

Vertical stratification of arthropod assemblages

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ABSTRACT

We review the information available on the vertical distribution of arthropods in tropical forests, especially rainforests. In these forests, faunal boundaries are likely to occur between the soil/litter layers, between these and the canopy, and in some instances between the upper canopy and lower levels. The major determinants of arthropod vertical distribution can be grouped in four categories: abiotic factors, forest physiognomy and tree architecture, resource availability, and arthropod behaviour *per se*. Many arthropod species are likely to forage at preferred levels within the rainforest canopy, to locate their preferred food resources, for example. Strict stratification in the canopy of closed and wet tropical forests has been reported for certain scavengers and fungal feeders, herbivores and ants but is less evident for generalist predators and biting flies. With respect to stratification of arthropods, the most evident and probably key distinction between temperate and tropical wet forests lies in the lack of pronounced vertical gradients (in microclimate and biotic factors) in the former. In particular, the presence of an upper canopy layer in closed tropical rainforests that is well delineated in terms of physiognomy and microclimate provides the most obvious explanation for the occurrence of richer and more distinctive arthropod assemblages in the uppermost parts of these forests compared with temperate forests. Overall, unambiguous data on the differential occupancy of vertical space by tropical forest arthropods remain few. With respect to the task of assembling and interpreting additional data, we stress the importance of appropriate methodology, of utilizing data available for temperate forests, of obtaining natural history information on the arthropods studied, and of placing investigations of canopy arthropods firmly in the context of the forest system as a whole.

INTRODUCTION

Vertical stratification (as opposed to altitudinal stratification) represents the distribution of organisms along the vertical plane (e.g. Dajoz, 1982) and is more or less well-marked depending on study systems (plant species in forests, plankton in lakes, microarthropods in soils, etc.). This chapter discusses the extent of vertical stratification of arthropods in tropical forests. For the sake of consistency, and as generally convenient locators of samples or observations, we generally employ the terms soil, litter, understorey, upper canopy, overstorey and canopy (the latter encompassing the three previous levels), as defined in Ch. 1. However, this is not intended to imply that these layers are necessarily well demarcated or that their fauna are necessarily distinct.

First, some necessary words of caution. One must agree with Smith (1973), for a similar argument about vegetational strata, that for rigorous demonstration of arthropod stratification, data must be collected at numerous, randomly located sampling points along vertical, ground-to-canopy transects. Because of the difficulties of canopy access, such data are virtually lacking. Data are often collected nonrandomly in the litter, understorey and upper canopy, more rarely in the midcanopy. For the few datasets available (see below), this gives an impression of faunal discontinuity among different putative strata, which is almost certainly an artefact. However, as discussed in the next section, faunal discontinuities may be real at the boundaries between the litter and understorey, and perhaps also between the canopy surface and the lower parts of the canopy.

Few resident arthropod species are to be found evenly distributed through any given tropical forest at any one time. In addition, different life stages may occupy different parts of a forest, and individuals too may move in response to temporal changes (daily rhythms,

weather, season) in their environment, or to fulfil varying needs (dispersal, mate-finding, etc.). Against this dynamic background, it is not surprising that there is inconsistency in just what is meant by 'stratification' as applied to arthropod assemblages. Following Intachat and Holloway (2000), we discriminate between (i) preferences in the vertical distribution of organisms from ground to the overstorey (aggregated as opposed to uniform or random distribution), and (ii) strong clumping of these preferences in true 'strata' within the vertical column, resulting in clear 'faunal boundaries' and distinct arthropod assemblages. We consider the latter to be strict stratification. We recognize, however, that assemblages may be time limited (e.g. evident only at certain seasons), and that for some species assemblage membership may be confined to a particular life stage. The distinction between (i) and (ii) above may require subtle statistical analysis (e.g. Rodgers & Kitching, 1998) and may also depend on the forest layers being compared (e.g. understorey versus midcanopy, understorey versus upper canopy, etc.).

Many entomologists have taken advantage of recent advances in canopy access to study canopy arthropods (see Ch. 2). Much of this recent ecological literature would leave the reader with the impression that the study of vertical stratification in tropical forests had not begun before the 1970s. On the contrary, there is a diverse literature, much of it in medical entomology journals, on much earlier efforts to study vertical stratification of biting flies and other economically important insects (e.g. Bates, 1944; Mattingly, 1949). Further, many observations on the vertical distribution of arthropods in tropical forests, made in the course of largely ground-based studies, stem from even earlier times. Many of the findings of the great Victorian naturalists such as Alfred Russell Wallace and Henry Bates (see Elton, 1973), along with those of their successors, remain instructive but represent a seemingly underappreciated resource. For many of the early investigators, the simple expedient of felling selected trees (or seeking out freshly fallen ones) provided the opportunity to collect many canopy arthropods (e.g. Bryant, 1919). Early efforts to study stratification outside of medical entomology included Allee (1926) on Barro Colorado Island, Panama and Hingston (1930, 1932) and associates in Guyana. The methods may have been primitive by today's standards, but the scale of samples taken on various kinds of platform suspended in trees remains impressive.

A particularly ground-breaking effort was the series of studies of Haddow *et al.* (1961), who used a 40 m tower, originally built at Mpanga, Uganda, in 1958 for mosquito studies. Haddow's team found that some climatic parameters showed little variation vertically (temperature and saturation deficiency, a measure of humidity), whereas others did (wind and light). Vertical stratification was observed in breeding sites of mosquitoes, but patterns of stratification varied among different insect groups. In some groups, males and females exhibited different patterns. In addition, because of the cycles involved in flight patterns, some kinds of trap gave biased views of overall population activities. Haddow's group also published some of the first detailed observations of insect behaviour above the canopy, noting especially the swarming activities of mosquitoes. The data were used in broader discussions of interactions between endogenous (genetic) and exogenous (environmental) components in determining patterns of insect behaviour (Corbet, 1966).

