represented by standing dead trees and 1.1 to 45.6 ton ha^{-1} represented by dead suspended wood (Martius & Bandeira, 1998). Connell *et al.* (1997) have also argued that 'subcanopy' (midcanopy) gaps, created by dead standing trees in the subcanopy, are commonplace in rainforests. Hence, the amount of dead suspended or standing wood temporarily available to xylophagous insects is likely to be considerable in such forests. In particular, this resource may increase the availability of habitats for wood-eating taxa able to develop in branches of small diameter (e.g. *Agrilus* spp., Curletti, 2000). Parenthetically, we note that the few remaining 'old-growth' temperate forests may also have substantial amounts of suspended dead and dying wood in their canopies.

The spatial distribution of these various plant resources is heterogeneous in the canopy (Table 5.1). Although leaves are plentiful in the canopy, most of them may be unsuitable, or at least suboptimal, for insect herbivores, as they may be too tough or unpalatable. Leaf availability may depend on the relative differences in palatability to insects between mature and young leaves. Many insect herbivores strongly prefer young over mature foliage, resulting in higher damage on younger than more mature leaves (e.g. Coley, 1983) and/or an aggregated insect distribution on young foliage (e.g. Basset, 1991d, 1996). Even, for example, on *Pourouma bicolor* Martius (Cecropiaceae) in Panama, a pioneer tree supposedly palatable (Coley, 1983), 95% of its associated leaf-chewing species are only able to attack young foliage (Basset, 2001a). There are, of course, many exceptions to this pattern. First, many leaf-mining and galling species are able to develop in mature leaves, sustaining a low growth rate but to some extent avoiding predators and parasitoids (e.g. Faeth, 1980). Second, large leaf-chewing insects with strong mandibles, such as some Orthoptera, Phasmida or Lepidoptera, may be able to cut through relatively tough mature foliage, (e.g. Saturniidae: Bernays & Janzen, 1988). In the same manner, some sap-sucking insects may be able to insert their stylets and feed on relatively tough tissues, such as phloem and xylem vessels (Pollard, 1968). Last, aggregation of conspecifics and collective feeding may overcome the initial toughness of leaves (e.g. Morris *et al.*, 1996).

The diversity and abundance of epiphytes in the canopy can sometimes be very high. For example, 109 species of epiphytes were growing on 20 m^2 of branch surface of several neighbouring trees in Ecuador (Nowicki, 1998). However, the ratio of epiphyte species to the total number of vascular plants, the epiphytic index, varies greatly among biogeographical regions. The epiphytic index, for example, is usually much higher in the neotropics than in Africa (Niedler *et al.*, 2001). The local occurrence of epiphytes also depends greatly on a variety of factors, such as rainfall, cloud cover, microclimatic gradients and host-tree structure, and epiphytes are particularly abundant in montane tropical forests (Niedler *et al.*, 2001). Nevertheless, their interactions with arthropods, and specifically with insect herbivores, have rarely been studied explicitly (e.g. Benzing, 1983; Lowman *et al.*, 1996, 1999; Schmidt & Zotz, 2000).

Live wood is rarely attacked by insects and where this does occur it usually involves the action of gall-making insects or bark beetles (e.g. Dajoz, 1980).

However, meristem feeders are more common and many bore into flower stalks, buds or young shoots. Likewise, the stems and tendrils of lianas represent important resources for tropical insects in the canopy (Ødegaard, 2000a). Dead suspended wood is exploited by many taxa, mostly beetles. Newly dead wood has a short persistence, and saproxylic beetles associated with this habitat may be more prone to disperse than counterparts inhabiting more decomposed wood (such as in the hollow trunks of living trees), which may persist for a longer period (Ranius & Hedin, 2001; see also Ch. 26).

The availability in time of these various resources to insect herbivores also differs (Table 5.1). The production of young foliage on trees greatly depends on their successional status, phenology and on rainfall (e.g. Coley, 1983). Rapid growth and high productivity in lianas, on the one hand, ensures that their leaves, stems and tendrils are available to insect herbivores most of the year (Hegarty & Caballé, 1991). On the other hand, the mature leaves of many vascular epiphytes are relatively tough and thick, and their leaf production is rather low (Zotz, 1995), so that they may be far less attractive to insect herbivores than are lianas. High-quality sap may also be difficult to track for sap-sucking insects and may be related to translocation of nitrogen, in leaves, flowers or seeds. Basset (1991d), for example, indicated that specialist psyllids attack different tissues of high nitrogen content, such as young foliages and flowers, on one species of rainforest tree in Australia. The occurrence of flowers, and particularly of fruits and seeds, in the canopy may represent the most difficult resource to track for insect herbivores. Setting aside specialized, presumably coevolved, pollinators, many flower visitors are not highly specific (e.g. Ødegaard, 2000a; Ch. 23). Accordingly, at least for generalist herbivores feeding on flowers (many Membracidae, Chrysomelidae, Curculionidae, etc.), it should not be too difficult to locate suitable resources, especially if the herbivores are reasonably good fliers (Chrysomelidae) or are dispersed and attended by ants (Membracidae). Locating adequate seeds or fruits, especially if their production is not annual, appears to be harder. Complex diapauses dependent on host phenology may be required to exploit these resources, as is known to occur in some temperate insect herbivores (e.g. Roques, 1988). To date, very little is known about such nonannual resources in the canopy of tropical rainforests and the insects that may thrive on them – with the possible exception of mass flowering of dipterocarps pollinated by thrips in south-east Asia (e.g. Appanah, 1993; see also Ch. 4).

