



# FOREST CANOPIES, ANIMAL DIVERSITY

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## GLOSSARY

- arbicolous** Living on the trees, or at least off the ground in shrubs and/or on tree trunks.
- emergent** A very tall tree that emerges above the general level of the forest canopy.
- epiphytic material** Live and dead canopy vascular and nonvascular plants, associated detritus, microbes, invertebrates, fungi, and crown humus.
- hectare** Metric equivalent of 2.47 acres.
- microhabitat** A small self-contained environmental unit occupied by a specific subset of interacting species of the forest (or any other community).
- scansorial** Using both the forest floor and canopy for movement and seeking resources.
- terra firme forest** Continuous hardwood forest of the nonflooded or upland parts of the Amazon rain forest.
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**THE FOREST CANOPY** is arguably the most species-rich environment on the planet and hence was termed the “last biotic frontier,” mainly because until very re-

cently it had been studied less than any place else, with the exception of the deep ocean floor and outer space. The reason for lack of study of the canopy was accessibility, and the evidence of the incredible species richness, mainly of tropical forests, is primarily the abundance of insects and their allies. This hyperdiverse and globally dominant group has adapted to every conceivable niche in the fine-grained physical and chemical architecture of the tree crowns. In less than three decades, canopy biology has become a mixed scientific discipline in its own right that is gradually gaining sophistication of both approach and access.

Tropical arbicolous (tree-living) arthropods were observed in the early 1800s in the “great forests near the equator in South America” and later that century were described by Henry Walter Bates. Even though Bates observed, described, and commented on the canopy fauna (as viewed from the ground and in recently felled trees), more than a century passed before Collyer designed an insecticide application technique that allowed a rigorous sampling regime for canopy arthropods. William Beebe and collaborators early in the twentieth century recognized that the canopy held biological treasures, but “gravitation and tree-trunks swarming with terrible ants” kept them at bay. Frank Chapman, a canopy pioneer (of sorts), viewed the treetops from his “tropical air castle” in Panama in the 1920s, but his interest was vertebrate oriented, his perch was a small tower, and his observations of insects and their relatives were casual. By the mid-1960s and early 1970s, a few workers in both basic and applied science were seriously

investigating canopy faunas of temperate and tropical forests in both the Western and Eastern Hemispheres. From the early 1980s until now, many workers have been improving methods of access and other techniques used to register, sample, and study the fauna (see reviews by Basset, Erwin, Malcolm, Moffett and Lowman, Munn and Loiselle, and Winchester in Lowman and Nadkarni, 1995; Moffett, 1993; Mitchell, 1987). Some of these workers have found that arthropods by far make up the fauna of the canopy (Erwin, 1982, 1988). Visiting and nesting bird, mammals, reptiles, and amphibians represent a mere 1% or less of the species and even less in the abundance of individuals in these groups (Robinson, 1986). There are no adequate measures of canopy nematodes, mollusks, or other nonarthropod microfauna groups.

What is meant by the forest canopy? Generally, the canopy, or tree crown, is thought of as that part of the tree including and above its first major lateral branches. The canopy of a single tree includes the crown rim (the leaves and small twigs that face the main insolation from the sun) and the crown interior (the main trunk and branches that gives a tree its characteristic shape). The canopy fauna is that component of animal life that inhabits the tree canopy and uses resources found there, such as food, nesting sites, transit routes, or hiding places. Hence, the forest canopy is collectively all the crowns of all the trees in an area. The canopy is often thought of as being stratified into emergents, one to three regular canopy strata, and an understory of smaller trees living in the shade of a more or less continuous overstory. All types of forests have their own describable characteristics, from the spruce forests of the Northwest Territories of Canada to the pine forest of Honduras, the dry forests of Costa Rica and Bolivia, and the Rinorea and Mauritia forests of the upper Manu River in Peru. It is through "whose eyes" one views the community, habitat, or microhabitat that determines the scale of investigation and subsequent contribution to the understanding of the environment—the beetles, the rats, the birds, the ocelots, the investigators, or perhaps even the trees.

