ARTHROPODS
OF TROPICAL FORESTS

Spatio-temporal Dynamics and Resource Use in the Canopy

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Canopy entomology, an expanding field of natural science

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In 1929, O. W. Richards and his colleagues hoisted light traps into the canopy of a Guyana forest and became the first to collect arthropods quantitatively from the canopy of any tropical rainforest (Hingston, 1930, 1932). Today, canopy science has become a novel, burgeoning and exciting field in the natural sciences, as evidenced by the ever increasing number of publications focussing on this habitat (Nadkarni & Parker, 1994; Nadkarni *et al.*, 1996). The vitality of canopy science can be traced back to a series of studies about the canopy flora and fauna in tropical forests performed about 20 years ago, in which entomology figured prominently (e.g. Hallé *et al.*, 1978; Perry, 1978; Wolda, 1979; Erwin & Scott, 1980; Nadkarni, 1981; Lowman & Box, 1983; Adis *et al.*, 1984; Stork, 1987a). This sparked a lively and continuing scientific interest in tropical forest canopies and their inhabitants (e.g. Nadkarni & Parker, 1994; Stork & Best, 1994; Lowman *et al.*, 1995; Stork *et al.*, 1997a,c).

The term 'canopy' has been used by different authors to mean rather different things. A definition gaining acceptance is the aggregate of every tree crown in the forest, including foliage, twigs, fine branches and epiphytes (Nadkarni, 1995). In a recent review of definitions, Moffett (2000) promotes the view that 'canopy' should be regarded as all elements of the vegetation above the ground and urges us to distance ourselves from the anthropocentric view that only high tree canopies deserve that designation. He supports this view by reference to agricultural science, in which even meadows are regarded as having canopies (e.g. Monteith, 1965). He reminds us of the tacit assumption underlying much of ecological science that processes and dynamics can be scaled up across many orders of magnitude. Of course, if this highly inclusive view of 'canopy' is adopted, then the science needs a careful set of definitions for the height subdivisions to which we must refer for descriptive clarity.

The term 'understorey' may be defined as the vegetation immediately above the forest floor and reachable by the observer or, if such measurements are available, the zone with less than 10% light transmittance (Parker & Brown, 2000). The French word *canopée* denotes the interface between the uppermost layer of leaves and the atmosphere (e.g. Hallé & Blanc, 1990). It has been translated as 'canopy surface' (e.g. Bell *et al.*, 1999) or 'outer canopy' (Moffett, 2000). Further, 'upper canopy' refers to the canopy surface and the volume immediately below (a few metres) that may be occupied by arthropods foraging specifically in the upper region of the canopy. This zone may be distinct only in tall, wet and closed tropical forests and its occurrence is discussed by several contributions in this volume (Chs. 22 and 27). Emergent trees and the air above the canopy may be termed the 'overstorey' as this layer is important for the dispersal of several arthropod groups (Amédégnato, 1997; Compton *et al.*, 2000). Note that use of the above terms does not necessarily mean that the forest is stratified: they are convenient to describe the origin of the material collected. Forest strata are best described in terms of segments of gradients, rather than height above the ground (Parker & Brown, 2000). For cogent descriptions of the canopy structure and canopy surface, see Bongers (2001) and Birnbaum (2001), respectively.

The expression 'canopy arthropods' also needs a brief explanation. Although some species spend their entire life cycle in the canopy ('canopy residents' *sensu* Moffett, 2000), others may live in the soil/litter habitat as immature stages and may move later into the canopy to feed on other resources as adults (Ch. 3). We use the term 'canopy arthropods' to refer to all those species that are dependent in any way on the canopy at least at some stage of their life cycle.

The role of forest canopies in key ecosystem processes within the biosphere, such as energy flows, biogeochemical cycling and the dynamics of regional and global climates, cannot be understated. The forest canopy is the principal site of energy assimilation in primary production, with ensuing intense interchange of oxygen, water vapour and carbon dioxide. Most photosynthetic activity in the biosphere occurs in the canopy, and forest canopies account for almost half of the carbon stored in terrestrial vegetation (e.g. Lowman & Nadkarni, 1995; Wright & Colley, 1996; Malhi & Grace, 2000).

In addition, scientists and the media have been captivated even more by the near countless species of animals and plants sustained by tropical forest canopies. The majority of these organisms is still unknown or undescribed. Erwin (1983a) termed the canopy of tropical forests 'the last biotic frontier', referring to the vast, but poorly studied, richness of organisms, particularly arthropods, resident in the canopy. This epithet and the underlying idea was seized upon and expanded by authors including Wilson (1992) and Moffett (1993). This volume focusses on arthropods of tropical canopies. Yet, canopies of all types, including temperate and tropical forests, play a crucial role in the maintenance of ecological processes and biodiversity. Since different forces may structure tropical and temperate systems (e.g. Turner *et al.*, 1996), comparative research is vital. We hope that this book will stimulate similar parallel efforts to bring together most of the information on arthropods of temperate canopies.