Perhaps the most obvious difference in terms of temporal availability of resources between the canopies of tropical and temperate forests is the higher predictability of these resources in the temperate forests. Consider tree leaves: temperate forests show a predictable succession of phenological events broadly synchronous among species, starting with bud break in spring and ending with senescence and leaf fall in autumn. This leads to a distinct succession of suites of insect herbivores during the course of the year (e.g. Dixon, 1976). In tropical forests, the diversity of plant species, their asynchronous phenology and their responses to climatic factors are such that such distinct patterns are unlikely to occur. However, patterns of leaf damage and herbivore activity may be more predictable in locations with well-marked dry seasons than in perhumid locations: compare Panama (Aide, 1992; Ch. 25), New Guinea (Novotny & Basset, 1998) and Guyana (Basset, 2000).

In addition to the higher specific variety of leaves and the coexistence of young and mature leaves for longer periods in the canopies of tropical forests, there is another important distinction differentiating them from temperate canopies. This relates to vertical structuring. Vertical complexity and stratification is higher in tropical forests than in temperate forests (Smith, 1973; Terborgh, 1985); in particular, vertical gradients in microclimatic and biotic gradients are much steeper in tropical rainforests than in temperate forests (e.g. Parker, 1995; Hallé, 1998). The quality of sunny and shaded leaves in tropical rainforests is, therefore, likely to differ substantially, even across conspecific plants. In wet tropical rainforests, this results not only in distinct faunas of herbivores foraging in the upper canopy and understorey, respectively (e.g. Amédégnato, 1997; Basset *et al.*, 2001a), but also in different herbivore assemblages feeding on conspecific seedlings/saplings and mature trees (Basset *et al.*, 1999; Basset, 2001a; Ch. 25). Note that studies relying largely on the examination of leaf damage are unable to demonstrate these faunal differences (e.g. Barone, 2000). Extreme heterogeneity in vertical abiotic and biotic gradients, such as in tall, closed, wet and tropical rainforests, may lead to a specialized herbivore fauna being restricted to the upper canopy layer (Basset *et al.*, 2001a; Ch. 3). Much of this paragraph has concerned leaves but similar arguments may

also apply to the quality of sap in the canopy of tropical forests.

To close this section, it is tempting to classify food resources according to their variability in carrying capacity over time or space. On the one hand, a large variability in carrying capacity over time (e.g. in the mass production of flowers or seeds) increases the benefit of dispersal and would select for a higher degree of mobility in insect consumers. On the other hand, a large variability in carrying capacity over space (e.g. in the occurrence of epiphytes or dead wood) would rather select for more resident individuals as, on average, dispersal would result in an individual reaching an environment worse than that it originated from (Ranius & Hedin, 2001). In turn, a large variability in carrying capacity over space could in some instances select for host-specificity in insects, while a large variability in carrying capacity over time could select for less-specialized species. However, since food resources in tropical canopies vary notoriously both in time and space (Table 5.1), the significance of this variability for insect herbivores remains difficult to evaluate. For example, one may predict that herbivores able to feed on mature leaves of epiphytes should be rather host specific, but data are presently lacking to evaluate this proposition.

ARE THERE KEYSTONE RESOURCES FOR INSECT HERBIVORES IN THE CANOPY?

Before attempting to answer this question, we need to discuss what might be the most commonly used plant resources in the canopy. It is difficult to answer this directly, but we can consider, as a guide, the number of species of insect herbivores restricted to particular resources (guilds), and the number of such species represented in large-scale collections from rainforest canopies (see Basset, 2001b for a list of such datasets). This compilation indicates that, among herbivores and in order of decreasing importance, Curculionidae, Lepidoptera, Chrysomelidae, Thysanoptera and Homoptera are often species rich in the canopy. The order of this list, of course, depends greatly on the aims of each study and the availability of taxonomic expertise to sort the material. However, if it has at least some relevance to the biological reality, then it suggests that leaves, sap and perhaps flowers (upon which many Curculionidae and Chrysomelidae feed) represent the most common resources used by insect herbivores in the canopy. Most likely, the young leaves of trees may be the most commonly used resource, but they could be locally supplanted by young leaves of lianas, which may be available for longer periods in the canopy. This generalization is complicated by issues related to leaf palatability and the local occurrence of confamilial or congeneric hosts (Novotny *et al.*, 2002a).

In considering the likely occurrence of keystone resources and the plant species that could provide them, we note that similar resources may be keystone in certain locations and not in others. For example, *Ficus* spp. are often considered as a keystone resource for canopy animals in the neotropics (Terborgh, 1986) and Malaysia (Lambert & Marshall, 1991), but not in Africa (Gautier-Hion & Michaloud, 1989) or in New Guinea (Basset *et al.*, 1997a). In the last study, the overlap of herbivores across *Ficus* spp. was high and precluded considering the leaves or figs of any particular species as a keystone resource. Despite many species of *Cecropia* being inhabited by ants, this genus has been deemed 'the most hospitable tree of the tropics' (Skutch, 1945). Many animal species feed on its leaves, nectar and inflorescences, food bodies and on the ants themselves. Despite being pioneer trees, the leaves of *Cecropia* ssp. are not highly palatable to insect herbivores (Y. Basset & H. Barrios, unpublished data) and these species do not support an unusually high species richness of folivorous insects (Y. Basset, personal observation). Examples such as these could be multiplied. We conclude that if keystone resources for insect herbivores do exist in the canopy of tropical forests, they are likely to be related to leaf resources and, most likely, will be of only local importance.

