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Conclusion: arthropods, canopies and interpretable patterns

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ABSTRACT

This synthesis chapter examines patterns of vertical stratification, temporal distribution, resource use and host specificity of arthropods in tropical rainforest canopies with particular regard to previous contributions in this volume. We stress research themes that are likely to be promising in future entomological research in tropical canopies and highlight lacunae in the understanding of arthropod distribution within tropical canopies. We are particularly interested in two simple questions that may stimulate further research on arthropods within tropical canopies. First, are distribution patterns of and resource use by arthropods congruent between geographical locations and, especially, forest types, such as lowland wet, lowland dry and montane tropical forests? Second, are particular arthropod taxa distributed similarly along vertical profiles in the forest and horizontally in the canopy? We discuss these and related issues from both evolutionary and conservation perspectives.

INTRODUCTION

This concluding chapter of the volume attempts to summarize spatial and temporal patterns of arthropod distribution in tropical forest canopies, with particular reference to the data presented in the preceding chapters. In particular, we emphasize congruent and/or different patterns among geographical locations, forest types and arthropod taxa for each of the three major research themes covered by this volume (vertical distribution, temporal patterns and resource use). The last section of the chapter discusses future directions of research relevant to canopy arthropods in the tropics, adding to the items already touched upon in Ch. 2.

VERTICAL GRADIENTS IN TROPICAL FORESTS

Congruent patterns among geographical locations and forest types?

One congruent pattern among geographical locations is the existence of distinct arthropod faunas in the lower (understorey) and higher parts (mid- and upper canopy) of rainforests, illustrated by all the contributions in this volume that discussed the vertical distribution of arthropods (Chs. 3, 6–11, 22, 25–27). This pattern is confirmed by several other studies in tropical rainforests (see reviews in Ch. 3 and in Basset *et al.*, 2001a) and contrasts with studies performed in temperate forests (e.g. Fowler, 1985; Le Corff & Marquis, 1999; Lowman *et al.*, 1993b).

Not unexpectedly, this pattern is most obvious when comparing the litter and canopy faunas (Ch. 9), but it is also apparent between the understorey and the upper canopy, particularly for insect herbivores (Chs. 3, 22 and 29). However, the extent to which a strict stratification of arthropod faunas exists from the litter to the overstorey is highly debatable (Ch. 3). Ant and bark beetle assemblages, for example, are not well stratified within the crowns of oaks in Sabah (Ch. 6). The extent of arthropod stratification may depend both on the arthropod taxa concerned (see below) and the forest type. For the latter, in addition to other determinants discussed in Ch. 3, at least three factors may affect arthropod stratification in tropical forests: (i) the vertical continuity of habitats; (ii) the physiognomy of the forest; and (iii) edaphic patterns.

First, differences in the continuity (or discontinuity) of available habitats for arthropods from the litter to the upper canopy may explain the extent of arthropod stratification (Basset, 2001b). For example, in montane rainforests, the trunks of trees often bear a thick cover of mosses and epiphytes and the canopy is often lower than in lowland rainforests (Richards, 1996). Accordingly, the continuity between the soil/litter and canopy in montane forests may be greater than in lowland forests, and this could explain the higher occurrence in the former of taxa well represented in the soil/litter habitat, such as Collembola, Acari and Arachnida (e.g. Stork & Brendell, 1990). Arthropod stratification would not be obvious in this case. Nadkarni & Longino (1990) reported relatively few differences in the fauna of suspended soils compared with that of the litter in a cloud forest in Costa Rica. Similarly, Sørensen (Ch. 9) reports few differences in the spider faunas of the understorey and the higher canopy of a montane forest in Tanzania.

Collembola seem to be particularly sensitive to forest type (Basset, 2001b) and this may be related to the high accumulation of organic matter in the canopy or slower decomposition rates, as discussed by Kitching *et al.* (1997) and Palacios-Vargas *et al.* (1998). Palacios-Vargas and Castaño-Meneses (Ch. 15) show that springtails can use both bromeliads on the ground and epiphytes in the canopy, migrating upward when water stress is considerable. As convincingly discussed by Shaw and Walter (Ch. 26), discrete and cryptic habitats may promote frequent inbreeding in arthropod species, thus leading to conservative arthropod assemblages. Depending on the vertical distribution of these habitats, this may also reinforce arthropod stratification in tropical forests.

Second, the forest physiognomy (i.e. forest cover and height of canopy), which is also related in part to the continuity of available habitats, may have substantial effects upon arthropod stratification. The leaf area index, for example, usually varies significantly from forest floor to the upper canopy (e.g. Parker, 1995) and this variance is maximal in tall wet tropical forests (Smith, 1973). Koike & Nagamitsu (Ch. 8) emphasize the need to measure adequately canopy structure and its influence on the flight patterns of certain taxa. A rather heterogeneous vertical distribution of values of the leaf area index may promote different insect flight patterns and, ultimately, different patterns of oviposition and vertical distribution.

In comparison with tall wet tropical forests, dry tropical forests and savanna forests are often characterized by more homogeneous environmental gradients, including abiotic and biotic factors such as illumination, relative humidity, leaf area index and the presence of flowers and seeds (e.g. Richards, 1996). Accordingly, it is less likely that arthropod faunas will be well stratified in dry forests or savannas. For example, E. Charles (personal communication) found a higher similarity of chrysomelid assemblages between the understorey and upper canopy of a dry forest than between these strata in a wet forest in Panama.