## I. CANOPY ARCHITECTURE, ANIMAL SUBSTRATE

A temperate forest is composed of both broad-leaved and coniferous trees, with one or the other sometimes occurring in near pure stands depending on the latitude and/or altitude and also on soil and drainage conditions.

Normally, there are few canopy vines or epiphytes and perhaps some wild grape or poison ivy vines. Soil and organic debris caches are few or absent in the tree crowns, except for tree holes which provide homes to numerous arthropod groups but few vertebrates. Temperate forests are subjected to cold and hot seasonal climate regimes as well as wet and dry periods. Great expanses of forest lose their leaves in the winter months, sap ceases its flow, and the forest "metabolism" comes to a slow resting state.

The temperate forest seemingly provides a great variety of substrates for the canopy fauna, but faunas are depauperate compared to those in tropical forests. Virtually no mammals are restricted to temperate forest canopies—only a few frogs and lizards. However, many bird species are restricted to the canopies, as they are in tropical forests. Among insects, for example, the beetle family Carabidae has 9% of its species living arboricolously in Maryland, 49% in Panama, and 60% or more at the equator in South America.

Tropical forests, on the other hand, have few if any coniferous trees; only forests at higher elevations and/or located closer to subtropical zones have coniferous trees. Tropical canopies are often (but not always) replete with vines and epiphytes, tree holes, and tank bromeliads, and there are soil mats among the roots of orchids, bromeliads, and aroid plants. In the early 1990s, Nadkarni and Longino demonstrated that epiphytic material is fraught with macroinvertebrates, and Coxson and Nadkarni later showed that epiphytic material is important in the acquisition, storage, and release of nutrients.

Lowland tropical forests are subjected to mild temperatures, without frost, but have both wet (sometimes severe) and dry seasons. Individual species of trees may be deciduous, but in general tropical forests are always green and there is a perpetual growing season. Substrates are constantly available for the fauna. Often, some microhabitats with their substrates are temporary in the sense that they remain in place for a season or two, but then their architectural structure collapses into a jumbled pile of organic detritus on the forest floor. Such microhabitats (e.g., a suspended fallen branch with its withering leaves) provide a home resource to thousands of arthropods in hundreds of species, many found only in this setting. Eventually, such a branch loses its dried leaves and crashes to the forest floor. However, a short distance away, another branch breaks from a standing tree and the process begins again. The arthropods of the old, disintegrating branch move to the new one. The microhabitat and its substrates are forever present across the forest; each individual branch

is ephemeral. The faunal members occupying such microhabitats are good at short-range dispersal.

## II. EXPLORING THE LAST BIOTIC FRONTIER

Until recently, the forest canopy was impossible to study well. Getting there was the limiting factor, and even after getting there (e.g., via ropes) it was difficult to find the target organisms. Modern devices such as aerial walkways (e.g., ACEER, Tiputini Biodiversity Station; Fig. 1), one- or two-person gondolas maneuvered along crane booms (e.g., in Panama at STRI), and web-rope techniques (see review by Moffett and Lowman in Lowman and Nadkarni, 1995) now allow real-time observations, sampling, and experiments anywhere in the canopy. Inflatable rafts that suspend mesh platforms resting on the upper crown rims of several trees have provided access from above, although this technique seems more suited to botanical work or leaf-mining insects, especially epiphytes and lianas. Insecticidal fogging techniques allow passive sampling of all arthropods resting on the surfaces of canopy plants (Erwin, 1995), and suspended window/malaise traps collect the active aerial fauna. Many of these techniques have been used during the past two decades; however, often they were simply used as collecting devices to garner speci-

mens for museums and/or for taxonomic studies, and for this purpose they are excellent. In some cases, ecological studies were desired, but the techniques were not properly applied and the results disappointing. It is important to first ask the questions and then design the experiments; in some cases, current canopy techniques can be powerful tools for answering questions. Unfortunately, although sampling is relatively easy, sample processing is time-consuming and laborious. For canopy fogging studies, after the sampling effort an average of 5 years was required before published products were achieved (Erwin, 1995). The main reason for this is a lack of funding for processing the results of fieldwork, even though the field studies were readily funded. Without processing, the data inherent for each specimen are unavailable for taxonomy or ecology studies. This is an historical funding problem and one of the reasons most studies examine but a few species from few samples.

