

# Tropical Forest Canopies: The Last Biotic Frontier

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More than 65 years ago, William Beebe (1917) wrote, "Yet another continent of life remains to be discovered, not upon earth, but one to two hundred feet above it. . . At present we know almost nothing of it. Up to now gravitation and tree-trunks swarming with terrible ants have kept us at bay, and of the tree-top life we have obtained only unconnected facts and specimens." Nothing much has changed in the last six decades to improve our knowledge of tropical forest canopies, the last biotic frontier. In addition, we are now faced with the projected loss of most of the tropical forest within the next 25 years at a rate of 7 to 12 million ha per year (U.S. National Research Council 1980).

In the early 1970s, I began studies of tropical forest canopy arthropods to gather new facts and connect old ones in such a way that current and future studies are enhanced to a maximum degree satisfying what Raven (1980a) called a need to "record coexistence and to be able to retrieve, for study, whole groups of organisms that occurred together for further analysis." My studies concern the tropical canopy beetle biota mainly, the general tropical arboreal arthropod fauna secondarily (but in an important way), and the relationship of these arthropod biotas to seasons, trophic adaptations, size distribution of taxa, ratios of higher taxa constituting the fauna, and richness of species and their distributions. These are all matters of importance in understanding tropical ecosystems. Results thus far have been startling! It is clear that, as we move into the 1980s and early 1990s, entomology's role and responsibility in tropical biology will increase dramatically.

Preliminary results and analyses indicate that there may be as many as 30 million species of insects, not 1.5 to 10 million as previously estimated (Erwin 1982), and that species of the tropics are, in general, restricted to very specific types of habitats within the supposedly "homogeneous green carpet of forest" which makes up the tropical "jungle." It is already clear

from my studies that most tropical arthropod species live in the tree tops where there are green leaves, fruits, flowers, and sunshine, and it is also clear that ants constitute the greatest number of individuals and biomass in the canopy as well as on the ground. To gather canopy arthropods for study and obtain data about forest canopies, I have employed a technique long used by mosquito control personnel—an insecticidal-fog-generating machine (see Fig.3)—which I modified for use in the tree tops.

## Methods of Canopy Fogging

The first attempt at true fogging of forest canopies seems to have been that of Roberts (1973). Others (Martin 1966, Gagné and Martin 1968) had earlier obtained canopy samples with hydraulic sprayers, but later

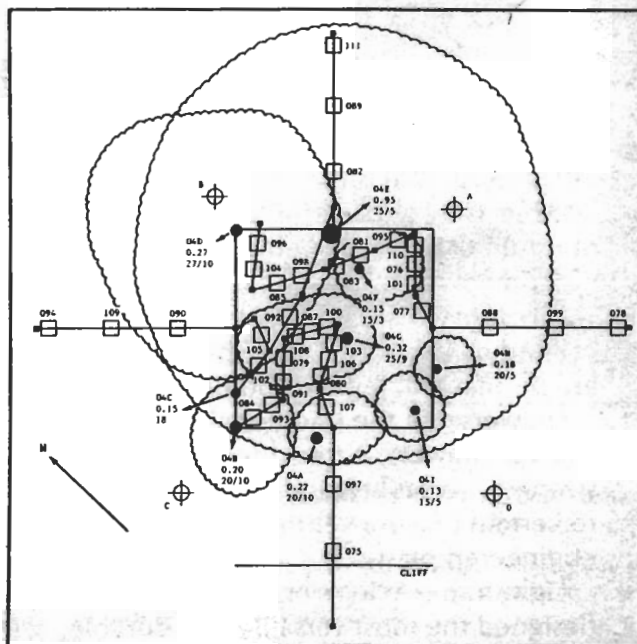


Fig. 1. Configuration of plot for canopy sampling at Tambopata Reserve, Peru, showing assigned tree numbers/letters, tray numbers, tree DBH, and canopy height/depth, and fogger pull-up sites (letters A-D). Plot size 12 by 12 m; tray size 1 m<sup>2</sup>.