Further, in dry (seasonal) rainforests, many tree species are deciduous or partly deciduous and nutrient cycling there may be quicker than in wet rainforests, where the foliage turnover of evergreen trees is slower. Canopy arthropods may possess a variety of adaptations to cope with gradual or sudden leaf exchange and increase in irradiance and water stress, or they may migrate to other locations, as is known to occur in a variety of moths (e.g. Janzen, 1988a). This suggests that arthropods may be pre-adapted to use habitats exhibiting varying leaf area indices. The data of Janzen (Ch. 33), for example, do not appear to indicate a stratification of saturniids in the dry forest of Guanacaste in Costa Rica.

It is also of interest to question whether the vertical distribution of habitats in mixed wet forests is similar to that in monodominant (or less speciose) wet forests, which may similarly promote arthropod stratification in both forest types. Again the physiognomy and leaf area index may appear superficially more homogeneous in monodominant than in mixed forests, and this may promote arthropod stratification in mixed forests. Schulze and Fielder (Ch. 7) report on the stratification of Pyraloidea in a dipterocarp forest, perhaps with more homogeneous environmental gradients than in highly diverse forests. They point out that differences are not extensive and that the moth assemblages of the understorey and upper canopy appear to be influenced by similar factors.

Last, edaphic factors may influence migrations from the forest floor to the canopy and, in consequence, arthropod stratification. Many soil taxa migrate upward in the canopy of Central Amazonian inundation forests in response to flooding (e.g. Adis, 1981, 1997a; Erwin & Adis, 1982). This results in distinct arthropod assemblages at different heights in the short term, but less so in the long term. In this case, the extent of arthropod stratification depends on the time frame being considered.

In sum, we predict that the extent of arthropod stratification will be relatively low in montane, dry and savanna forests, and perhaps also in subtropical forests, but higher in tall wet tropical forests. Disturbance and opening of the canopy in the last is likely to affect significantly populations of canopy arthropods there.

Congruent patterns among arthropod taxa?

This issue has already been discussed at length in Ch. 3. Following the same approach, we discuss whether patterns of vertical distribution seem to be congruent for representatives of different feeding guilds, in light of the various contributions of this volume.

With regard to scavengers, fungal-feeders and dead-wood eaters, Winchester and Behan-Pelletier (Ch. 10) show that the habitat represented by suspended soils is modified by height, and that these effects can have implications for the composition of arthropod assemblages between 32 and 42 m. The review compiled by Prinzing and Woas (Ch. 24) indicates that many factors, including ecophysiological conditions, immigration from population pools and interspecific interactions, can affect the redistribution of springtails and mites among different habitats. Most likely, these patterns of redistribution are responsible for the faunal differences observed between the forest floor and the canopy. Itioka *et al.* (Ch. 12) report that the Blattodea respond positively to humus accumulation in the canopy, following flowering in dipterocarp forests, possibly promoting vertical migrations of this taxon. Barrios (Ch. 25) indicates that the scavenging fauna is more abundant on seedlings of *Castilla elastica* in the understorey than on conspecific mature trees in the canopy. These observations stress that habitats for scavengers and fungal-feeders, such as dead wood and associated fungi, appear to be relatively discontinuous and discrete along a vertical transect of rainforest (Ch. 26). Consequently, we might expect rather different assemblages of scavengers and fungal-feeders at different heights in rainforests, perhaps with a specialized fauna able to cope with the harsh environmental conditions of the upper canopy. However, the abundance and diversity of this guild should be highest near ground level (see Ch. 3).

With regard to herbivores, particularly insect herbivores, De Dijn (Ch. 11) notes the highest abundance and diversity of Homoptera is in the canopy in Surinam. Itioka *et al.* (Ch. 12) stress that anthophilous insects respond best to general flowering in the canopy of dipterocarp forests in Malaysia. Amédégnato (Ch. 22) discusses the stratification of habitats available to grasshoppers in the Amazon and the different assemblages occurring at different heights. In Panama, Barrios (Ch. 25) shows that mature trees of *C. elastica* are foraged and fed upon by a more abundant and diverse fauna of herbivores than their conspecific seedlings and saplings in the understorey. In chapter 27, Basset *et al.* compare the assemblages of insect herbivores in the understorey and upper canopy in Gabon, showing that their abundance and diversity is higher in the latter. They emphasize the low faunal turnover across the two strata, both during day and night.

There are also exceptions to this pattern of higher abundance and diversity of insect herbivores in the higher part of the canopy compared with the understorey, and this parallels the available literature (see Ch. 3). Although Schulze and Fiedler (Ch. 7) observed distinct assemblages of Pyraloidea in the understorey and upper canopy of a dipterocarp forest in Malaysia, species richness was highest in the understorey. As the authors note, whether this results from the low diversity of Lepidoptera that feed on dipterocarps in general is not known. Scolytinae were rather indifferent to height when their fine distribution in the crown of oaks in Malaysia was considered (Ch. 6). The influence of illumination on different arthropod resources, such as dead or live wood and leaves, warrants further investigation.

In sum, since many food resources, such as leaves, flowers and fruits, are more abundant in the upper canopy than in the understorey of wet rainforests, the abundance and diversity of many herbivore taxa are expected to be higher in the former strata. Differences in foliage quality between the upper canopy and understorey may induce a clear stratification of herbivores, as reported in several studies, particularly when taxa have a narrow host range (see details in Chs. 3 and 5).

Within the predatory and parasitoidal guilds, generalist predators such as spiders appear to be more diverse at ground level and the similarity of their assemblages in the understorey and canopy is rather high in Tanzania (Ch. 9). Others, such as wasps, forage indifferently in both the understorey and canopy and do not respond well to flowering events in the canopy (Ch. 12). On *C. elastica*, both insect predators and parasitoids were more abundant on mature trees than on conspecific seedlings or saplings (Ch. 25). As already noted in Ch. 3, the extent of stratification of predators and parasitoids depends on whether or not they specialize on certain prey or host species and whether they can tolerate environmental differences across different forest levels.