Tropical forest canopies represent fascinating environments for entomologists and ecologists for many reasons. First, with the exceptional diversity of their arthropod communities, tropical forest canopies may be the most species-rich habitat on Earth (e.g. Erwin, 1983a), although the soil/litter of tropical forests is another strong contender (e.g. André *et al.*, 1994; Hammond, 1994; Stork, 1988). Most of the contributions in this volume confirm the impressive diversity of canopy arthropods in the tropics.

Second, despite increasing interest in their study, the fauna of tropical canopies remains largely unknown and has been the subject of much controversy among entomologists and ecologists. Even the simplest questions remain unanswered, such as: how many arthropod species live in the canopy of various tree species and forest types, what is their resource base, or how have their ecological niches evolved (e.g. May, 1994). For example, the deceptively simple question as to whether tropical canopy herbivores are more or less specialized than their temperate counterparts, or than counterparts foraging in the understorey, is far from answered (e.g. Basset, 1992a; Gaston, 1993). Several contributions in this volume address these issues (Chs. 5, 21, 22 and 29).

Third, tropical canopies represent a key arena in which biologists can study the interactions of multiple species within communities and test hypotheses on evolution and coevolution. Studies of tropical environments and their organisms have contributed significantly to the advancement of modern ecology (Chazdon & Whitmore, 2002). Canopy ecology is a young, 'frontier' science, exploring a largely unknown environment, establishing basic patterns and developing nascent theories. We expect that synecological studies of canopy organisms, documenting the rich variety of their interactions in this complex habitat, will boost our ability to generate and test evolutionary scenarios. Because of the high diversity of canopy arthropods, they also represent model organisms for studying macroecology and discovering general patterns and rules in nature (Lawton, 1999). The synecology of arthropod assemblages in the canopy is a central theme of several contributions in this volume (Chs. 19, 20, 26, 29, 30 and 33).

Last, rapid habitat loss in tropical forests makes their canopy inhabitants particularly vulnerable to endangerment or even extinction. Dissemination of scientific information to foster scientific interest in canopy arthropod communities is crucial for the survival of canopy communities, as well as for those who study them. For example, sound estimates of species loss cannot be inferred from ground-based studies alone; data on the distribution and ecology of canopy arthropods are essential to predict the effects of forest disturbance and fragmentation on species loss (e.g. Willott, 1999; Kitching *et al.*, 2000). These issues are discussed in Chs. 18, 28 and 34.

Most of the biological activity in tropical rainforests is concentrated in the upper canopy rather than the understorey (e.g. Hallé & Blanc, 1990; Parker, 1995). Many abiotic and biotic characteristics of the canopy are different from those in the underlying understorey. The higher illumination levels in the canopy promote rapid rates of photosynthesis, which, in turn, promotes high plant production, thereby sustaining a more abundant and diverse community of animals than in the understorey (Wright & Colley, 1996). The vertical stratification of resources and organisms is one of the key characteristics of tropical forests, particularly of wet forests. Many contributions in this volume explore how different and unique canopy arthropods are compared with their counterparts in the understorey (Chs. 6–8, 11, 25 and 27), or in the soil/litter habitat (Chs. 9, 10, 24 and 26).

Other characteristics promoting a distinctive canopy fauna relate to the discrete distribution of resources in the canopy. The high rate of plant production in the canopy is often not continuous (e.g. van Schaik *et al.*, 1993), thus shaping specific strategies and life histories in insect herbivores and their associated assemblages of predators and parasitoids. This important theme is addressed by several contributions (Chs. 4, 12, 14–16). Others emphasize the temporal scale at which these complex interactions occur, from diel activity patterns (Chs. 23, 27 and 28) to transannual effects (Ch. 13).

Arthropods and their food resources may experience different microclimates within the heterogeneous environment of tropical forests (e.g. Lowman, 1995; DeVries *et al.*, 1999a). This is most apparent along the vertical gradients of closed wet tropical forests, but it also occurs horizontally when natural tree falls modify the structure of the canopy. Several contributions examine the spatial distribution of particular resources and its consequences for canopy arthropods: the physical qualities of leaves (Ch. 31), the accumulation of litter (Ch. 10) and the presence of epiphytes (Ch. 17), vines (Ch. 31) or flowers (Chs. 20 and 23).

Many of the earlier studies of canopy arthropods took primarily a faunistical approach (reviews in Erwin, 1989, 1995; Stork & Hammond, 1997; Basset 2001b). They often relied upon indirect sampling methods, such as light trapping or pyrethrum knockdown (canopy fogging). Workers were limited to ground level and arthropod life histories and population dynamics could only be inferred indirectly from their data. In addition to improvements in fogging techniques, recent methodological developments in canopy access (some reviewed in Moffett & Lowman, 1995) allow the observation of canopy arthropods *in situ* and their live collection.

Today, methods of canopy access that are favoured by entomologists include construction cranes, canopy towers, canopy rafts, aerial sledges, aerial walkways or single rope techniques (see Ch. 2). Collecting methods are accordingly more diverse and reflect the increasing complexity of the questions that are pursued by canopy biologists and entomologists. The contributions in the present volume truly reflect this revolution in canopy access, sampling methodologies and the consequent maturation of research.