METHODOLOGICAL PROBLEMS IN THE STUDY OF RESOURCE USE BY HERBIVORES

Herbivore 'communities' as they are usually studied represent ensembles *sensu* Fauth *et al.* (1996): that is, sets of species delimited by their common phylogeny (they are insects), use of resources (feeding on plants) and physical location (in a forest canopy). These ensembles are intersections of three principally different species groups: taxa (groups of species of common descent), guilds (groups of species that exploit the same class of environmental resource in a similar way) and communities (groups of species occurring in the same place at the same time). These ensembles invite further dissection

with regard to their phylogeny, resource use and spatio-temporal distribution.

Herbivore phylogeny and studies of resource use

Phylogeny shapes not only the composition of herbivore assemblages but also the way they are studied. Even primarily ecological studies are often limited in their scope to certain taxa, rather than guilds, usually for methodological rather than logical reasons. For instance, 23 of the 30 contributions amenable to comparison in this volume focussed primarily on taxa, rather than guilds. This is perhaps inevitable, but we should be at least aware of the fact that the taxonomic tradition shapes our knowledge of rainforest ecosystems as it makes some ecological interactions more likely and others less likely to be studied – which may bear little relationship to their 'real' importance.

Ecological relationships across taxa of herbivores, where each requires a different method of study, are particularly poorly known. For instance, lepidopteran caterpillars and leaf-cutter ants are perhaps the two most important taxa of insect herbivores (as measured by their leaf damage) in Neotropical rainforests (Barone, 1998; Leigh, 1999); however, as far as we are aware, there is no study addressing their mutual interactions in a rainforest ecosystem. Similarly poorly explored are interactions between insect and vertebrate herbivores competing for leaf resources in rainforests (however, see Estrada & Coates-Estrada, 1986). Seed predation by vertebrates and invertebrates is perhaps a well-known exception to this pattern (e.g. Janzen, 1971a; Lamprey *et al.*, 1974), originating from long-term interests in rainforest regeneration.

In contrast, many studies focus on groups of species that do not represent any coherent ecological or evolutionary units. For instance, modern analyses have demonstrated that the Auchenorrhyncha, a favourite group for ecological studies (e.g. Wolda, 1979; Novotny, 1993), is not monophyletic (Sorensen *et al.*, 1995). It includes species from three different guilds, phloem-, xylem- and mesophyll-feeders (Novotny & Wilson, 1997), and some of these guilds are of multiple evolutionary origin, either within the Auchenorrhyncha (xylem-feeders) or elsewhere (the two other guilds). A similarly questionable unit for ecological analysis is the microlepidoptera. Ecological analyses of such groups are difficult to interpret, as they are neither taxa nor guilds. Ecological patterns, such as body size distribution, can often be analysed only when these groups are further divided into separate taxa or guilds (Novotny & Basset, 1999; Hodkinson & Casson, 2000).

There is a great imbalance in our level of knowledge among taxonomic groups in the canopy. Coleoptera is by far the most often studied arthropod order (Basset, 2001b). Likewise, 8 out of 12 contributions dealing with specific herbivore taxa in this volume focus on beetles. We can only guess at our overall level of ignorance of insect–plant interactions in the canopy, given such an overwhelming reliance on studies of Coleoptera. Consider, for example, the full tally of species likely to be herbivorous within a large and relatively well-known area such as Australia (which extends well into the tropical zone). We summed 14 300 species of beetles likely to be herbivores and 21 400 species of non-beetle herbivores (from the Lepidoptera, Hemiptera, Orthoptera, etc.) in Waterhouse (1991). The actual numbers may be influenced by a range of factors, not all of which are biological, that are themselves unimportant. The main point is that there is a far from negligible fraction of herbivores in the canopy that is not beetles, and we should also attempt to study this fraction. How many studies to date, for example, have reported on canopy tortricids or cicadellids in the tropics?

Resource use and spatial distribution of herbivores

Many studies of resource use by herbivores are unduly restricted to a particular habitat, even where the herbivores they study use resources from several habitats. This is particularly frequent in habitats that require specific methods of study or access, including the canopies of rainforests. This is an important bias in the study of canopy herbivores, which are often dependent on extracanopy resources or environments during a part of their life cycle.

As already emphasized, beetles rank as one of the most popular foci in the studies of rainforest insects, particularly by canopy fogging techniques (e.g. 9 from 14 assemblage studies in Stork *et al.* (1997a) were restricted to beetles). Numerous studies addressed their local species richness (Erwin & Scott, 1980; Basset *et al.*, 1996a; Ødegaard *et al.*, 2000; Missa, 2000), β-diversity (Allison *et al.*, 1997), host specificity (Mawdsley & Stork, 1997; Ødegaard *et al.*, 2000,

Ch. 29), colonization dynamics (Floren & Linsenmair, 1998a) or patterns of body size (Morse *et al.*, 1988). All this effort, however, has been concentrated almost exclusively on the adults, which are often the only life stage present in the canopy (Basset & Novotny, 1999; Novotny *et al.*, 1999b). Resource utilization by adults of herbivore beetles in the canopy can be of rather marginal importance compared with that by their larvae, which develop in wood, flowers, seeds or roots. Some of these larval resources may be present in the canopy but an appreciable proportion of beetle larvae must originate from dead wood and roots in the understorey and soil. Further, there is an indication that some adult beetles may not feed at all in the canopy (Y. Basset & H. Barrios, unpublished data). Therefore, larvae, as the more host-specific stage, are conceivably the key stage to be studied if we want to understand the composition and dynamics of canopy beetles, despite the fact that they only rarely reside in the canopy. Unfortunately, larval biology is particularly poorly known for beetle herbivores in rainforests (Jolivet & Hawkeswood, 1995; Tavakilian *et al.*, 1997). A redirection of effort may be indicated, for example to lepidopteran herbivores where the larvae are clearly visible, can be readily collected and can be bred through to produce identifiable adults.