For Malaysia, Simon *et al.* (Ch. 6) report that alate ants prefer the lower parts of the crown, where litter accumulates and they are more likely to establish a nest, but that ant workers forage indiscriminately over the whole crowns. Ants are also most abundant in suspended soils situated in the lower part of the canopy (Ch. 10). Both De Dijn (Ch. 11) in Surinam and Barrios (Ch. 9) in Panama indicate that ants are more abundant in the understorey than in the upper canopy. As discussed in Ch. 3, strict stratification of ant species in the canopy may sometimes occur, but the abundance and biomass of ants may not necessarily be higher in the canopy than near ground level, and their observed distributions may depend on nesting ecology.

In sum, many arthropod species are likely to forage at preferred levels within the rainforest canopy. Strict stratification in closed and wet tropical forests has been reported for certain scavengers and fungal-feeders, herbivores and ants, but it appears less likely for generalist predators and biting flies (see Ch. 3).

Stratification and speciation in the canopy

Beyond the effects of latitudinal gradients and ambient available environmental energy (e.g. Turner *et al.*, 1996; Kolasa *et al.*, 1998; Gaston, 2000), additional hypotheses have been suggested to explain high species richness in tropical rainforests (e.g. Simpson & Haffer, 1978; Endler, 1982; Erwin & Adis, 1982; Brown, 1999; Schneider *et al.*, 1999; Gascon *et al.*, 2000; Hubbell, 2001; Whittaker *et al.*, 2001). These are as follows.

1. The island hypothesis, in which the formation of numerous islands caused by high sea levels during the Tertiary period subsequently resulted in species differentiation.
2. The riverine barrier hypothesis, in which emerging rivers during the Quaternary period separated species and caused them to diverge.
3. The montane isolate hypothesis, in which periods of low rainfall stranded animal populations on different parts of rainforested mountains, where they subsequently diverged.
4. The Pleistocene refuge hypothesis, in which rainforests shrank during a cool and dry period. The biota left in the fragments diverged and then rejoined expanding rainforest tracks during subsequent warming and moistening of the climate.
5. The gradient hypothesis, in which speciation results from the action of diversifying selection across environmental gradients.
6. The peripheral divergence hypothesis, in which peripheral areas of forest receive gene flow and dispersing individuals from fewer directions than do central populations with forests on all sides. This allows more differentiation to occur in peripheral populations.
7. Sympatric speciation may result from ecological separation, such as in the case of fig wasps feeding on different plants.

Basically, hypotheses 1–4 emphasize geographic isolation as the driving force behind speciation, whereas 5–7 represent the outcome of ecology-driven speciation processes. Geographic speciation has long been held as the most important factor regulating speciation in tropical forests and it may indeed be notable, despite recent criticisms of the Pleistocene refuge hypothesis (e.g. Colinvaux, 1998).

Recent studies suggest that natural selection across habitat gradients, without significant geographic or genetic isolation, may also be an important process in animal speciation in tropical rainforests (e.g. Schneider *et al.*, 1999; Bridle *et al.*, 2001). In other words, isolation through vicariance in rainforests may in certain cases be insufficient to produce phenotypic divergence among populations and, therefore, may be less important in species formation than previously thought (Schneider *et al.*, 1999). For example, Schneider *et al.* (1999) compared mitochondrial and morphological divergence in ground-dwelling rainforest lizards in Australia and concluded that natural selection operating across ecological gradients can be more important than geographic isolation in similar habitats in generating phenotypic diversity. Their study contrasted lizards occurring in rainforests, savannas and on the forest edge. One could summarize their findings by stating that 'species are more likely to evolve if they live at the rainforest edge' (Brown, 1999).

Following this line of reasoning, we consider that an ecotone such as the upper canopy (or canopy surface) of closed wet tropical forests may represent a significant arena for natural selection promoting speciation, especially for small organisms such as arthropods. For these taxa, environmental gradients from the canopy to the overstorey may be similar to those occurring from the forest interior to the edge. The implications for the conservation of rainforest biota may be important. First, it may be imperative to preserve the processes that promote genetic variation in rainforest species (Erwin, 1991c; Brown, 1999; Schneider *et al.*, 1999; Levin & Levin, 2002). Second, a distinct arthropod fauna restricted to the upper canopy of tropical rainforest may represent one of the biotas that is most endangered by anthropogenic disturbance (Basset *et al.*, 2001a). In brief, there is enough inferential evidence to stimulate entomologists to pay more attention to the arthropods of the upper canopy and the gradients of environmental factors that they must face there.

TEMPORAL PATTERNS IN TROPICAL CANOPIES

Congruent patterns among geographical locations and forest types?

Temporal patterns of distribution in canopy arthropods may be compared at three different scales of increasing resolution: (i) among forest types, especially between wet and dry forests; (ii) among host or support plants; and (iii) between undisturbed and disturbed forest sites. With regard to the first scale of resolution, many temporal factors shape the structure of arthropod communities. Some, including both climatic and biotic factors (such as biotic resource tracking, resource competition and predation), are often predictable and act at the regional scale (Ch. 4). Others appear to be stochastic and may act at a much finer scale (Chs. 18, 19 and 23), although spatial scale and predictability may not be related necessarily.

Even when considering a particular host-plant species in differing geographical situations, historical factors may constrain the local diversity of its associated arthropods (e.g. Cornell & Lawton, 1992). Gruner and Polhemus (Ch. 13), for example, in their analysis of *Metrosideros* sp. in Hawaii over a 4-million-year period, conclude that ecological factors affecting arthropod densities are significant at the scale of the ecosystem, but are less significant at the level of the forest patch or individual tree. They also contend that if *Metrosideros* sp. is a recent arrival in Hawaii, then contemporary arthropod assemblages are a subset of the regional species pool that has shifted hosts within a short evolutionary time. Interestingly, the situation appears similar for *Ficus* spp. and its associated herbivores in New Guinea (Basset & Novotny, 1999).