In this review, we first discuss the compartmentalization of tropical forests and the extent of arthropod stratification there. We then examine the information available on gradients of species richness, discuss determinants of arthropod stratification in tropical forests and comment upon the extent of stratification across different arthropod guilds.

COMPARTMENTALIZATION AND THE EXTENT OF ARTHROPOD STRATIFICATION IN TROPICAL FORESTS

There is a large body of literature originating from the study of forest entomology in temperate areas showing that (i) the soil fauna is stratified among different soil layers (e.g. Gisin, 1943; Stebayeva, 1975); (ii) the soil/litter fauna is in large measure distinct from that of the forest above (e.g. Luczak, 1966; Cherrill & Sanderson, 1994; Osler & Beattie, 2001); (iii) many arthropods, especially herbivores, show vertical preferences in their distribution within the canopy (e.g. Morris, 1963; Nielsen, 1978; Gross & Fritz, 1982; Philipson & Thompson, 1983; Bogacheva, 1984); however (iv) distinct herbivore or other arthropod assemblages are not generally recognizable at different canopy levels, even, in the case of leaf-feeders, between the foliage of seedlings and that of conspecific mature trees (e.g. Fowler, 1985; Godfray, 1985; Schowalter & Ganio, 1998; Le Corff & Marquis,

1999). Item (iii) is well known to forest entomologists and often results in stratified sampling of pest populations (e.g. Morris, 1960).

Are these findings equally applicable to tropical forests? Available evidence suggests this is generally so for conclusions (i) and (ii) (e.g. Duviard & Pollet, 1973; Schal & Bell, 1986; Adis *et al.*, 1989; Hammond, 1990; Longino & Nadkarni, 1990; Longino & Colwell, 1997; Brühl *et al.*, 1998; Rodgers & Kitching, 1998). Items (iii) and (iv) are more difficult to evaluate, and discussion of them forms the substance of the present review. Before examining vertical gradients of species richness within tropical forests, we must first comment on the compartmentalization of these forests and related topics in general. Differences in the vertical distribution of arthropods in different forest types (e.g. montane, dry, lowland) are discussed in the concluding chapter of this book.

What is immediately clear is that variability is not expressed in most instances entirely or even mainly in terms of vertical strata. Indeed, it is arguable that, once away from the forest floor, strictly vertical stratification is not the norm. Nevertheless, in the canopy, using the term in its broadest sense, some stratification is evident. For example, the extremes in physical conditions experienced at the interface between the forest and the free air above justify the recognition of this uppermost part of a forest as a distinct stratum. Many abiotic and biotic characteristics of the upper canopy of closed tropical rainforests are different from forest layers below, especially from the understorey. For example, in a rainforest in Cameroon, the characteristics of the canopy surface are more akin to chaparral shrub vegetation than to familiar rainforest understorey vegetation (Bell *et al.*, 1999). Whereas the upper canopy receives close to 100% of the solar energy, less than 1% of this energy reaches the understorey (Parker, 1995). Average light availability decreases up to two orders of magnitude over short distances from the external surface to a few centimetres inside the canopy (e.g. Mulkey *et al.*, 1996). Levels of ultraviolet, fluctuation of relative humidity and air temperature, and wind speed are notably higher in the upper canopy than in the understorey (e.g. Blanc, 1990; Parker, 1995; Barker, 1996). Water condensation at night is frequent within the upper canopy but absent in the understorey (e.g. Blanc, 1990). The leaf area density and the abundance of young leaves, flowers and seeds are also usually higher in the upper canopy than beneath

(Parker, 1995; Hallé, 1998). Leaf turnover and nitrogen translocation, upon which many sap-sucking insects depend, are well marked in the upper canopy (Basset, 1991e; 2001a). The leaf buds of the upper canopy appear to be extremely well protected against desiccation and herbivory (Bell *et al.*, 1999). Further, levels of secondary metabolites that are biologically active within individual trees are much higher in leaves of the upper canopy than in leaves situated at the base of the crown (Hallé, 1998; Downum *et al.*, 2001).

Beneath the upper canopy, vertical strata are much less clearly demarcated in terms of the physical and biotic features most likely to determine arthropod distributions. There are obvious exceptions: for example, individual tree cavities may exhibit clear internal vertical stratification. Are there alternative or better ways of talking about a forest in terms of 'naming of the parts'? This is not a trivial matter as the answer may have a direct bearing on how we go about studying and reporting on within-forest distribution. In much of the space between the ground surface and the upper canopy, a useful approach may be to deal with 'compartments', for example, the main trunk area of trees, 'free space', other spatially defined blocks of the canopy, and the habitats/microhabitats such as fungus fruiting bodies, carrion, inflorescences and so forth, distributed within them.

Although a growing body of literature on 'stratification' in tropical forests exists mainly from the 1970s, few datasets on the composition of arthropod assemblages in tree crowns are extensive enough to evaluate whether these are truly stratified or compartmentalized (but see the contributions in Part II). The main shortcomings responsible for this situation are the absence of any reference to the composition of assemblages found at lower levels; the comparison of the distribution of various taxa that differ significantly in biology; and a lack of uniformity in the methods used to sample or appraise different assemblages, sometimes even among different putative strata.