## III. RESULTS OF STUDIES

### A. Invertebrates

Recent findings by Adis in the central Amazon Basin and by Erwin in the western part of the basin demonstrated that there are as many as  $6.4 \times 10^{12}$  terrestrial arthropods per hectare. A recent 3-year study of virgin



FIGURE I The rainforest canopy of the western Amazon Basin from the canopy walkway of the ACEER Biological Station.

terra firme forest near Yasuni National Park in Ecuador by Erwin found an estimated 60,000 species per hectare in the canopy alone. This figure was determined by counting the actual species in the samples of several well-known groups and comparing their proportions in the samples with their known described taxonomic diversity. The predatory beetle genus, *Agra* (Fig. 2), has more than 2000 species found only in Neotropical forest canopies and scattered remnants of subtropical forest canopies in southern Texas and northern Argentina. The herbivorous weevil genus, *Apion*, likely has more than 10,000 species. In only 100 9-m<sup>2</sup> samples of canopy column from 1 ha of virgin terra firme forest near Yasuni National Park in Ecuador, there are more than 700 species of the homopteran family, Membracidae, which were found along with 308 species of the beetle family, Carabidae, and 178 species of the spider family, Theridiidae.

“Biodiversity” by any other name is “Terrestrial arthropods”—that is, insects, spiders, mites, centipedes, millipedes, and their lesser known allies.

Forest canopy studies of terrestrial arthropods are few (Erwin, 1995). Many of these studies currently concentrate on host specificity as a herbivore or parasite that eats only one other species of plant or animal. However, there is another class of specificity that is very important in understanding biodiversity that has

received almost no study: “where” species hide and rest. This is not random but rather species specific (T. L. Erwin, unpublished data).

Terrestrial arthropods are found in “hotels” and “restaurants” or “in transit” between the two (Fig. 3). Often, insects and their allies eat, mate, and oviposit in the restaurant or at the food source, for example, on fungi or in suspended dry palm fronds. These insects may hide during the day under debris or under bark near the fungus or on the palm debris, but they never roam far from the vicinity of the food source, except to locate new food sources when the old one is depleted. Members of other species eat in one place and then move to cover for a resting period, i.e., the hotel. An example of this is the subfamily Alleculinae of the beetle family Tenebrionidae. These beetles feed on lichens and moss on tree trunks at night and spend the day (hiding, resting, and possibly sleeping) in suspended dry leaves elsewhere in the forest. Many species found in the forest canopy during the day (utilizing leaves, fruits, and/or flowers) hide and rest at night in the understory (e.g., various pollen-feeding beetles and the larger butterflies).

Insects particularly, and some of their allies, have adapted to nearly every physical feature of the planet, and the canopy is no exception. Many beetles have special feet for walking on leaves; some even have modified setae on their feet to slow them down upon landing from rapid flight (Fig. 4). Because they are in an environment with raptorious birds, lizards, and frogs, many insect species have evolved camouflage coloration.

Climate is the main constraint on terrestrial invertebrates. In the temperate zones, it is the winter cold and



FIGURE 2 *Agra cowilsoni* Erwin, a species of Colombia, South America.

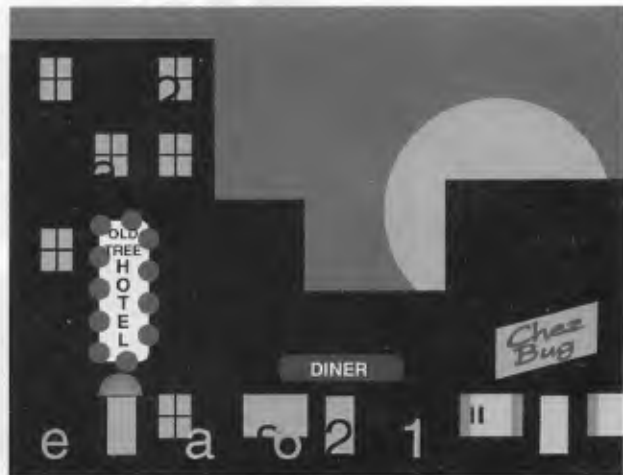


FIGURE 3 Humorous depiction of where “bugs” live and eat.