In the tropics, congeneric species of herbivores may sometimes have quite different life histories and/or forage in different habitats (e.g. Basset *et al.*, 2001b). Accordingly, it is difficult to provide a list of the most common higher taxa that are most likely to be restricted to the canopy in both their larval and adult stages. Many (but not all) Eumolpinae, Galerucinae, Alticinae, and Entiminae feed on roots as larvae and are, therefore, unlikely to fall into this category. Most Cerambycidae, Anthribidae, Brentidae, Cossoninae, Molytinae, Zygopinae, Scolytinae and Platypodinae feed on wood and/or fungi. They may breed either in the dead wood of the understorey or litter or in the dead suspended wood of the canopy. The final category of taxa is most likely to have representatives associated with the canopy throughout their life cycle: the Hispinae (leaf-rollers/miners), Attelabidae (leaf-rollers), Chlamisinae (stem feeders), Baridinae (stem and flower feeders), Anthonominae, Tychiinae (flower feeders), Bruchinae and Curculioninae (seed eaters). Note that a speciose taxon such as the Cryptorhynchinae defies such crude classification, its members feeding on a variety of resources (sources for larval food resources: Anderson, 1995; Jolivet & Hawkeswood, 1995). Turning from the Coleoptera, the Derbidae, one of the most species-rich hemipteran families on rainforest vegetation (Casson & Hodkinson, 1991), can be found in the canopy only as adults while their immatures, suspected to be fungal-feeders (O'Brien & Wilson, 1985), are virtually unknown. Similarly, the nymphs of the most abundant species of sap-sucking insect present in the canopy of mature *Pourouma bicolor* trees in Panama, *Bebaiotes* sp. (Achilixiidae), are also unknown and may well live in the understorey or litter (Basset, 2001a).

It is clear that canopy assemblages of herbivorous insects cannot be studied in isolation from those of other parts of the rainforest ecosystem. It is unfortunate and ironical that most canopy studies target Coleoptera, a taxon including many representatives not restricted to the canopy habitat throughout their life cycle. Other taxa of insect herbivores may either feed during their whole life cycle in the canopy (presumably most Thysanoptera, Hemiptera and Orthoptera) or feed as larvae in the canopy with subsequent small intake of food as adults in the canopy also (presumably most Lepidoptera and Diptera).

Numerous studies infer resource use by canopy insects from their spatial distribution in the rainforest, rather than from direct observation of their feeding habits. This approach is often chosen more for convenience than any other reason. However, the diverse rainforest vegetation is particularly unsuitable for such inferences concerning usually highly mobile insect herbivores. For example, capture–recapture studies of butterflies yielded average dispersal distances from one to several hundreds of metres (Scott, 1975; Mallet, 1986; Novotny *et al.*, 1991) and these are probably underestimates. Fig wasps, thought to be poor fliers, may disperse distances up to 10 km (Nason *et al.*, 1996). Colonization by herbivores of isolated *Passiflora* plants located 50 m away from conspecifics was as rapid as those not so isolated (Thomas, 1990b). Although data on herbivore dispersal in rainforests are scarce, it can be safely assumed that each rainforest tree is within dispersal distance of a herbivore fauna from plants growing at least in the surrounding hectare, but most likely from a larger area of the forest. Dispersal distances of only 400 m correspond to a 50 ha area becoming a source of herbivore colonizers as well as of transient 'tourist' species. Three plots of this size from humid

rainforests included respectively 305, 817 and 1171 species of plants with diameter at breast height > 1 cm (Plotkin *et al.*, 2000), not to mention smaller lianas, epiphytes and nonvascular plants. Dispersal of herbivores from such a large number of plant species represents a significant source of noise impeding inference on resource use from spatial distribution of herbivores among plants.

Resource use by herbivores in an ecological context

Most ecological data are contextual: that is, they make sense only in connection with other data. Resource use can be most profitably studied either as the use of the various types of resource (leaves, wood, flowers, seeds, etc.) provided by a single tree (or a population of a single tree species) or as the use of a particular resource across the whole plant community. Ideally, both approaches should be combined, however, in practice, no study has been fully successful in implementing either of these two protocols. Basset (1993) studied various resources in the canopy of a single tree species whereas Janzen (1988a and subsequent unpublished studies) focussed on folivorous caterpillars but included all plant species in a tropical forest. Several other studies of herbivores have selected a subset of local rainforest vegetation, including either closely related species (flower eaters: Compton & Hawkins, 1992; seed eaters: Hopkins, 1983; leaf chewers: Marquis, 1991), distantly related species (seed eaters: Janzen, 1980a; leaf chewers: Basset, 1996; wood borers: Tavakilian *et al.*, 1997), or a mixture of closely, distantly and locally abundant species (leaf chewers: Barone, 1998; Novotny *et al.*, 1999b, 2002a; Ødegaard, 2000a).

The task of studying resource use across many classes of resource on many plant species by many species of herbivore is daunting but is probably the only approach that will bring substantial progress in our understanding of herbivore assemblages in rainforests. Most of the studies to date take a narrow focus targeting specific interactions among a tiny subset of species from the whole ecosystem, which may be interesting in its own right but does not contribute much to the understanding of the whole ecosystem (Godfray *et al.*, 1999). This point is illustrated by recent progress in the study of rainforest vegetation, which has benefited from detailed studies of a large proportion of plant species across relatively large (50 ha) areas (Condit, 1997).