As discussed in the next section, most arthropod species in most forests are effectively confined to the lowest layers (soil and soil surface habitats). Nevertheless, many species associated with soil and soil surface habitats are represented in samples taken from compartments above the forest floor, where they are often best regarded as vagrants, tourists or, at most, short-term visitors (e.g. Adis, 1984b; Hammond, 1990); others

are more appropriately regarded as 'stratum generalists' (Hammond *et al.*, 1997). Knowledge of the assemblages tied to these lowest forest strata is, therefore, essential (e.g. Haddow, 1961) if sample data from the canopy are to be used effectively in the characterization of the various assemblages occupying the upper levels of a forest.

Many studies have found, in general, significant differences in composition and abundance of arthropods at different vertical levels in the trees, but questions of what is actually being sampled and the lack of understanding of the biology of the organisms have limited the conclusions that can be drawn. Some studies find greater abundance at higher levels (e.g. Basset *et al.*, 1992), whereas others find greater abundance at lower levels (e.g. Wolda *et al.*, 1998) or no significant differences are observed (e.g. Intachat & Holloway, 2000). Further, a large body of literature focusses on arthropod samples obtained from the forest 'canopy', usually referring to samples obtained 15 m or more above the ground, by various methods (reviewed in Basset, 2001b). Most studies with insecticidal fogging (e.g. Erwin, 1995), light traps (e.g. Sutton, 1983; Wolda *et al.*, 1998) or by felling trees (e.g. Amédégnato, 1997; Basset *et al.*, 1999) do not sample the upper canopy selectively and efficiently. Improved canopy access (Ch. 2) has allowed entomologists to refine their sampling protocols, in order to obtain replicated samples of the upper canopy and question whether stratification is maintained both during day and at night (Basset *et al.*, 2001a), or during seasonal events (Ch. 7).

Based on a review of recent literature, we argue in the following sections that vertical stratification may be more distinct in tropical than temperate forests but may only concern certain taxa during certain life stages.

VERTICAL GRADIENTS OF SPECIES RICHNESS: SOIL VERSUS CANOPY FAUNA

Globally, are arthropod faunas more species rich in the canopy than in the soil of tropical rainforests? This question (although not the only one of relevance: see Basset *et al.*, 1996a) has been central to global estimates of arthropod species richness derived from surveys of arboreal arthropods on particular host trees (e.g. Erwin, 1982; May, 1990). Erwin (1982) contended that the canopy fauna was the most species rich but the subsequent evidence seems contrary (e.g. Hammond, 1990, 1995; André *et al.*, 1992; Hammond *et al.*, 1997; Walter *et al.*, 1998).

It is worth reiterating that the problem of generalizing for all taxa and forest types remains. There are four additional issues, both for and against Erwin's contention, that are relevant to this particular debate. First, it is difficult to compare soil and canopy faunas, since they need to be surveyed by different sampling methods (see Ch. 9). For example, extremely high densities of springtails occur in the canopy of certain dry forests in Mexico (Palacios-Vargas *et al.*, 1998) but how do they compare with springtail densities in the soil and litter? Sample size is different and not directly comparable. Furthermore, the number of individuals collected is not a valid criterion in this context, since it is highly dependent on the amount of habitat sampled. The volume of habitat sampled may be a better descriptor of sample size, but it is difficult to estimate for the canopy habitat.

Second, Acari are often dominant but underestimated in arboreal habitats (e.g. Walter, 1995), whereas they are relatively well sampled in soil and litter habitats. Since this taxon is dominant in the soil of rainforests (e.g. Stork, 1988), comparison between the faunas of soil and canopy must ensure that Acari have been well sampled in the latter. To date, no tropical study has had sufficient scope to survey representatively *all* arthropod taxa within a vertical transect of forest.

Third, assessing the diversity of soil versus canopy biota evidently also depends on patterns of β -diversity. If faunal turnover is rather high in the canopy (because of the relatively high specialization of insect herbivores and associated specific predators and parasitoids on particular host-tree species, see Ch. 5), compared with that in the soil, it may be inappropriate to compare the diversity of equivalent projected areas of canopy and soil. Monodominant stands aside, the β -diversity of canopy communities may be much higher than that of soil communities in rainforests. For example, the β -diversity (and 'host specificity') of soil mites is very low in Australia (Osler & Beattie, 2001). Note, however, that at the appropriate scale a correlation between below-ground and above-ground biodiversity may exist (Hooper *et al.*, 2000). In particular, plant diversity, because of the production of diverse root exudates, can lead to increased diversity of mutualistic soil microflora, the first link of a cascade of effects resulting in increased diversity of other soil animals (Lavelle *et al.*, 1995).

Last, as emphasized repeatedly (e.g. Hammond, 1990; Basset & Samuelson, 1996; Chs. 2 and 5), faunal

comparisons rely on the taxonomic study of adult specimens, and juveniles are rarely accounted for, be they spiders or beetles. The most likely situation is for juveniles to develop in the soil, to move up into the canopy as adults and to feed and disperse from there (e.g. Hammond, 1990; Basset & Samuelson, 1996). In addition, one must factor in seasonal migrations upward into the canopy, especially during flooding (e.g. Adis, 1981, 1997a; Erwin & Adis, 1982). Do we always study the soil and canopy fauna separately in these conditions?