It is of interest that certain arthropod taxa in various forests growing under extreme amplitudes of rainfall show similar temporal patterns, moving upward in the canopy during the most unfavourable periods. In dry forests in Mexico, springtails migrate upwards into bromeliads to escape water stress during the dry season, increasing the diversity in the canopy (Ch. 15). In inundated forests of the Amazon, Carabidae, Pseudoscorpiones, Chilopoda and many other taxa also migrate upwards in the canopy during flooding (e.g. Adis, 1981, 1997a; Erwin & Adis, 1982). There is a seasonal component in arthropod vertical distribution that may be obvious in tropical forests enduring large climatic amplitudes. Similarly, arthropod vertical migrations may occur in montane forests during the most unfavourable periods (perhaps moving down during the coolest periods).

Other effects may be more subtle, as indicated by the study of Wagner (Ch. 14) in Uganda. There, arthropod seasonality depends on forest type and local irrigation (i.e. swamp forest), even in forest plots located close to each other. Wagner stresses that in this case seasonal factors and habitat structure are more important than host specificity in explaining assemblage composition and structure. This is an excellent illustration of the contention that temporal variation may be as important as spatial variation in tropical canopies (See Ch. 4). In Uganda, many small beetles aggregate in trees during the dry season without any long-lasting association with the trees: yet another example of migration during an unfavourable period.

In Ch. 4, Didham and Springate explain convincingly the effects of host phylogeny on the patterns of temporal distribution of arthropods in tropical canopies (see also Ch. 16 for an example of such patterns). Host phylogeny includes factors acting at the second scale of resolution, as listed above. Didham and Springate refer to host traits such as tree phenology, growth rate and senescence pattern to predict cascading effects on arthropod assemblages. Host phenology and growth rates, in affecting the amount or quality of resources available to insect herbivores, are prime factors in this equation. Despite this, it is perhaps frustrating to realize that, to date, we have basically no data comparing the influence of phenology of evergreen versus deciduous hosts on the structure of associated arthropod assemblages.

Patterns of tree senescence are also likely to affect deeply the resources available to arthropods. Senescence may affect the balance between live and dead wood in the canopy and the amount of suspended soils, but it may also promote the growth of other plants, such as epiphytes. This, in turn, may affect the seasonality of arthropods – the working hypothesis of Stuntz *et al.* (Ch. 17). In particular, the presence of epiphytes in the crowns of host trees could act as an environmental buffer for arthropods during the dry season. The hypothesis is attractive but not supported by the data put forward in Ch. 17 for *Annona glabra*, its epiphytes and their arthropod inhabitants in Panama.

Didham and Springate (Ch. 4) also suggest that at the third scale of resolution, the disturbance of originally similar forest sites, host phylogeny most likely leads to changes in long-term temporal variation in the structure of arthropod assemblages. Indeed, Schowalter and Ganio (Ch. 28) report that annual patterns of arthropod abundance are often related to hurricane disturbance or drought in the neotropics. In their study, herbivores had variable but important effects on canopy structure (notably leaf loss), depending on tree species. Leaf loss may influence canopy porosity (i.e. penetration of light, water and air flow) and hence the turnover of water, carbon and other nutrients.

Congruent patterns among arthropod taxa?

To discuss congruence and differences of temporal patterns among arthropod taxa in the canopy, it is best to examine patterns at the following three scales: (i) diel activity patterns; (ii) seasonal patterns (i.e. within an annual cycle); and (iii) multiannual patterns. With regard to the first, several studies showed convincingly that different arthropod taxa forage either during day or during the night in the canopy (e.g. Hammond, 1990; Basset & Springate, 1992; Springate & Basset, 1996; Compton *et al.*, 2000; Basset *et al.*, 2001a; Ch. 27). Some subdominant ant species, for example, are active either during day or night, sharing territory with other ants (Ch. 30). Most of these studies also indicate that arthropod diel activity is overall higher during the day than at night in rainforests. Schowalter and Ganio (Ch. 28) report distinct diel patterns for different taxa but overall find little difference in arthropod activity during day and night. Their methods targeted rather inactive insects and did not specifically monitor arthropod activity.

Since scents are often better propagated when the relative humidity is high (i.e. at night), fungal-feeders or scavengers relying to some extent on scents for the location of their food resources may be particularly active during night. Conversely, herbivores that may rely to some extent on vision (guided by foliage reflectance etc.) may be particularly active during day. The studies cited above generally reflect these trends, although no generalization is possible at the species level. Each guild includes representative species that may be more active during either day or night, resulting in distinct faunas foraging during day or night.

Janzen (1983a) proposed that herbivores in rainforests might be more active during night than day, to escape day-active predators and parasitoids. Various studies using different methods (e.g. Springate & Basset, 1996; Novotny *et al.*, 1999a) showed that this was unlikely. Night was confirmed as a relatively enemy-free time, which, however, was not exploited to the fullest by herbivores.

With regard to seasonal patterns, several studies emphasized differences in the seasonal distribution of both arthropod guilds and species in the canopy during the annual cycle (e.g. Wolda, 1978b; Basset, 1991c; Ribeiro & Pimmenta, 1991; Janzen, 1993b; Kato *et al.*, 1995; DeVries *et al.*, 1997; Chs. 7, 15 and 16). In addition, the seasonal distribution of arthropods intimately associated with certain host trees may be affected by certain traits such as host phenology and growth, often dependent on host phylogeny, as well as on other abiotic and biotic factors (Ch. 4). Therefore, seasonal patterns are likely to be highly variable and difficult to predict, unless arthropods specialize on a particular resource. Indeed, two studies in New Guinea and Guyana indicated that specialist herbivores are likely to be more seasonal (and predictable) than generalist herbivores (Novotny & Basset, 1998; Basset, 2000).