Long-term studies on a relatively large scale are also desirable inasmuch as they are likely to be the best approach to understanding how insect herbivores exploit highly fluctuating resources through time. This subject has been little studied in the canopy and in the tropics in general. Insects specializing on intermittently available resources may finely tune their activities to the phenology of the host, by diapausing if necessary (e.g. Janzen, 1971b; Rockwood, 1974; Denlinger, 1986); switch among other resources within the same host plant, such as young leaves and flowers (e.g. Basset, 1991d); or switch to secondary hosts (cf. Basset, 2000 for seedling insects).

ECOLOGICAL SPECIALIZATION AND RESOURCE USE

Spatial and temporal dynamics of plant resources

The plant's availability, nutritional quality, antiherbivore defences and the associated predators, parasites and competitors are the principal factors circumscribing the plant–herbivore interaction from the viewpoint of the plant (Michaud, 1990). Plant traits must be evaluated in the context of the herbivore's response to them – its efficiency in locating the plant, utilizing the plant's nutrients and its ability to counteract, tolerate or circumvent the plant's defences and the associated parasites, predators and competitors (Novotny, 1994).

The plant's availability to herbivores is determined by its spatial distribution and the temporal variability of its populations. Short-lived plants with unpredictable population dynamics, particularly pioneers in early stages of secondary succession, are colonized, in temperate forests at least, predominately by generalist herbivores (Jaenike, 1990). The temporal variability of plant populations may be less constraining in rainforests, where ecological succession often starts with pioneer trees rather than with annual herbs. Woody pioneers, although short lived compared with other trees, nevertheless represent a sufficiently predictable and 'permanent' resource to be colonized by specialized herbivores (Leps *et al.*, 2001).

Plant rarity may be a more important factor constraining plant use by specialists. Dixon *et al.* (1987) suggested that low species diversity of aphids in the tropics is a result of poor colonization efficiency and

high host specificity of aphids combined with low population density of many plant species in rainforests. An interesting, but unexplored, question is whether this lack of aphids is compensated by higher species richness in other phloem feeders.

Unfortunately, information on herbivore communities on rare plants is limited, as they are particularly difficult to study in rainforests. Most of the studies (e.g. Basset, 1996; Barone, 1998; Basset & Novotny, 1999) are, for practical reasons, focussed on common plant species. Rainforest flora includes many species of epiphytes such as orchids (Gentry, 1990), which are often rare, small in size and sometimes relatively short lived. These species would be prime candidates for the study of the effects of plant abundance on their use by herbivores in the canopy. We await such studies.

Individual plants can escape from specialized herbivores when they grow far from their conspecifics, but such escape may require extremely low population densities for woody plants, which are generally long lived and large (Thomas, 1990b). In contrast, seedlings grow often <100 m from the canopy of their parent tree, but as small resource units separated from the canopy by a steep vertical gradient of microclimatic conditions they host mostly generalist herbivores (Basset, 1999b) at lower densities than in the canopy (Basset *et al.*, 1999). Seeds, which are small and ephemeral resources, can escape from their herbivores more easily when they are isolated; that is, when they disperse far from their parent tree. Seed infestation by a bruchid beetle on *Scheelea* palm seeds, for instance, declined between 16 and 100 m away from the parent tree (Wright, 1983). Mast fruiting represents an efficient means of escape in time by seeds from their predators (Toy *et al.*, 1992) but is relatively rare in rainforests.

Unlike whole plants, specific plant resources exploited by herbivores in the rainforests are often short lived and unpredictable. Young leaves are a high-quality, rare and short-lived resource for herbivores (Scriber & Slansky, 1981; Coley & Aide, 1991) and their availability is an important determinant of species diversity in leaf-chewing communities (Basset, 1996; Basset & Novotny, 1999). The rate of damage to young leaves by herbivores is several times higher than for mature leaves (Coley & Barone, 1996) and is higher in rainforests than in any other forest type (Coley & Aide, 1991). Some rainforest species developed costly strategies, such as delayed greening of expanding leaves, in order to limit their potential for damage by herbivores (Kursar & Coley, 1992). Plants with unpredictable, synchronous production of rapidly expanding and maturing leaves would be expected to be colonized by more generalist communities of herbivores than those with young leaves continuously available, but this proposition remains untested. In support of this, the proportion of specialist herbivores on distantly related species of New Guinean trees depended in part on the availability of young foliage all year round (Basset, 1996).

Plant defences and enemies of herbivores

Tropical vegetation is renowned for its high diversity and incidence of alkaloids (Levin, 1976), latex and other secondary metabolites (Coley & Barone, 1996), but also for a diversity of counter-adaptations by herbivores. For instance, plants with a novel antiherbivore defence – latex and resin canals – were probably temporarily freed from herbivore pressure and diversified more than their sister lineages not possessing this defence (Farrell *et al.*, 1991). A variety of counter-measures, including vein cutting and leaf trenching, which interrupts latex or resin flow, are, however, common among contemporaneous herbivores (Dussourd & Eisner, 1987; Becerra, 1994), and lactiferous rainforest trees, such as *Ficus*, support herbivore communities as diverse as those on nonlactiferous plants (Basset & Novotny, 1999; Novotny *et al.*, 1999b).