DETERMINANTS OF ARTHROPOD STRATIFICATION IN TROPICAL FORESTS

This and the following section are more relevant to the canopy fauna *per se*. Several popular hypotheses involving concepts such as tree architecture (Lawton, 1983), resource concentration (Root, 1973) or resource base (Price, 1992) could explain vertical gradients of insect diversity in tropical rainforests. These explanations are not mutually exclusive and can account only partially for the observed gradients. There may be many, most likely interrelated, factors that may induce arthropod stratification in the canopy of tropical rainforests. Depending on vegetation type, latitude and so on, some factors may be locally more significant than others. We discuss four categories of determinants with reference to how they may tune arthropod behaviour, from a coarse to a finer scale of behaviour: (i) abiotic factors; (ii) forest physiognomy and tree architecture; (iii) resource availability; and (iv) arthropod behaviour *per se*, including search for enemy-free space and dispersal. Each of these categories of determinants influences the lower one in the hierarchy but, for the sake of simplicity, we will discuss them separately.

Abiotic factors

Abiotic factors such as light, levels of ultraviolet, air temperature, relative humidity, wind and water condensation, to cite but a few, may have direct as well as indirect effects (i.e. through their strong influence upon other determinants) on arthropod stratification. Their significance should not be underestimated. Bates (1944), for example, recorded the flight of different species of mosquitoes at various heights in the canopy in Columbia. He noted that it is easy to find sections of the forest in which light is greater at ground level

than in the canopy, but the gradients of humidity and temperature seem never to be reversed by local conditions in the canopy. He also observed that mosquitoes react primarily to the humidity gradient, not to the light gradient. Accordingly, arthropod stratification could be maintained readily in tropical forests by strong gradients of abiotic factors alone. Similarly, the stratification of bark beetles in a lowland rainforest in the Ivory Coast is maintained by differences in relative humidity along the vertical transect (Cachan, 1974). The vertical distribution of Diptera in lowland dipterocarp forests in Malaysia is significantly affected by wind speed and minimum air temperature (Ng & Lee, 1980).

The quantity and quality of sunlight may also influence strongly the photosynthetic process at different levels in the forest, both in terms of primary and secondary metabolites. This, in turn, is likely to influence the quantity and quality of resources available to insect herbivores and their vertical distribution (see further discussion in Ch. 5). For example, most insect herbivores feeding on the Australian rainforest tree *Argyrodendron actinophyllum* Edlin respond primarily to the availability of young foliage, which depends directly on the local light regime. In this case, stratification is not well marked as it depends on local differences in illumination within tree crowns, which can vary substantially among individual trees (Basset, 1992c).

Wind speed within different forest layers may influence significantly insect flight in temperate forests (e.g. Nielsen, 1987), but this has not been well studied in tropical forests (Ng & Lee, 1980). Schal (1982) reported that, in Costa Rica, cockroaches stratify vertically both inter- and intraspecifically along micrometeorological gradients. This observation relates to the ascent of warm air and pheromone dispersion at night and represents a mate-finding strategy. Perching of dung beetles on the foliage also perhaps represents a form of behavioural thermoregulation and/or a strategy to maximize the detection of scents in the air and a consequent resource partitioning (e.g. Young, 1984; Davis, 1999b). Other factors, such as dust accumulation on the foliage, with effects that have been well studied for rainforest vertebrates (e.g. Ungar *et al.*, 1995), could also influence the vertical distribution of arthropods.

Forest physiognomy and tree architecture

The forest physiognomy, including features such as the height of the canopy, the disposition of large tree

trunks, the leaf area index, the occurrence of free space (openness) and so forth, as well as the tree architecture (Lawton, 1983: height, biomass, size and abundance of leaves, flowers, seeds, etc.), represents resources in their own right. However, these features also have a bearing on the way that the 'primary' resources are distributed and may influence arthropod foraging activity. For example, the localization of flight height in Lepidoptera is not so developed in the more open forests of lesser stature such as lowland forests of Sulawesi and Seram, compared with that in tall Bornean forests (J. D. Holloway, personal observation). In addition, the extent of faunal stratification may depend on the slope of the terrain (Sutton, 1983) and on local flooding regimes (e.g. Adis, 1997a).

Tree architecture, including the varying biomass of conspecific seedlings, saplings and trees, is a significant determinant of the richness of associated insect herbivores in tropical trees (e.g. Basset *et al.*, 1999; Basset, 2001a; Caraglio *et al.*, 2001; Chs. 5 and 25). Differences in the volume of habitat available often correlate with resource availability (e.g. higher occurrence of young foliage, flowers and seeds in mature trees than in seedlings or saplings).

Studies of vegetational strata in temperate and tropical forests suggest two possible further hypotheses for the maintenance of arthropod stratification in tropical forests (Smith, 1973).

1. Plant stratification, by providing clear 'flight paths' for insects, birds and bats above and below each stratum, may increase the probability of pollination or seed dispersal. In other words, production of open areas in the canopy through stratification may have selective value.
2. Canopy-level predation on tree flowers, fruits, buds and leaves may select for aggregation of the foliage of different plant species into one or more common strata. If many tree species produce mature foliage at a common level (as opposed to each species producing mature foliage at its own characteristic level above the ground), any herbivore specializing in a particular species would need to spend more time and energy searching for its host. So stratification might confer protection against herbivory.

Despite the proven existence of clear flight paths for arthropods in rainforests (e.g. Shelly, 1988; Ch. 8), it is difficult to comment on the validity of the first hypothe-

sis without further data. Recent and comprehensive data about the host specificity of tropical insect herbivores, including several tens of replicates of both individuals and tree species, suggest that many insect species specialize at the generic or familial, rather than specific, plant level (Novotny *et al.*, 1999b, 2002a). For mixed and botanically diverse forests, such data would not appear to support the second hypothesis.