Resource availability over time also greatly influences multiannual patterns of arthropod distribution (Chs. 4, 12 and 32). For example, arthropod guilds specializing on different resources respond differently to general flowering in dipterocarp forests (Ch. 12). Further, multiannual modification of the resource base (Price, 1992) available to arthropod assemblages through natural disturbance, such as El Niño events, may also affect them greatly and trigger cascading effects (Ch. 28).

Are temporal patterns similar in the understorey and upper canopy?

Most likely, the answer to this question will depend on the availability and predictability of resources in these two forest strata, and on other factors discussed by Didham and Springate (Ch. 4). The interpretation of patterns may also prove to be different depending on whether detailed information exists on arthropods and their resources. Schulze and Fiedler (Ch. 7) indicate that seasonal fluctuations of pyraloid moths appear to be similar in both strata, and that both faunas are probably influenced by similar factors in the understorey and upper canopy. This may be related to the relatively uniform floral composition of this forest, perhaps providing a more uniform temporal environment with synchronous leaf-flush, flowering and fruiting. Without information about the resources used by the moths collected, it is difficult to discuss this contention.

Itioka *et al.* (Ch. 12) show that generalist predators foraging both in the understorey and upper canopy do not respond strongly to general flowering; that is, their seasonal patterns are similar in both strata. Patterns may be different for more specialized species, as noted above. For example, the seasonal availability of the young foliage of mature trees of *Pourouma bicolor* in Panama is significantly less variable than that of conspecific saplings (Basset, 2001a). Since certain herbivore species specialize on *Pourouma* sp. saplings in the understorey, their seasonal distribution is likely to differ from that of counterparts specializing on mature foliage in the canopy. Alternatively, understorey specialists may be more generalist with regard to plant use, a hypothesis that is also plausible. In Guyana, insect herbivores foraging on seedlings included a majority of generalist species (Basset, 1999b). In any case, the high leaf turnover in the upper canopy of rainforests, compared with their understorey (e.g. van Schaik *et al.*, 1993; Coley & Kursar, 1996), is likely to have a significant influence on herbivore seasonality.

RESOURCE USE IN TROPICAL CANOPIES

Congruent patterns among geographical locations and forest types?

What are the most significant differences in terms of habitat and resource use among different types of tropical forest? In the tropics, most studies interested in altitudinal gradients have focussed on litter and understorey arthropods, often targeting specific taxa (e.g. Janzen *et al.*, 1976; Wolda, 1987; Hanski & Niemelä, 1990; Holloway *et al.*, 1990; Olson, 1994a). Altitudinal transects targeting canopy arthropods have been more rarely employed (e.g. Gagné, 1979; Stork & Brendell, 1990; Allison *et al.*, 1997) and specific studies on the fauna of canopies in montane forests are even scarcer (e.g. Chs. 6 and 9). Often, these studies show bell-shaped curves of diversity, with maxima at the transition zone of lowland and montane forests, diminishing thereafter with increasing and decreasing altitude. Mid-elevation diversity appears to be inflated by faunal overlap from both lower and higher elevation zones (e.g. Lees *et al.*, 1999).

In addition to the high continuity of habitats from the ground to the canopy, discussed above, the harshness of the climate in montane forests is also likely to affect the habitats available to arthropods there. For example, the ratio of ants to other taxa appears to decrease from lowland wet forests to montane forests (Stork & Brendell 1990; Basset, 2001b). Montane rainforest may be too cold to allow ants to forage efficiently or for their larvae to develop fast enough (Brown 1973), or the resource base may be too low to allow large populations of their homopteran associates to exist. In lowland forests, high ratios of ants to Homoptera are more common and this may be partly related to mutualism and the tending of homopterans in the canopy in favourable situations (Basset, 2001b).

Although information on the effects of altitudinal gradients on canopy arthropods is relatively scarce, that on the effects of rainfall gradients is more abundant, as evidenced by several contributions in this volume. Ribeiro (Ch. 31) reviews the major differences between tropical savannas and wet forests. The former experience more leaf damage and support higher abundance of more host-specific herbivores and more gall-forming species than the latter. These differences appear to reflect the concentrated plant resources in savannas (as opposed to diluted resources in mixed tropical forests – the 'trees as islands' of Janzen (1968, 1973c) – and evolutionary responses to sclerophylly. Ribeiro also suggests that the canopy surface in savannas is rather different from that in tall wet forests, and its properties need to be better studied.

In support of Ribeiro's views, Mody *et al.* (Ch. 19) stress that African savanna trees can support high numbers of arthropods and a species richness intermediate between that on temperate and tropical trees (see also Krüger & McGavin, 1998a). Further, beetles, but not so much ants, show a high fidelity to both tree species and individual trees among study years. The data clearly stress the individual trees as the source of variation for arthropod assemblages. Even if the structure of the arthropod assemblage varies little between years on these trees, it is difficult to predict from one conspecific tree to the other. In a dry (deciduous) forest in Costa Rica, many species of saturniid moths are rather specialized (Janzen, 1988a; Ch. 33). In a wetter, semideciduous forest in Panama, Ødegaard (2000c; Ch. 21) shows that many phytophagous beetles, dominated by Chrysomelidae and Curculionidae, appear relatively specialized, many dependent upon lianas.