Tropical rainforest, and the canopy in particular, is an environment with a high risk of predation, generated mostly by ants (Jeanne, 1979; Olson, 1992; Novotny *et al.*, 1999a). A large proportion of rainforest plants attract ants using extrafloral nectaries (Pemberton, 1998) and obligate ant–plant mutualisms are also common (Jolivet, 1996a). Insect herbivores, that is potential prey, can respond using a variety of defence strategies – the avoidance of enemy-filled space – or succumb to predators. A wide range of these responses are probably common, but we lack a broader picture of how intense pressure from predators shapes herbivore assemblages. Intense foraging by ants can be responsible for a low abundance of externally feeding herbivores (particularly of those that are poorly defended) in rainforest canopies. Externally feeding larvae of beetles are conspicuously missing from rainforest assemblages. Among leaf-beetles, the scarcity of freely feeding

larvae in rainforest canopies results in the prevalence of Eumolpinae, Galerucinae and Alticinae in most assemblages (Stork, 1987a; Farrell & Erwin, 1988; Basset & Samuelson, 1996; Wagner, 1997; Novotny *et al.*, 1999b) since all species of Eumolpinae and many Galerucinae and Alticinae have subterranean, root-feeding larvae (Jolivet & Hawkeswood, 1995). In contrast, approximately 70% of the 560 chrysomelid species from Central Europe have leaf-feeding larvae (Warchalowski, 1985; J. Bezdek, personal communication).

Feeding on roots as larvae may be one strategy developed by beetles to specialize on and stay tuned to the host phenology by using translocation clues in the root tissues, thus predicting the optimum timing for adult emergence and feeding on young leaves in the canopy. At the same time, they may avoid potential predators such as ants. Another strategy is to develop relatively mobile nymphs that feed freely in the canopy and that can either tolerate/escape ants (Orthoptera, some Hemiptera) or are tended by them (Coccoidea, Membracidae, Aphididae, etc.). Larvae of Lepidoptera, which are relatively species rich in the canopy, specialize on concealed resources (leaf rolls, leaf-mines and galls, stems, flowers and seeds), appear to be highly toxic (as are the few beetle larvae free-feeding on the foliage: e.g. Jolivet, 1987) or themselves associate with ants (e.g. Lycaenidae: Kitching, 1987; Fiedler, 1995).

A high incidence and wide variety of chemical defences against predators and parasitoids among tropical herbivores (Sime & Brower, 1998) have been proposed as explanations of the low species diversity of certain host-specific parasitoid taxa in the tropics (Gauld *et al.*, 1992). Since these defences can also be effective against predators, we speculate that high predation pressure by ants indirectly reduces the resource base and hence the species richness of parasitoids of herbivorous insects. High predation risk can influence also the host specificity of herbivores, as diet specialists seem to be better protected from predators than are generalists (Dyer, 1995).

One example: *Coelomera* attacking *Pourouma* in Panama

Consider a specific example that illustrates the constraints acting on the distribution of specific herbivores in rainforests and the wide range and nature of data required for identifying and interpreting such causal effects. Basset (2001a) studied the herbivorous fauna feeding on saplings and mature trees of *Pourouma bicolor* (Cecropiaceae), a pioneer tree, in a wet forest in Panama. There was very little faunal overlap between saplings and mature trees. In particular, the most abundant leaf-chewing species on mature trees was *Coelomera* sp. (Chrysomelidae: Galerucinae). The 35 known species of this Neotropical genus feed on Cecropiaceae and appear to be quite specialized (e.g. Jolivet, 1987). Both the adults and the free-living larvae feed on young leaves and shelter within the large stipules of trees. If disturbed, both adults and larvae exude a nauseating fluid, which may act as chemical defence. Adults, larvae and their characteristic leaf damage were not observed on saplings of *P. bicolor* in the 6 ha plot studied.

From the viewpoint of this specialized species, trees may be more hospitable than saplings for at least five possible reasons, all subject to debate.

1. Production of young foliage at the study site was three times higher, and more predictable, in trees than in saplings.
2. The presence of more abundant, larger and stronger stipules in trees than in saplings may protect *Coelomera* sp. from desiccation and predation.
3. Leaf palatability may be higher on trees than on saplings; the main factors affecting leaf palatability may be leaf toughness and chemistry, since leaf pubescence is superficially similar on both host stages. However, tree leaves are tougher and, when damaged, exude more latex than those of the saplings. If overall leaf palatability is higher on trees than on saplings, perhaps permitting higher loads of chewers on trees, then the foliage of saplings must be extremely well defended, as has been found in some other tropical trees (e.g. Langenheim & Stubblebine, 1983). In fact, 89% of larvae tested in multiple choice feeding experiments on *P. bicolor* in captivity preferred young leaves from trees over young leaves from saplings ($n = 18$), but adults fed on both ($n = 3$). Consequently, this issue cannot be resolved without a thorough chemical analysis of the leaf material.
4. Microclimatic effects must be of consequence and may represent a behavioural barrier for many insects dispersing either in the sunny upper canopy or in the shady understorey (e.g. Moore *et al.*, 1988). These

effects may be significant even when the host is a pioneer species and grows in relatively more open forest, such as in the present case.

5. Enemy-free space may also account for the patterns of distribution of *Coleomera* sp. The abundance of insect predators and parasitoids was higher on trees than on saplings; ants showed the reverse trend. Other predators (mostly spiders) had similar levels of abundance on both host stages. Accordingly, it is difficult to comment on the relative importance of enemy-free space on saplings and trees for *Coelomera* sp. It may further depend on the success of its defences against particular enemies, including vertebrate predators, and would require behavioural studies.

The conclusion of this short example is that, although it is difficult enough to outline the distribution of herbivores in the rainforest, it is far more complex to establish what might be the causal factors behind the observed distributions.

PATTERNS OF HOST SPECIFICITY

There are sound optimality arguments in support of the evolution of both narrow and broad host-plant ranges in rainforest insects (Basset, 1992a). In short, high diversity of chemical defences displayed by rainforest plants and high predation pressure by generalist predators have been suggested as agents selecting for restricted host range in herbivores, while high spatial variability, scarcity and unpredictability of resources, especially of young foliage, are suggested as factors promoting the evolution of polyphagy. Nevertheless, the predominance of specialists (at plant-specific, generic or familial levels) found in many taxa of herbivorous insect cannot be fully explained by optimality arguments and may well reflect an elevated speciation/extinction ratio in specialized versus polyphagous lineages (Jermy, 1993; Menken, 1996).