Resource availability

Resource availability and its use by insect herbivores in the canopy are discussed in more details in Ch. 5. As already emphasized, the quantity and quality of resources for herbivores (young foliage, flowers, fruits, seeds, etc.) differ between the understorey and upper canopy and globally this should result in higher abundance/diversity of herbivores in the upper canopy, as well as the occurrence of strata specialists (e.g. Basset *et al.*, 1992, 2001a; Basset, 2001a; Chs. 5 and 25). The major volume of tropical forests is in the canopy, and a wide range of habitats are scattered or non-existent in the understorey. For example, the greater part of production and structural diversity of lianas occur in the mid- or upper canopy (Hegarty & Caballé, 1991) and many herbivores specialize on them (e.g. Stork, 1987a; Ødegaard, 2000a). Low values of leaf area index in the understorey, as compared with that in the upper canopy, are likely to affect not only the resources available to insect herbivores but also how they can escape their potential enemies.

The quality of resources may also represent a significant factor. Hallé (1998) has argued that the exposure of canopies should result in high concentration and diversities of compounds, either developmentally controlled or induced by light, wind, desiccation and/or exposure to herbivores and pathogens. Yet, the evidence for increases in compounds relative to the understorey is meagre and primarily from colorimetric assays for tannins and total phenols (Coley & Barone, 1996). Recently, Downum *et al.* (2001) showed that the crowns of rainforest trees produce significantly more secondary compounds and at higher concentrations than do understorey saplings. Some of the compounds are biologically active and could help to reduce damage from herbivory and disease. The canopy samples from each species showed dramatic increases (by more than four times) for the number of compounds and their relative concentrations. The greatest number of

compounds was produced from tree crowns: those exclusively from the crowns were half or more of the total number of compounds detected although a few compounds were produced in the understorey alone. These differences may result in discrete habitats, depending on the age and physiognomy of the forest stand but also on the ecological characteristics of the host plant (taxonomic isolation, height, crown volume, growth patterns and phenology). In turn, this would select for rather specialized herbivores either in the upper canopy or understorey. Accordingly, plant phylogeny may well influence both temporal patterns (Ch. 4) and the vertical stratification of arthropod assemblages in rainforests.

Certain resources are evidently more abundant in the understorey and near the ground, such as dead wood, litter, dung, fallen fruits, carrion, the availability of specific prey, and so on. These resources may attract different assemblages specific to the understorey (e.g. Davis *et al.*, 1997; DeVries & Walla, 2001; Schulze *et al.*, 2001). For example, most dung beetles are more species rich near the ground but certain species specialize on perched dung (Davis *et al.*, 1997). These canopy species rarely forage near the ground in primary forests but may sometimes be present at ground level in logged forests, tracking their preferred resources (Davis & Sutton, 1998).

Many adults of herminiine Noctuidae fly at low levels, where the larvae feed on litter and detritus (Holloway, 1984b; as Hypeninae). This poses the question 'to what extent is there resource fidelity?' For holometabolous flying insects, larval densities, pupation sites and adult flight levels may (e.g. Beccaloni, 1997; Willmott *et al.*, 2001) or may not (e.g. Van Klinken & Walter, 2001) be correlated. Is a larval/adult correlation to be deemed stronger if the intervening pupation site level is different (canopy larvae dropping to pupate in litter)? Is such a correlation stronger in taxa where the adults do not feed so resources are not 'pulling' in different directions (foliage versus nectar/fruit/carrion/salts)? Once again, these questions highlight the difficulty of interpreting distributional data and putative stratification without considering the entire life cycle of the species studied.

Arthropod behaviour

Specific patterns of arthropod behaviour may generate preferred distribution in the vertical plane and, per-

haps more rarely, strict stratification. One example of the latter could be mimicry rings, where groups of species become locked into interdependence in some way at a certain level in the forest (e.g. Papageorgis, 1975; Mallet & Joron, 1999). For example, the mimicry rings of ithomiines (Nymphalidae) show some patterns in flight height (e.g. Medina *et al.*, Beccaloni, 1997; DeVries *et al.*, 1999b; 1996) that may be tuned to local predator knowledge and could be a response to different guilds of predators that forage in different habitats (Beccaloni, 1997).

As for preferred vertical distributions, it is well known that sexual differences in adult butterfly behaviour may be resource based and may lead to observations of flight at different forest levels (e.g. Holloway, 1984c). For example, the males of papilionids and pierids are more prone to disperse and fly more in the open, whereas females are less often observed and fly more in the forest interior, searching for oviposition sites. Phenomena such as hill-topping and migration (and the response to light) are usually dominated by male butterflies. In addition, certain groups, such as Nymphalidae or Lycaenidae, may be more or less territorial, with males favouring sunlight gaps for perching (e.g. the Amathusiinae) or occupying specific areas of the forest floor (Holloway, 1984c; Novotny *et al.*, 1991).

Enemy-free space (e.g. Schal & Bell (1986) for cockroaches), competition (Enders (1974) for spiders) and aggregation of conspecifics are other factors that may induce preferences for particular forest levels, and perhaps stratification in tropical forests. Adult Japanese beetles, *Popillia japonica* Newman (Scarabaeidae), aggregate and feed most heavily in the upper canopy of their host plants. However, they begin to feed in the upper canopy for reasons unrelated to host nutritional variation (e.g. behavioural thermoregulation, visual orientation to the host silhouette), and top-down defoliation follows as additional beetles are attracted to feeding-induced volatiles acting as aggregation kairomones (Rowe & Potter, 1996).