In contrast, recent studies using large sample sizes in wet forests indicate relatively lower proportions of highly specialized herbivores (e.g. Basset, 1999b; Basset & Novotny, 1999; Novotny *et al.*, 1999b, 2002a,b; Ch. 29). It is possible that the proportion of insect herbivores that are specialized may decrease as one moves from savannas through dry to increasingly wetter tropical forests. Possible explanations may include the increasing dilution of hosts in mixed wet forests and the resulting constraints on host location (e.g. Basset, 1992a); and the increasing number of taxonomically related hosts in mixed wet forests, favouring host switches (e.g. Novotny *et al.*, 1999b, 2002a; Ch. 5).

Congruent patterns among arthropod taxa?

We discuss briefly here the ecological specialization (habitat and resource use) of a certain number of taxa, that is, their 'niche width', with particular emphasis on the studies reported in this volume. Care must be taken to distinguish habitat and resource specialists in certain cases (Ch. 18). In Panama, for example, the caterpillars of the nymphalid *Tigridia acesta* (L.) were only collected from the saplings of *P. bicolor*, not from conspecific mature trees (Basset, 2001a). They would feed on the young foliage of trees, but with apparent difficulty. This species probably occurs rarely if at all, on the foliage of mature *P. bicolor*. It may be restricted to saplings of *Pourouma* spp. in the understorey but feed also on relatively small and shaded *Cecropia* spp. in the understorey, as indicated by host records (Young, 1986; DeVries, 1987a). The adults prefer to fly in the understorey (DeVries & Walla, 2001). This could be an example of a habitat specialist (in the understorey) able to feed on different resources (various Cecropiaceae). A similar situation is observed in many species of herbivorous beetles that specialize on roots or wood as larvae but perform 'maturation feeding' on a range of hosts in the canopy as adults (Ch. 15; and see paragraph on grasshoppers, below).

Shaw and Walter (Ch. 26) show that primitive arthropods may be common in tree hollows in the canopy because of frequent inbreeding in these discrete habitats. In particular, mites are diverse in these habitats and also occur in nests of vertebrates, which provide many transitional forms from free-living to ectocommensal or parasitic. Therefore, sampling from cryptic canopy habitats is important to understand mite evolution. Tropical forest canopies are likely to include many such discrete habitats and associated specialized arthropod inhabitants. Other arthropods, such as free-feeding herbivores, are often good fliers that disperse readily and may not be so closely tied to particular habitats. However, it is this latter category of arthropods that are most likely to be collected in the canopy by fogging or trapping. Hence, our estimates of niche breadth may be biased against cryptic arthropods when relying solely on these collecting methods. Further, cryptic arthropods may also redistribute in subtle ways among habitats (Ch. 24).

The full life cycle of most canopy arthropods is unknown (but see Paarmann & Paarmann, 1997). One other notable exception is represented by the canopy grasshoppers of the Amazon, which have been well studied by Amédégnato (1997; Ch. 22). Their spatial distribution is extremely complex as they exploit different types of food from the litter to the overstorey, lay eggs on different substrates and represent different assemblages in the succession of the vegetation. They include both specialists and generalists and it is very possible that many species show rather narrow habitat specificity (oviposition substrate, stratification), but a wider use of plant resources.

Recent studies of beetle assemblages by fogging in wet forests (e.g. Basset *et al.*, 1996a; Chs. 14, 18 and 19) indicate that many representatives of this taxon may not be as host specific as early fogging studies claimed (e.g. Erwin & Scott, 1980). In particular, Kitching *et al.* (Ch. 29) show that as inter-tree taxonomic distance increases, there is a clear decline in beetle similarity for faunal assemblages. However, inconsistencies emerge when taxonomic sample size gets smaller, as different taxa do not respond similarly.

Using a different approach based on collecting *in situ*, Ødegaard (Ch. 33) records that each plant species studied in a small area of dry forest in Panama supported an average of 51 species of phytophagous beetles. Effective specialization was 13.9 beetle species per plant, so that host specificity in the whole forest was estimated to be 7–10%. Such a forest may harbour 1600–2000 species of phytophagous beetles, but probably only 40% of the species belongs to described taxa. This last figure scales the magnitude of the task awaiting taxonomists, even in a country where the arthropod fauna has been reasonably well studied, such as Panama. The estimates of species richness appear surprisingly low and probably result from the small area being studied (the crane perimeter) and low replicates in terms of individual trees. Here again, estimates of host specificity are lower than early guesses of 20% of beetle species being host specific (Erwin, 1982).

Beetles feeding on flowers appear not to be very host specific and they may form random assemblages not consistent in space and time (Ch. 23). Beetles may be flying from far away to reach the flower resources. Flowering events are significant since they represent a conspicuous, easy to access resource and further provide important meeting points ('concourses') for conspecific insects. Indeed, loose niches in plant–pollinator systems within rainforest canopies appear relatively common and often involve generalist plant–pollinator relationships (Ch. 32). Although this remains to be proven, flower visitors may be specialized with regard to habitat (flowers in the canopy, or understorey, perhaps certain features of flowers), but less discriminating with regard to the identity of the flowers.

Janzen (Ch. 33) provides a comprehensive overview of host use for 31 saturniid species on 370 woody dicot species, representing 66 families, in a dry forest in Costa Rica. Comparable datasets, even for other Lepidoptera, are currently not available. Janzen notes the difference between oviposition and feeding records, and focusses on the latter. Although many species are rather specialized, probably few can really be considered as being monophagous. A similar pattern exists in leaf-chewing insects in lowland wet forests of New Guinea (Novotny *et al.*, 2002a). Interestingly, many plant species or families locally available in the study area in Costa Rica are not fed upon, even by the most polyphagous species. Further, Janzen contends that saturniid–plant interaction at Guanacaste probably do not result from intricate pairwise coevolution, but rather from ecological 'fitting' (Janzen, 1985b) of immigrant species. He predicts that these patterns may apply to other diverse tropical canopy and large caterpillars.