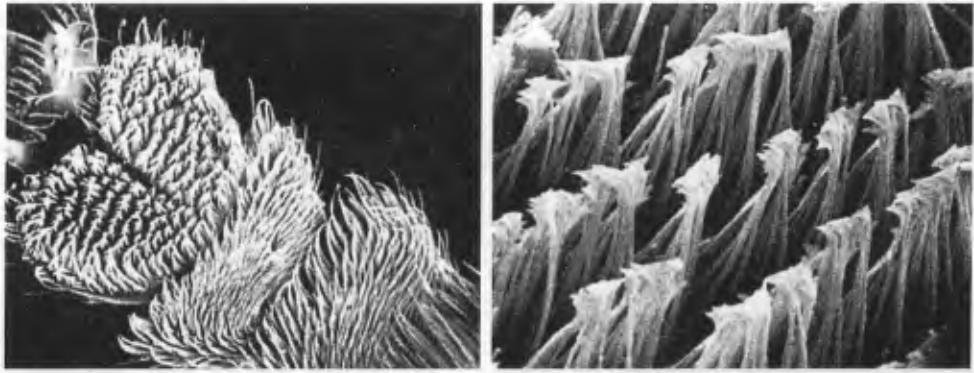


FIGURE 4 Setae of an arboreal beetle's tarsi used for landing and stopping quickly.

dryness; in the equatorial tropics, it is the dry season for some and the rainy season for others, with the temperature far less of an influence than it is in the far north or south. Many herbivores must contend with plants that produce toxic chemicals or other defensive systems. All insects must also deal with other insects that predate, parasitize, or carry bacteria, fungi, or other insect diseases. Hammond, Stork, and others, in their studies of insects in the Sulawesi dipterocarp forests, and Miller, Basset, and others in New Guinea found much less insect diversity and richness than Erwin and his teams in the Neotropical forests. Hammond also found in southwest Asia that the canopy fauna was not as delimited from the understory fauna as it is in the Amazon Basin. Unfortunately, all these teams used different methodology; hence, much of their results are not comparable. It is certain, however, that the Old World tropical forests are not as biodiverse as those in the New World, nor are the forests of Costa Rica and Panama as diverse as those of the Amazon Basin. Disparate regional richness is one of the main problems in estimating the number of species on the planet. Another is the incredible richness of terrestrial arthropod species and the fact that scientists likely know less than 3–5% of them if published estimates of 30–50 million extant species are close to reality. Stork (1988) has even gone so far as to suggest that there could be 80 million species on the planet.

## B. Vertebrates

Availability of food year-round constrains vertebrates from living strictly in canopies (see reviews by Emmons and Malcolm in Lowman and Nadkarni, 1995). Only in evergreen rain forests is there a continuous supply of food (albeit somewhat dispersed and sporadic) for

phytophagous and insectivorous vertebrates. In deciduous forests, most species also forage on the ground or hibernate when food supplies are short. Almost all canopy mammals live in evergreen tropical forests, but even there most are scansorial. Timing and distribution of food resources are the critical controlling factors. Among all nonflying vertebrates, anurans and lizards and to a lesser extent snakes are the most important truly canopy creatures. Birds and bats are also exceedingly important components. All these groups except snakes account for vertebrate predator-driven evolution on the far more dominant invertebrates of the canopy. For example (as Blake, Karr, Robinson, Servat, Terbourg, and others have shown), throughout the tropics approximately 50% of birds are strictly insectivores, whereas another 8% take insects and nectar.

Morphological adaptations that allow canopy life include feet that can firmly grip the finely architected substrate of twigs, leaves, and scaly bark. Emmons, in her many articles on Neotropical mammals, demonstrated that among these animals, those with the ability to “jump” avoided wasting energy and time by descending and climbing new trees to find resources; hence, more true canopy species have this ability. This is certainly true also of frogs and lizards. However, it is the flying forms—birds and, to a lesser extent, bats—that account for most of the treetop vertebrate fauna. Physiological adaptations that allow vertebrate canopy life include the ability to subsist on diets of fruit, flowers, leaves, or insects and their allies. Among mammals, fruit eaters are dominant.