Gagné (1979 [based on work done in 1973]) switched to the use of a resonant-pulse fogger. Roberts' (1973) discussion of field methods describes almost exactly the techniques of Montgomery and Lubin in the first fogging of lowland seasonal forest in Panama (see Erwin and Scott [1980]) and subsequent studies in Venezuela and Brazil. The only difference was the adoption by them of Gagné's (1979) use of Dyna-fog machine and suspended cloth and plastic sheets for the collection of insect rain. For later studies, Montgomery ran the suspended sheets along a 50-m transect with sheets paired and the fogger hoisted four or five times along and over the transect. For the last study in Manaus operated by Montgomery (in August 1979), I introduced molded plastic funnel trays, with 4-oz (ca. 118-ml) plastic collecting bottles screwed beneath (Fig. 4), in place of the cloth sheets to protect the more delicate specimens which were damaged with the suspended-sheet technique. These plastic trays also served for better assessment of which insects fell from which tree, because they were more easily positioned and mapped. However, because of both major and minor problems in the systems described above, I undertook a reassessment of the entire sampling regime and arrived at a new design (Fig. 1). This design has been described in some detail (Erwin 1983) and is currently in use in Peru by me at the Tropical Forest Canopy Laboratory of the Smithsonian Institution's National Museum of Natural History.

Briefly, it consists of the following sequence of events. First, forest types at the site are delimited and selected (at the Peru site there are six types of forests). Then 144-m<sup>2</sup> plots are established by locating a tree with large upper branches which will sustain a pulley system; this tree then becomes the north point of the plot. A plot (see plot map, Fig. 1) is established by selection of three more trees with suitable branches which delimit a vertical column with four sides, 12 m to a side, and as high as the canopy top in that particular forest type. This plot is suitably surveyed and marked; perpendicularly, at the middle of each side, a 15-m line is marked off. With the aid of a line-throwing gun (Fig. 2), pulleys are placed as high as possible in the four trees



Fig. 2. Line-throwing gun used to establish rope and pulley system in canopy. Attached spinning reel aids in line retrieval.

and to the outside of the plot (not directly over it). Over these pulleys, "pull-up" ropes are set and tied off for hoisting the Dyna-fog machine during fogging operations. Within the plot area of 144 m<sup>2</sup>, lines are tied horizontally between trees in a non-arbitrary way at a height of about 2 m.

Arrangement of trays (Fig. 1 and 5) is scattered depending upon availability and position of trees on which to tie the support lines. On these "clotheslines" are suspended 25 trays, each 1 m<sup>2</sup> in surface area relative to the ground, as sampling surfaces to catch the "rain" of dead arthropods after fogging the canopy. The trays are collapsible plastic with square aluminum frames and are funnel-form; at the bottom of the funnel is screwed a 4-oz plastic bottle with 70% alcohol preservative. Outside the plot area, perpendicular to each side, are strung additional trays at 5-m intervals to catch individuals which leave the fogged area before dying and dropping.

In addition, these outlier trays collect wind drift, should there be any, thus providing a measure of the success rate of capture within the plot area, and also telling something of the kind of species with higher escape capabilities. Other tests of internal consistency



Fig. 3. Radio-controlled Dyna-fog machine in canopy being rotated through 90° angle.

are run at selected sites; for example, sites are refogged a few days later to determine recolonization. Once the set-up is in order for fogging, preparations are made to return to the site early the next day when there is little or no wind blowing. Although the commercial Dyna-fog machine is normally hand operated, I attached a small, radio-controlled servo unit to the on/off lever so that the fog could be automatically turned on while up in the canopy. The radio-controlled fogging machine is started and hoisted into the upper canopy; the fog is turned on by the radio, and it is run for one min at a dial setting of "5" (density of fog) as the fogger is lowered to 15 m above the forest floor.

The process is repeated at each of the four corners. Formulation of the insecticide is set to provide 40,000 m<sup>3</sup> of fog during this 4-min period, thus completely over-fogging the amount of canopy available in the plot (about 3,000 to 4,000 m<sup>3</sup>). As the fogger is moved down through the vertical distance to 15 m at each of the four pull-ups, it is rotated 90°. In this way, the entire 3,000 to 4,000 m<sup>3</sup> of canopy is actually over-fogged—enough to make up for any variables such as deeper canopy, denser foliage, wind, or pull-up lines being slightly away from corners,

etc. It is the "over-fog" capability which allows comparison between samples; replicate series in each forest type are used to show sample comparability.

The number of plots needed per forest type to assure adequate coverage of tree species present is now under study. Drop-time is 2 hours from the end of fogging at each plot. Material is then collected from the trays and subsequently transferred from 4-oz bottles of 4-dram (ca. 7.1-g) vials for return to the processing laboratory in Washington. Measures are made electronically (Erwin 1978), and all data (including species numbers, counts, and measures, and all information about tree sizes and positions, species, and ages) are stored as computer readable and accessible.

### Observations and Preliminary Results

The most important conclusion reached in studies to date is a substantiation of the prediction (Erwin 1981a, Erwin and Adis 1982) that most tropical-canopy arthropods are restricted to specific forest types. Of the 1,080 species of adult Coleoptera analyzed in the fogging collections from four forest types at Manaus, Brazil, (Erwin 1983), 83% are restricted to one kind of forest, 14% are restricted to two forest types. To know that, in terms of insects at least, geographically small biotopes are unique to thousands of species is of importance when setting aside tracts of land for conservation and natural gene resource banks.