In an ingenious experiment, Jaffé *et al.* (Ch. 20) show that flowers in a savanna display more features that repel ants than do canopy flowers in a wet forest. Canopy flowers appear to be adapted to tolerate ants. This sheds some new light on the intricate relationships between ants and plants. It also suggests that specialized ecological interactions or coevolutionary processes have occurred less commonly in the canopy of wet forests than in savannas.

The emerging picture from this compilation of studies is that tropical canopy arthropods may be less specialized than previously thought with regard to resource use (early arguments: Beaver, 1979; Basset, 1992a). At the same time, they may be more specialized than previously thought with regard to habitat use, particularly with regard to specific habitats situated within different strata in tall wet forests (see Ch. 3). The conservation implications are not comforting, implying that small levels of disturbance that alter arthropod habitats, breaking the canopy surface for example, may have significant negative consequences.

IMPROVING OUR KNOWLEDGE OF CANOPY ARTHROPODS IN THE TROPICS

Themes currently lacking in canopy entomology and future directions of research

In biogeographic terms, most of our knowledge originates from the neotropical region (12 contributions out of 28 in this volume and see Basset, 2001b). African canopies are poorly known, heavily threatened by anthropogenic disturbance and deserve a concerted rapid 'action plan' for their study. Lowland wet forests are also the most studied forest type (Basset, 2001b). Research should also be expanded to focus on montane forests, savannas and dry forests, the last representing one of the most endangered tropical biomes (Janzen, 1988c). Data on resource and habitat use, among other things, for particular higher taxa occurring in different types of tropical forest would be most useful. To date, these data are mostly restricted to butterflies (e.g. Spitzer *et al.*, 1993; Brown & Hutchings, 1997), which are neither particularly speciose nor particularly tied to forest canopies (Basset *et al.*, 1998). In addition, next to nothing is known about how insect herbivores, for example, use resources in monodominant and mixed wet lowland forests, respectively. Monodominant stands are relatively common in the tropics (e.g. Hart, 1990) and their comparative study would certainly be a most instructive example. Since monodominant species often grow slowly (e.g. Hart, 1990), they may be well defended chemically and relatively unpalatable to insects; consequently, they may support a relatively high proportion of generalist insect herbivores (Basset, 1999b).

It has already been emphasized that our current knowledge of canopy arthropods is strongly biased towards beetles and ants (Ch. 5). Taxonomical biasses against invertebrates are reviewed elsewhere (Basset, 2001b); see also Ch. 16 for a plea to study Dipteran assemblages in the canopy. In particular, insect predators and parasitoids (mostly Hymenoptera Parasitica) are two guilds for which the information relevant to tropical canopies is particularly scarce. Apart from studies of community structure focussing on predator–prey ratios (e.g. Gaston *et al.*, 1992; Basset, 1995, Krüger & McGavin, 2001) and predatory arboreal ants (review in Ch. 30), few studies have been concerned with these guilds and the relevant arthropod taxa. Hymenopteran parasitoids are particularly diverse in tropical canopies (e.g. Noyes, 1989b; Askew, 1990; Stork, 1991; Horstmann *et al.*, 1999), but their autoecology and synecology have been rarely studied (e.g. Memmott *et al.*, 1993; Godfray *et al.*, 1999).

With regard to other resources available and prominent in canopies, sap-sucking and fruit-feeding/seed-eating herbivores have been rarely studied (see Ch. 5). For the last group, although studies of postdispersal seed attack by insects are plentiful, studies of predispersal attack in the canopies of tropical forests are few (e.g. Janzen, 1983b; Forget, 1994; Delobel *et al.*, 1995; Peredo Cervantes *et al.*, 1999). Predispersal seed predation is most likely to be limited by either predator satiation or environmental factors affecting adult oviposition and larval development, whereas postdispersal predation may reach 100% through an expansion of the insect population in highly disturbed forest habitats (e.g. Wright, 1990).

The significance of the upper canopy has been stressed several times in this volume. In particular, the data of Basset *et al.* (Ch. 27) suggest that insect herbivores of the upper canopy may be resident and well adapted to environmental conditions there. Whether the fauna collected in the upper canopy is very specialized and whether it is different from that foraging a few metres below in the canopy represents a key follow-up question for exploration. Since the upper canopy may well be distinguished from the lower canopy only in closed, relatively flat and undisturbed rainforests, the implications for the conservation of tropical rainforest arthropods may also be important. In this context, it is perhaps surprising that the biological significance of the 'inversion surface' (*surface d'inversion*) of Oldeman (1974) has never been assessed for the arthropod fauna and, particularly, for insect herbivores. Briefly, this is the zone where water becomes the limiting factor for tree growth and where photosynthesis is performed with a minimum of transpiration. It roughly corresponds to the first branching of dominant trees (Oldeman, 1974). In French Guiana, Sterck and Bongers (2001) recently showed that regressions of plant traits against tree height were linear with study trees below 25 m in height, and become nonlinear with taller trees. Light availability was not considered to be an important selection force acting on architectural changes with tree height. Thus, branching patterns in the upper canopy may be different from those below (e.g. Hallé *et al.*, 1978; Bell *et al.*, 1999; Sterck & Bongers, 2001), with likely consequences for the arthropod fauna.

The consequences of the high leaf turnover in the upper canopy (e.g. van Schaik *et al.*, 1993; Coley & Kursar, 1996) should not be underestimated for insect herbivores, which are often highly dependent on windows of availability of young foliage (e.g. Aide & Londoño, 1989; Basset, 1991d). High leaf turnover may select for extremely specialized herbivores feeding on young foliage, providing that the resource base is large enough (Basset, 1996a); for specialists feeding on mature foliage and able to cope with its toughness and low nutrient content; or for generalists feeding on young foliage. It would be particularly stimulating to compare the habitat and resource use of arthropods in the understorey and upper canopy of tall wet forests. In the same vein, a study of faunal similarity between the upper canopy and forest gaps in a wet forest would be of the utmost interest to understand what proportion of fauna may be lost when the upper canopy is disturbed by logging.