As shown by Duellman, Dial, and others, among canopy anurans and lizards, nearly all are primarily insect predators. Birds are overwhelming insectivorous in the canopy fauna, with approximately 40% in the upper Amazonian and 48% at Costa Rica's La Selva

Biological Station. Malcolm, in summarizing the few articles on the subject, estimates that 15% of mammal species are arboreal/scansorial in temperate woodlands, whereas between 45 and 61% exhibit this behavior in tropical forests. In Duellman's 1990 list of anurans and reptiles from Neotropical forest, 36% are strictly arbicolous, whereas 8% are scansorial. Among birds, Blake and others found that scansorial species using the understory and ground were more numerous than strictly canopy species (51 and 42%, respectively), at their site in Costa Rica.

In summary, although canopy vertebrates are important in driving part of invertebrate evolution in the forest canopy, they have not overwhelmingly radiated into or made use of the canopy, as have the invertebrates. For example, the total vertebrate fauna known at Cocha Cashu, Peru, is approximately 800 species (approximately 45% of which are arbicolous or scansorial), whereas at a nearby location there are nearly 900 species of the beetle family Carabidae, of which more than 50% are strictly arbicolous. In Ecuador, near Yasuni National Park, there are in excess of 600 species of the homopteran family Membracidae in a single hectare, 100% of which are strictly arbicolous.

#### IV. CONCLUSIONS

Although animals may use the air for dispersal, they live on substrate. Here, they eat, mate, hide, and walk. Forest canopies are rich in species because they offer a three-dimensional array of varying substrates that directly receive the sun's energy with little filtering.

Although much has been and is being accomplished by faunal studies of the forest canopy, there is still much to do. There are missing data links between vertebrates and invertebrates and between both of these and the plant food and plant architecture on which they depend, and data is also missing on the influence of the canopy physical features on the fauna such as microclimates (see Parker's review in Lowman and Nadkarni, 1995). Each subsystem is receiving at least some attention, but the new discipline of canopy biology is in its infancy. Is it too late? The forests and their species-rich canopies are rapidly disappearing (World Resources Institute, 1993).

Topics of current investigation include canopy insect  $\beta$  diversity and measures of host specificity, the latter particularly in leaf-feeding beetles. Both areas of study were driven by earlier, somewhat naïve estimates of millions of species extant on the planet (Erwin, 1982; Stork, 1988; May, 1990; Casson and Hodkinson, 1991;

Gaston, 1991). Although some of these studies may have been internally consistent within the parameters set for the estimations, no one had really gotten a handle on the true meaning of "host" specificity, biocomplexity of tropical forests, the influence of tropical biotope mosaics,  $\beta$  diversity or what is known as species turnover in space and/or time, or the disparities of richness among continents or even the disparity among regions within continents.

Even so, our current rudimentary knowledge indicates that we are losing hundreds, even thousands, of invertebrate species with "scorched earth" programs such as that in Rondonia, Brazil, clear-cutting of Borneo and other southern Asian forests, and other losses in Haiti, Puerto Rico, Hawaii, the western Amazon Basin, Madagascar, and so on.

Conservation strategies are currently dominated by data on vertebrates (Kremen *et al.*, 1993; Samways, 1994); however, invertebrates are rapidly becoming sufficiently known to include them in analyses that are directed toward preservation of forest communities; to this end, the collective human conscience will soon be dealing with real extinction processes equivalent to those in the past, from the Permian to the Cretaceous. We are living at the beginning of the so-called "sixth extinction crisis" sensu Niles Eldridge of the American Museum of Natural History. Amelioration of the impact of this crisis rests on a better knowledge of the natural world around us and the development of conservation strategies that consider what we, Earth's managers (whether we like it or not), want future evolution to look like, as so well described by David Quammen (1998).

#### See Also the Following Articles

AMAZON ECOSYSTEMS • ARTHROPODS, AMAZONIAN • BEETLES • FOREST CANOPIES, PLANT DIVERSITY • FOREST ECOLOGY • INVERTEBRATES, TERRESTRIAL, OVERVIEW • TROPICAL ECOSYSTEMS

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