Another major finding is that the central Amazonian mixed-water forest (flooded by both white and black water each year) is the richest by far (of the four forest types studied) in insect species, indicating its general richness in other biota and its probable higher nutritional state in comparison with other forest types. However, the terra firme forest (nonflooded) is the richest in terms of restricted species and second richest in number of species, whereas the white-water forest (based on one transect) is the richest in terms of individuals. The richness of restricted species in the



Fig. 4. Sampling tray full of insects at site in Manaus, Brazil.

terra firme forest can be explained partly by the fact that this forest type seems to carry a higher load of smaller species (1-mm class); another possible explanation is the susceptibility of terra firme forests to refugial fractionation during the Tertiary (Prance 1982a), thus providing a greater chance of isolation of gene pools and resultant species formation.

The richness of individuals in the white-water forest is possibly due to the disturbed nature of the habitat and its continuous distribution over large distances (many rivers of the upper Amazon basin and the main lower channel). The white-water system is in a constant state of disturbance during flooding and probably acts like a pioneer community; thus, a few species produce high numbers of dispersants; note also that small beetles, those with potentially greater dispersal problems, are relatively few in this habitat, whereas the terra firme forest has the highest number of small species. The white-water forest has the fewest species, although the result is based on a single transect and must be regarded as tentative. The plants in this transect, however, are more continuously distributed over wide areas (i.e., along white-water riverine systems and gallery forest away from Amazonia proper) than are plants of the other types of forest (Prance 1982b); thus, it is likely that insect species are also more widespread.

Among adult Coleoptera, first the weevils (Curculionidae) and then leaf beetles (Chrysomelidae) are the dominant forms of canopy life; both are herbivorous. No other groups at any trophic level approach the richness of species of these two families. Darkling beetles (Tenebrionidae) are the dominant scavengers, fungus weevils (Anthribidae) and handsome fungus beetles (Endomychidae) are the dominant fungivores, and ladybird beetles (Coccinellidae) and rove beetles (Staphylinidae) are the dominant predators. In terms of size (mean length), scarab beetles (Scarabaeidae) are the largest herbivores by far, Tenebrionidae are the largest scavengers, Anthribidae are the largest fungivores, and firefly beetles (Lampyridae) are the largest predators.

These findings support my prediction that there may be as many as 30 million species of insects (Erwin 1982). I arrived at this figure by extrapolation from my study of beetles of the tree *Luehea seemannii* in Panama's seasonal lowland forest. This tree is a medium-sized seasonal forest evergreen with an open canopy and large and wide-spaced leaves. The 19 trees sampled had few epiphytes or lianas. In fogging samples from three seasons, 1,200+ species of beetles were collected. Tables #1 and 2 show the distribution of trophic types of the species collected and an estimated host specifically for each category. *Luehea* therefore carries an estimated load of 13.5% host specific species. An average tropical forest has about 70 generic-group trees per ha like *Luehea*; therefore, there could be 11,410 host-specific species of beetles per ha, or 163 per genus-group tree species. My fogging samples were then composed of 163 restricted species and 1,038 species that could be found anywhere in the vicinity, on perhaps any tree.

Table 1. Numbers of estimated host-specific species per trophic group on *Luehea Semannii* (data from Erwin and Scott [1980])

Trophic group	No. of species	% host specific (estimated)	No. host specific (estimated)
Herbivores	682	20%	136
Predators	296	5%	15
Fungivores	69	10%	7
Scavengers	96	5%	5
<b>Total</b>	<b>1,200 +</b>		<b>163</b>

Table 2. Numbers of estimated host-specific species per trophic group in four forest types near Manaus, Brazil (data from Erwin [1983])

Trophic group	No. of species	% host specific (estimated)	No. host specific (estimated)
Herbivores	795	20%	159
Predators	145	5%	7
Fungivores	29	10%	3
Scavengers	100	5%	5
<b>Total</b>	<b>1,069</b>		<b>174</b>