Recent advances in community models could help us to understand better the effects of fluctuating resources in the canopy on arthropod assemblages. In particular, nonequilibrium models explain diversity as a balance between immigration and extinction, with the species composition itself constantly changing (e.g. Bell, 2001; Hubbell, 2001; Chave *et al.*, 2002). Roubik *et al.* (Ch. 32) show that this approach is promising for studying flower resources and their associated visitors, but it may also be relevant to other resources and their associated arthropods, as well as to the study of arthropod vertical distribution, especially when daily or seasonal vertical migrations occur (see Ch. 3).

Our knowledge of canopy arthropods in the tropics is particularly thin when discussing food-webs (Godfray *et al.*, 1999). However, this situation is unlikely to improve for tall wet forests unless the important issues of canopy access and replication can be solved (Ch. 2). More humbly, we will have to initiate work in plantations (e.g. Memmott *et al.*, 1993) or forests with easily accessible canopies, such as savannas (Ch. 31). As our methods of study, databases and canopy science mature, we may be able to seek the answer to more ambitious questions and to perform more consequential studies.

How to study canopy arthropods inexpensively

Most tropical forests are situated in the Third World. As a consequence, local entomologists rarely have the opportunity to study tropical canopies with sufficient infrastructure and funding (Kitching & Clarke, 1989) and the present volume reflects this unfortunate state of affairs. Long-term arthropod studies are more likely to originate from international collaborative programmes based in the tropics, often well funded by developed countries (e.g. Guanacaste area: Janzen, 1998; La Selva: Longino & Colwell, 1997; Barro Colorado Island: Leigh, 1999; Manaus: Fonseca *et al.*, 1998; Lambir Hills: Yumoto *et al.*, 1996; Danum Valley: Marshall & Swaine, 1992). Unfortunately, most of these programmes are based in the neotropics.

We emphasize here that it is crucial to encourage the study of canopy arthropods by local entomologists. It can be achieved through the above-mentioned programmes, although concentration of resources and research may not always be desirable, particularly when studying highly heterogeneous environments. The other strategy is to implement inexpensive methods of collecting and studying arthropods in canopies, such as those presented by De Dijn, and Koike and Nagamitsu in Chs. 8 and 11. Arguably, there are methodological problems related to the use of these methods, but these are no more severe than for many other collecting methods. The key point is to be aware of the limitations of the method selected, to ensure that it is relevant to the question(s) asked, and that it will allow a straightforward interpretation of the data (e.g. Basset *et al.*, 1997b). A supplementary approach is to train local parataxonomists to help with the research (Ch. 2).

Conservation of tropical canopies and their inhabitants

This is an important topic of research (see Soulé & Orians, 2001; Ch. 2, 18 and 34). In Malaysia, loss of diversity in selectively logged forests is not drastic compared with the diversity of primary forests (Ch. 34). Alteration in guilds and loss of species is obvious only in exotic plantations. Still, these provide refuges for the fauna, providing that the understorey is well developed (unlike in oil palm plantations). It is not clear whether these considerations would still apply if the fauna of the upper canopy had been specifically targeted by the study (see Willott, 1999).

In contrast to these rather optimistic views, Floren & Linsenmair (Ch. 18) report, also from Malaysia, strong effects of anthropogenic disturbance. For example, 40 years after disturbance, the fauna of the disturbed forest is still different from that in the primary forest. There is a transition from deterministically structured communities to random ones through forest succession. In particular, assemblages of Coleoptera and Formicidae show deterministic patterns in disturbed forests, whereas nonequilibrium conditions mediate species coexistence in primary forests (random assemblages). This argument in itself is worthy of further investigation since, for example, ant mosaics appear to exist and are deterministically structured in primary rainforests (Ch. 30; counter-argument in Floren & Linsenmair, 2000a).

What are the effects on arboreal arthropods of the opening of the canopy after the creation of natural or anthropogenic gaps? Do the upper canopy and its fauna 'fall' to the ground? As far as insect herbivores are concerned, the short answer to this is most likely no, since forest gaps typically include a different set of plant species (pioneers) than are present in the mature canopy (shade-tolerant species), and many insect species are relatively specialized. In addition, herbivores foraging on mature trees in Guyana do not invade conspecific seedlings subsisting in logged and more illuminated patches (Basset *et al.*, 2001b). Taxa less tied to resources occurring specifically in the upper canopy, such as dung beetles, do not appear to suffer much from canopy loss and survive well in the understorey of disturbed forests (Davis & Sutton, 1998). This and related issues warrant further investigations.

And . . . how many species?

We cannot close this volume without commenting briefly on the fundamental question of how many species; this has been at the core of early studies in canopy entomology in the tropics (e.g. Erwin, 1982; Stork, 1988). It is becoming increasingly clear that global estimates of biodiversity cannot be based on a handful of canopy studies. There are various reasons for this but most significantly it is because of the tremendous variance in the distribution of arthropod diversity among biogeographical locations and forest types (e.g. May, 1990; Thomas, 1990a; Basset *et al.*, 1996a; Ødegaard, 2000c; Novotny *et al.*, 2002b). The research has now shifted towards understanding how biodiversity is distributed in tropical forests, how it is maintained and how it can be preserved from anthropogenic disturbance. We hope that this volume has brought some element of response to these questions, has stimulated confirmed canopy entomologists to seek even more ambitious investigations, preferably of a collaborative nature, and that it will stimulate students to pay attention to one of the most fascinating habitats on Earth and its little-known inhabitants.