Monophagy, oligophagy and polyphagy

There are many species of insect that are restricted to single species of tree (Connor *et al.*, 1980; Claridge & Wilson, 1981). Where we have sufficiently complete information, as is the case with, say, butterflies and fruit-flies, then characteristic distributions of host specificity emerge. Figure 5.1 presents data on the known food plants of the entire butterfly fauna of the Australian

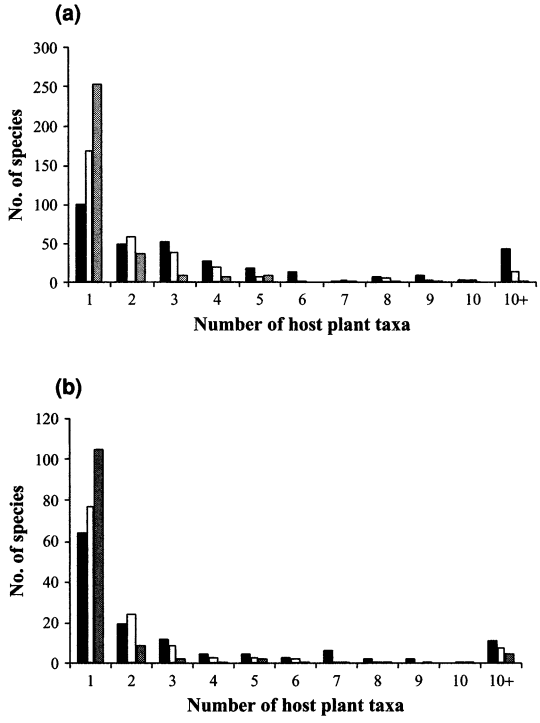

Fig. 5.1. Host plant taxa used as food. (a) The number of species of butterflies of the Australian continent feeding on 1, 2, . . . , 10 + plant taxa (extracted from Braby, 2000). (b) The number of species of the tephritid fruit-flies of south-east Asia feeding on 1, 2, . . . , 10 + plant taxa (extracted from Allwood *et al.*, 1999). Closed bars, plant species; open bars, plant genera; grey bars, plant families.

continent and on the tephritid fruit-flies of south-east Asia (Allwood *et al.*, 1999; Braby, 2000). In fact, these data show that for both groups functional monophagy is the commonest feeding pattern across all species. Relative to the entire fauna, this monophagy becomes even more marked when the analysis is done at the level of the plant genus and greater still at the the family level. That having been said, there are many herbivore species showing all grades of nonmonophagy from the exploitation of two taxa of plant through to *Bactrocera papayae* Drew & Hancock (Tephritidae), which is recorded as feeding on an astounding 193 species of plants in 114 genera in 50 families! Figure 5.2 is redrawn from Novotny *et al.* (2002a) and shows the host-plant ranges at a variety of taxonomic levels for three groups of herbivores in lowland forest in Papua New Guinea. The figure underlines the

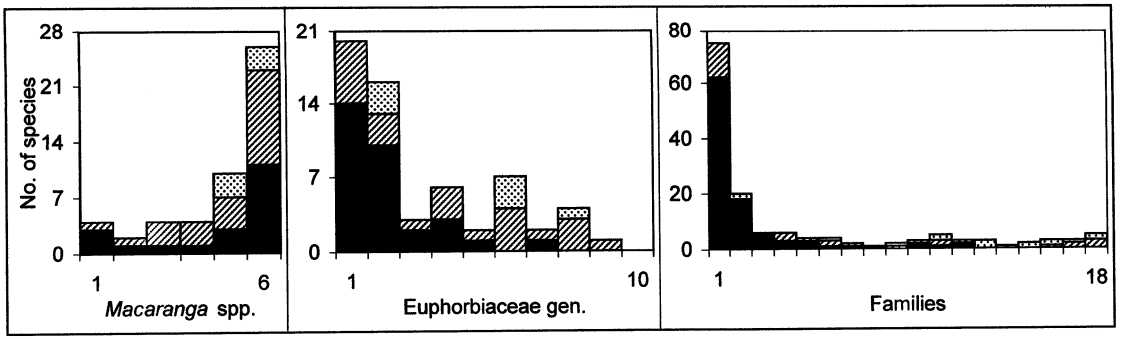

Fig. 5.2. Host-plant range of leaf-chewing insects on congeneric *Macaranga* species, on hosts from different genera of Euphorbiaceae and on hosts from different families of flowering plants. Black bars, Lepidoptera; hatched bars, Coleoptera; stippled bars, orthopteroids.

fact that within a fauna different groups of herbivores may show dramatically different degrees of host-plant fidelity. In the herbivorous Lepidoptera, Coleoptera and orthopteroids of a New Guinea forest, the Lepidoptera showed the greatest degree of host specificity (although within the plants examined this was most apparent at the generic level), followed by the Coleoptera. The orthopteroids were in general the most catholic feeders of the groups being compared. Even simple comparisons of the kind presented here can lead to oversimplistic interpretations. Janzen (Ch. 33) discusses at length the various sorts of polyphagy exhibited within the Costa Rican Saturniidae. He notes cases where the species may show polyphagy but individuals do not; the contrasting situations where even single individuals may be polyphagous; the extraordinary increase in food-plant range that may occur during an outbreak population; and, finally, the restraints on potential polyphagy by limits in the diversity of the local flora. All of these considerations lead us, further, to caution that even the best of datasets should not be assumed to be final and complete. Even in the butterflies, there are many familiar species where the full range of food-plants is poorly understood, particularly in the case of monocot feeders such as the Satyrinae and Hesperioidea.