Finally, arthropod dispersal may or may not promote strict stratification. Fig wasps in Borneo, for example, disperse mostly in the overstorey even where species are associated with host trees that do not fruit in the canopy. In this case, once the fig wasps detect the species-specific volatiles released by their host figs, they then may fly down into the canopy, where the lower wind speeds allow them to fly actively upwind to their hosts

(Compton *et al.*, 2000). In Uganda, many mosquitoes that feed almost exclusively at ground level may rise to the canopy after sunset and form substantial swarms in the overstorey (Haddow, 1961; Haddow & Corbet, 1961a; Haddow & Ssenkubuge, 1965).

With the above list of determinants in mind (abiotic factors, forest structure, disposition of habitats/resources and arthropod behaviour *per se*), the explanation for observed stratification of arthropods in forest may be sought through consideration of these factors. Unfortunately, our current knowledge of the autoecology of canopy arthropods in tropical forests is in most cases crude. For now, we will discuss resource availability and its influence on the vertical distribution of arthropods by contrasting representative taxa from different feeding guilds.

VERTICAL GRADIENTS AND ARTHROPOD GUILDS

We review briefly and separately the extent of stratification for the following guilds: biting flies; scavengers and fungal-feeders, including dead wood eaters; herbivores, including pollinators; predators and parasitoids; and ants.

Biting flies

There is a large body of information on both the vertical and horizontal distribution of representatives of the biting flies in tropical rainforests, originating from studies in medical entomology. The food resources of the guild do not appear to be well segregated along the vertical plane. However, foraging of biting flies is often influenced by abiotic factors such as humidity and light (e.g. Bates, 1944) and this may induce strong preferences for particular forest levels, depending on the structure of the forest. Indeed, stratification of adult biting flies does not appear to be well marked, although most species do show height preferences and, collectively, are often more abundant in the understorey (e.g. Ceratopogonidae: Arias & Freitas, 1982; Aguiar *et al.*, 1985; Azevedo *et al.*, 1993; Veras & Castellon, 1998; Culicidae: Bates, 1944; Mattingly, 1949; Murillo *et al.*, 1988). This pattern appears to be similar for larvae in their breeding sites (e.g. Galindo *et al.*, 1956; Corbet, 1961a; Lounibos, 1981; Lopes *et al.*, 1983; Murillo *et al.*, 1988). Certain species of Ceratopogonidae are well known to prefer foraging at canopy level (e.g. Arias &

Freitas, 1982; Aguiar *et al.*, 1985), and some Culicidae move to feed from canopy to ground and vice versa during daily vertical migrations (e.g. Haddow, 1961; Haddow & Ssenkubuge, 1965; Deane *et al.*, 1984). The latter phenomenon is of considerable medical importance, as it provides a link between the fauna of the forest canopy and that at ground level, including humans (Haddow & Ssenkubuge, 1965). Phytotelmata, particularly those provided by Bromeliaceae, are favourable breeding sites for many culicid vectors of human malaria and filariasis (e.g. Pittendrigh, 1948; Zavortink, 1973; Lounibos, 1981).

Scavengers, fungal-feeders and dead wood eaters

As well as the information presented in this volume (see notably Chs. 10 and 24), several studies more specifically targeting the scavenging and fungal-feeding fauna report on upward migrations in the canopy (e.g. Adis, 1984b), distinct faunas in the litter and canopy and associated flight preferences (e.g. Cachan, 1964; Schal, 1982; Walter, 1983; Young, 1983; Schal & Bell, 1986; Hammond, 1990; Rodgers & Kitching, 1998; Yanoviak, 1999; De Abreu *et al.*, 2001; Van Klinken & Walter, 2001), or the higher species richness and/or abundance in the litter compared with the canopy (e.g. Nadkarni & Longino, 1990; Paoletti *et al.*, 1991; Basset *et al.*, 1992, 2001a; Davis *et al.*, 1997; Hammond *et al.*, 1997; Walter *et al.*, 1998; Basset, 2001a).

Habitats for this guild, such as dead wood and associated fungi, appear to be relatively discontinuous and discrete along a vertical transect of rainforest (Ch. 25). This may limit the dispersal of some forest floor species higher up in the canopy and maintain distinct assemblages at different levels (Rodgers & Kitching, 1998). Although the amount of dead wood and suspended soil may not be negligible in the canopy, their abundance is highest at ground level (Nadkarni & Longino, 1990; Martius & Bandeira, 1998). In addition, the low relative humidity in the upper canopy may hinder fungal growth there. Consequently, we would 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. These conditions include greater illumination, more wind and frequent cycles of wetting/drying (Dajoz, 2000). Strict stratification could, therefore, occur for this guild. To date,

selective data relevant to the upper canopy and comparison with the lower levels of the forest are rare but indicate a clear stratification for representatives of Collembola, Acari and Buprestidae of the genus *Agrilus* (Rodgers & Kitching, 1998; Walter *et al.*, 1998; Curletti, 2000; Basset *et al.*, 2001a). However, the abundance and diversity of this guild should be highest near the ground (Hammond, 1990).