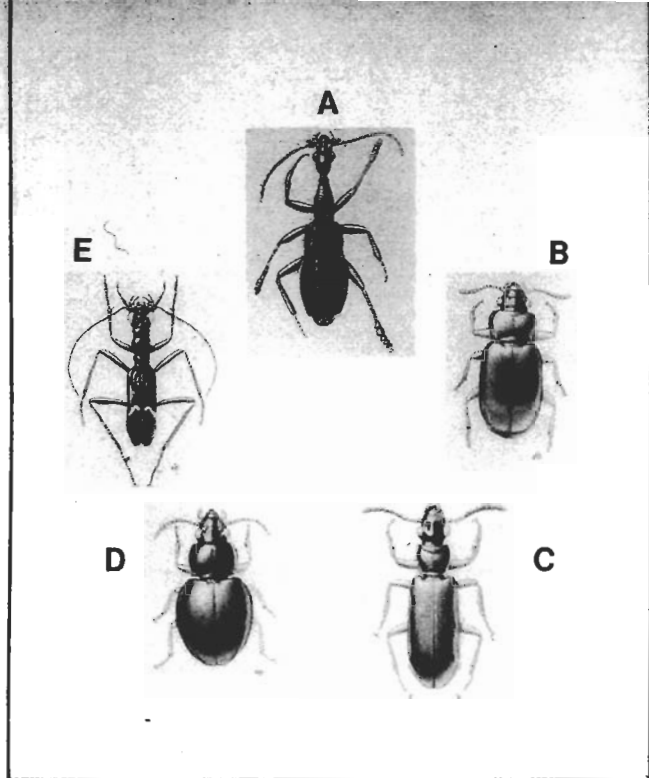


Fig. 5. Various arboreal carabid beetles often found in tropical forests: (a) *Agra dora*; (b) *Miotachys* sp.; (c) *Pachyteles* sp.; (d) *Xystosomus insularis*; (e) *Iresia pulchra*.

Adding the 11,410 restricted species per ha and the 1,038 transient species gives 12,448 beetles species per ha for the canopy alone. Beetles make up an estimated 40% of all insect species; therefore, there are 31,120 species of insects in the canopy of 1 ha of tropical forest. My own observations indicate that the canopy is at least twice as rich in species as the forest floor, so conservatively I added one-third more species to the canopy figure, arriving at a grand total of 41,389 species per 1 ha of seasonal forest in Panama. If one considers that there are about 50,000 species of trees, the same simple mathematics says there are as many as 30 million species of insects!

#### Biota Potential

As has been amply documented (Raven 1980b), 45% of the pharmaceuticals in use today are derived, in part, directly from plants. It is these same plants, plus others, that insects of the tropics eat (or avoid eating). Is it not worth studies to discover how the enzyme systems of such a vast array of tropical canopy insects allow them to digest their chemically protected or chemically laced food sources, or conversely, how plants avoid the multitude of herbivorous insects? Most canopy samples have an abundance of new species and even some new genera of parasitic Hymenoptera. Do we not use such efficient little insects in biological control? Are there not among these some unknown beneficial treasures to be found, mass reared, and released? Chemicals produced by certain beetle larvae (living in deserts and subtropics), when

wafted before ants, force the ants to run away (Erwin 1981b). Do we not need ant repellents in the southern United States for the fire ants? Do we not need to know, in these days of genetic engineering, what the world holds in the way of genetic diversity and genetic variability?

It seems that humanity has copied nature, adapted nature, even directly used nature throughout history, and for the most part it has been beneficial, at least for humankind. With the entomological richness now being discovered by canopy sampling, it seems it is time to broaden our approach and strengthen our efforts of study, so that the potential of the last biotic frontier is also developed beneficially, both for humanity and for the perpetuation of natural habitats.

#### Summary

Based on canopy arthropod samples taken by an insecticide-fogging technique, it appears that a high percentage of species, at least the beetles, are confined to one type of forest. Of the four forest types in the Manaus, Brazil, area, the mixed-water inundation forest is richest in numbers of individuals. The terra firme, or nonflooded forest, contains the highest number of restricted species. The white-water forest species are, on average, larger than species of the other three forest types studied; the species of the terra firme forest are the smallest. In all forests, 97% of the beetle species are less than 8 mm in total length. Herbivores are the largest species, and fungivores are the smallest. Weevils and leaf-beetles (Curculionidae and Chrysomelidae, respectively) are by far the dominant forms of beetle life in the canopy. However, in all samples in all forests thus far fogged, including recent studies in Peru, ants (Formicidae) are dominant in number of individuals and biomass. Parasitic Hymenoptera and Diptera are abundant in most samples. Recent recruitment studies in Peru indicate that ants rapidly and dominantly move into the canopy area within 10 days after fogging.

Data gathered and analyzed thus far clearly support



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the prediction that there may be as many as 30 million species of insects in the world, given the number of forest types in the Amazon basin alone. It is suggested that concentrated efforts from the entomological community begin to focus on the beneficial potential of this tropical treasure house of genetic diversity.

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