Highly specific phytophages are generally presumed to have coevolved to varying degrees (but note the important comments in Ch. 33). Sometimes this level of coevolution is extreme. Gall-formers (Askew, 1980), some leaf-miners (Common, 1990), specialized seed predators (Janzen, 1970; Oberprieler, 2003) and so forth are cases in point. Often even insects that we regard as 'specialists' – such as the large assemblage of oak associates in the cool temperate regions (Kennedy & Southwood, 1984; see also the general treatment of Lawton & Schröder, 1977) – are, in fact, oligophages, specializing not in a single species but in a particular genus or group of related genera. Further, even within that set of host species, not all will be equally selected – and the preferred set may change from place to place within the range of the herbivore. The degree to which such oligophagous specialization is obligate or facultative will reflect the chemical characteristics of the plants involved. Examples of sets of herbivore getting ecologically 'marooned' so to speak by the chemical peculiarities of their host plants, however, are widespread within both the gymnosperms and the angiosperms. Examples that have featured in recent important studies include the coniferophagous weevil family Nemonychidae (Farrell, 1998) and the assemblage of specialized herbivores on the angiospermatous Asclepiadaceae, Moraceae and Apocynaceae (Futuyma & Moreno, 1988; Dobler & Farrell, 1999). Of course, many insects are genuinely polyphagous and are able to feed on a very wide range of host plants. Generally, such polyphages will still avoid some of the more chemically challenging groups of plants but nevertheless remain remarkably catholic.

Considerations of this kind have lead to the redefinition of host-plant specificity as a statistical concept better represented by distributions of levels of exploitation of a range of host species and the degree of exploitation of each by particular herbivores. Diserud and Ødegaard (2000) use a beta binomial model for this purpose while Mawdsley and Stork (1997) follow May

(1990) in calculating a weighted sum reflecting the number of co-hosts for each insect species encountered on a focal tree. Both of these approaches ideally require complete species lists for each tree species: a requirement that is rarely met even for temperate forests (but see Ward & Spalding, 1993) and that remains a distant dream for tropical systems.

A diversity of herbivores

Differing degrees of specialization among different major groups of herbivore restrict the degree to which conclusions about one group may be generalized to all of the Insecta. Novotny and his co-workers (2002a) have demonstrated recently that, even though a simple power curve readily represents the relationship between insect herbivores and tree species within a tropical rainforest in northern New Guinea, different orders of insects have quite different exponent values, reflecting the degree of specialization characteristic of each. Of the three major herbivorous orders, the Lepidoptera showed the greatest degree of specialization followed by the Coleoptera and, finally, the Orthoptera.

Insect–plant associations often exhibit considerable evolutionary conservatism and are also a product of chance historical events. In consequence, we can expect phylogenetic relationships among host plants to account for a significant part of the similarities observed in the contemporary assemblages of herbivores, these similarities being only partially attributable to causal effects of local and/or regional factors (Farrell & Mitter, 1993; Losos, 1996). There is no theoretical framework for predicting whether host specificity and species richness of insects feeding locally on rainforest tree species can be attributed largely to local processes, to regional processes or, being a result of idiosyncrasies of evolutionary history of plant–herbivore interactions, to neither of them. Empirical studies taking into consideration the whole range of local and regional variables, as well as the phylogeny of host plants, are, therefore, much needed, especially in the tropics.

CONCLUSIONS

The study of insect herbivores and their resource use in the canopy of tropical rainforests represents a formidable challenge. We need sampling efforts, sampling universes, observations and results of experiments that are commensurate with the size and scope of the study system, possibly one of the most species-rich on Earth. To date, no study has been able to provide us with data that may be useful to extrapolate patterns at the forest level. Studies are too short in duration, too restricted in terms of insect or plant taxa, too restricted in terms of spatial or temporal replicates originating from the study hosts, or they do not provide direct observations of insect–plant interactions and feeding records. No matter what mathematics is applied to a poor, unrepresentative dataset, the result is going to be equivocal.

To remedy this, we need to increase our knowledge by:

- increasing the focus on taxa other than beetles and comparing patterns of plant use by these various taxa
- increasing plant replicates so as to include a representative subset of the forest stand, in terms of phylogeny, abundance and biomass
- increasing spatial replicates so as to include replicated blocks (sites) within the forest and sufficient replicates of conspecific plants: the number of replicates needed most likely will depend on plant characteristics, such as phylogeny, abundance, ecological plasticity, phenology, and so on (although, for these reasons, it is difficult to recommend a figure, as many as 50 or 100 replicates are indicated (*cf.* Basset & Novotny, 1999; Novotny *et al.*, 1999b, 2002a)
- increasing temporal replicates so as to include supra-annual events
- studying the relationships between the canopy and soil/litter faunas.

This list may look rather depressing, especially when considering the difficulties of canopy access and the associated physical and financial constraints. Where do we start? A 'canopy station' (see Ch. 2) would greatly help to get representative and sufficient replicates both spatially and temporally, and to develop long-term experiments. Numerous replicates and experiments could be obtained or performed by local parataxonomists (e.g. Novotny *et al.*, 1997; Basset *et al.*, 2000) and they could be productively trained by experienced and professional tree-climbers to access many parts of the canopy. Perhaps the biggest challenge of all may be to

develop the framework within which canopy ecologists and taxonomists can (and will) work together to achieve these goals.

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