Herbivores

Given that the food resources for many herbivores, such as leaves, flowers and fruits, are more abundant in the upper canopy than in the understorey of wet rainforests (e.g. Hallé, 1998; Ch. 5), the abundance and diversity of many herbivorous taxa should be higher in the former strata. This appears to be the case for homopterans, herbivorous beetles, flower-visiting butterflies, caterpillars, fig wasps and certain euglossine bees (e.g. Wolda, 1979; Erwin, 1982; Sutton *et al.*, 1983a; Basset *et al.*, 1992, 1999, 2001a; Spitzer *et al.*, 1993; Kato *et al.*, 1995; De Oliveira & Campos, 1996; Compton *et al.*, 2000; Basset, 2001a; Schulze *et al.*, 2001; E. Charles, personal communication). Differences in foliage quality between the upper canopy and understorey (e.g. Downum *et al.*, 2001; see above and Ch. 5) may induce a clear stratification of herbivores, as reported in several studies (e.g. Amédégnato, 1997; Basset, 2001a; Basset *et al.*, 2001a; Ch. 25), particularly when taxa have a narrow host range, such as is the case for many gall-makers and leaf-miners (Medianero, 1999; Valderrama, 1999: faunal overlap between the upper canopy and understorey <1%). For many herbivorous beetles, this stratification may be complex, with juvenile stages feeding in the soil on roots and the adults feeding at different levels in the canopy (Basset & Samuelson, 1996; E. Charles, personal communication).

Exceptions to these 'general' patterns are also common. Fruit-feeding nymphalid butterflies and geometrid moths appear to be more active, abundant or species rich in the understorey than in the upper canopy (e.g. DeVries, 1987b; DeVries *et al.*, 1997; DeVries & Walla, 2001; Schulze & Fiedler, 1998; Intachat & Holloway, 2000; Schulze *et al.*, 2001). In general, bees do not forage consistently by strata. However, some understorey specialists are known, and species that prefer to forage in the upper canopy may have specific physiological traits, such as capacity for heat loss during flight, or may be nocturnal (Roubik, 1993; Roubik *et al.*, 1995).

This lack of concordance may be a result of differences in resource use and preferences across life stage, since larval distribution and adult flight behaviour may not necessarily be correlated. In some cases, juvenile stages may be feeding actively in the canopy, but adults may be dispersing in more open parts of the forests, such as in the understorey (in pristine forests) or overstorey. Indeed, sometimes they may not feed at all.

A few words should be said here about the Janzen-Connell model. In brief, this model states that patterns of herbivore attack below the parent tree are density dependent and decrease with increasing distance from the parent tree (Janzen, 1970; Connell, 1971). This process could promote botanical diversity by prohibiting establishment of young trees near conspecific parents (e.g. Janzen, 1970; Connell, 1971). One of the implicit assumptions in this model is that most insect herbivores that feed on seedlings are specialists that originate from and feed on the parent tree (Leigh, 1994). This assumption has repeatedly proven false when examining the distribution of insect herbivores on conspecific seedlings and mature trees in different tropical wet forests (Basset *et al.*, 1999; Basset, 2001a; Willmott *et al.*, 2001; Ch. 25); data considering leaf damage, such as Barone (2000) are unconvincing for reasons discussed in Basset & Höft (1994) and Hadwen *et al.* (1998). Janzen (1970) formulated the model when studying an insect-plant system in a dry forest in Costa Rica. This suggests that the model and its assumptions may be valid in situations where few barriers to the dispersal or maintenance of insect herbivores exist between mature trees and their conspecific seedlings. Alternatively, the model may apply only to postdispersal attack of seeds and may be irrelevant to attack upon seedlings or saplings near the parent tree.

Predators and parasitoids

The stratification and migrations of carabid beetles have been well studied in the Amazon (Adis, 1982; Erwin & Adis, 1982). Nevertheless, in general, few data exist on specific groups of predators and parasitoids in tropical canopies (Godfray *et al.*, 1999). Most data refer to levels of abundance and do not detail distribution patterns for specific species. For example, in Panama, the abundance of insect predators and parasitoids, but not that of spiders, was higher on the foliage of mature *Pourouma bicolor* Martius than on conspecific saplings (Basset,

2001a). In Gabon, parasitoids, particularly Scelionidae, were more abundant and active in the upper canopy than in the understorey (Basset *et al.*, 2001a). In Borneo, Encyrtidae are more abundant in the overstorey and upper canopy than in the understorey, but Mymaridae show the reverse trend (Compton *et al.*, 2000).

The extent of stratification of these groups probably depends on whether they specialize on certain prey/hosts or not. Generalist predators may not be strata specific, depending on whether they can tolerate environmental differences among different strata. Specialist predators and parasitoids are more likely to forage within the discrete habitats of their prey, as is known to occur for certain temperate species (e.g. Hollier & Belshaw, 1993; Redborg & Redborg, 2000) and are, therefore, more likely to be restricted to certain forest strata. Note that tropical parasitoids are not necessarily host specific, as many target egg masses of different arthropod hosts (Noyes, 1989b).

Ants

Depending on their nesting ecology, ant assemblages may often be distinct along vertical transects of rainforests (e.g. Wilson, 1959; Itino & Yamane, 1995; Brühl *et al.*, 1998; Yanoviak & Kaspari, 2000). Strict stratification has been reported in several studies (e.g. Longino & Nadkarni, 1990; Brühl *et al.*, 1998). One extreme specialization is represented by the famous ant gardens occurring in the canopy of neotropical forests (e.g. Wheeler, 1942; Davidson, 1988; Cedeño *et al.*, 1999). Although many studies have reported a high abundance or diversity of ants in the canopy of tropical rainforests (e.g. Erwin, 1983b; Stork, 1987b; Wilson, 1987; Tobin, 1991; Basset *et al.*, 1992; Dejean *et al.*, 1999), this is not a general rule. Often, it reflects but a few ant species able to feed on plant and homopteran exudates in the canopy, but which also may prey on other arthropods (e.g. Tobin, 1991; Itino & Yamane, 1995; Davidson, 1997; Kaspari & Yanoviak, 2001; Ch. 30). The choice of support trees by arboreal ants is not random (Ch. 30) and is perhaps related to the abundance and fitness of ant-attended homopterans on putative host trees.

One example is particularly eloquent. In one lowland forest in southern Cameroon, ants were significantly more abundant in the upper canopy than in the understorey, and many were attending Coccoidea in the upper canopy (Basset *et al.*, 1992; Dejean *et al.*, 2000e).

Not far from there, in a similar lowland rainforest in central Gabon, the reverse trend occurred. In this case, Psylloidea were much more abundant than Coccoidea and few homopterans were attended by ants in the upper canopy (Dejean *et al.*, 2000b; Basset *et al.*, 2001a).

In short, many arthropod species are likely to forage at preferred levels within the rainforest canopy, in order to locate their preferred food resources. Reinforcing this tendency, as well as acting in their own right, are the additional determinants of stratification discussed in the previous section. 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.

CONCLUSIONS

One essential difference between temperate and tropical wet forests may well prove to be the lack of pronounced vertical gradients in the former because of the less drastic vertical changes in microclimate and biotic factors (see Ch. 24). Although the upper canopy of wet tropical rainforests is often structurally and environmentally distinct from lower forest levels (e.g. Bell *et al.*, 1999), this stratum (or the extent of its distinctiveness), seems to be lacking in temperate forests. Lowman *et al.* (1993b) have suggested that the upper canopy of a temperate forest has proportionally fewer niches available to organisms compared with tropical forests. This, and the discontinuity of available habitats, could explain the stronger stratification observed in tropical forests and their richer fauna compared with temperate forests. Vertical gradients of species richness within wet tropical rainforests may be akin to gradients of latitudinal richness, when considered as a result of the control exerted by solar energy over organic diversity in conditions of unlimited water resources (Turner *et al.*, 1987).

One goal in planning new research on the spatial distribution of arthropods in tropical forest canopies should be to understand how these arthropods are distributed through the forest as a whole. Without this context, and especially when attempting to interpret the results of mass sampling, the composition of assemblages will be difficult to establish and the unique features of assemblages hard to determine. Assessing under what conditions a distinct upper canopy layer and its more or less specific fauna is maintained is also a research priority.

Much remains to be gained by examining what is known of stratification and compartmentalization of forest arthropod assemblages where these are best documented: in parts of the northern temperate zone (e.g. Dajoz, 1980; Strong *et al.*, 1984; Barbosa & Wagner, 1989; Schowalter, 2000). Of course, the extent to which the situation in a moist temperate forest may be extrapolated to the tropics is uncertain. Still, our understanding of arthropod distribution (vertical or horizontal) will progress considerably following appropriate comparisons of temperate and tropical systems.

To improve protocols and satisfy the rigour demanded by Smith (1973), sampling artefacts and biases need to be factored out, particularly where a bait such as light or fruit is being used, as it may pull an insect away from its usual 'cruising level' (see for example Byers *et al.* (1989) for calibration of flight height distribution in bark beetles and DeVries & Walla (2001) for mark-recapture studies). The simplest solution to these problems is to avoid any method of sampling that involves attractants, especially those, such as light, that are responded to from some distance. For valid comparisons, a prerequisite is for samples to be of the same type. However, even when the same method of sampling is employed, results obtained may be strongly affected by variables such as the mobility/activity levels of the arthropods themselves (e.g. pitfall traps, Malaise traps) or trap 'apparency' (e.g. pan traps), which, in turn, may be largely a function of structural differences (such as 'openness') in the immediate environment. Further, a minimum number of replicates is obviously needed to factor out site effects (Basset *et al.*, 2001a; DeVries & Walla, 2001) and it would be preferable to obtain selective samples along the whole vertical transect, not just from the understorey and upper canopy. There may be preference for traps that sample passively (suction, Malaise, intercept), though these rarely provide useful samples of groups like Lepidoptera.

It is difficult to draw general conclusions about the vertical distribution of insects in tropical forests. Long-term studies, such as those of Roubik (1993) and DeVries & Walla (2001), suggest that temporal movements up and down in response to changes in the environment (food and nectar sources, as well as microclimate) and in the insect populations (mating behaviours, for example) are of critical importance and can only be understood with long-term observations. With respect to vertical

stratification, data concerning samples of insects taken while in flight will always present a particular problem. Appropriate understanding of the biology of the individual species involved will, however, help to determine whether such data have any bearing on vertical gradients or stratification of some persistence, or merely catalogue the numbers of short-term or occasional visitors to a particular canopy level. Last, an improved framework for describing the within-forest distributions of arthropod species is badly needed. Ideally, this should reflect, at least in some measure, the ways in which arthropods themselves experience the heterogeneity of their setting.

In the context of tropical forests, the most evident explanations for a pronounced stratification of arthropod assemblages are marked vertical gradients of environmental factors and discontinuities in the occurrence of available habitats. These characteristics are most strikingly exhibited by tall, closed, mixed and wet rainforests growing on flat terrain. Since these same forests are those under the greatest threat, particularly from logging, the study of arthropod vertical distribution in situations where stratification is most evident may, besides its taxonomic, ecological and evolutionary interests, also have important implications in conservation biology.

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