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LIFE ON VEGETATION : A FRAMEWORK FOR CANOPY BIOLOGY

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Canopy biology, a subject limited to trees by many practitioners (e.g., Lowman et al. 1995), has experienced a scarcity of conceptual thought about what makes treetops, as such, unique and thus worthy of separate discussion. In truth, all aspects of ecology in trees presumably grade imperceptibly with the processes on other, smaller aboveground vegetation. On these grounds, I recently proposed (Moffett 2000) that forest biologists should expand their outlook of canopies to embrace aboveground terrestrial vegetation in general. Here I explore this idea by distinguishing six "areas of investigation" that bear on the general relationships between any plant matrix and the species residing within it (Table 1).

Of course, many studies make points in two or more of the "areas." Furthermore, the areas frequently interrelate, with aspects of one often covarying with those of another. Still, I have been surprised how cleanly most results in the literature can be partitioned along these lines. I suggest that by framing some of their questions in regard to these subjects, researchers can contribute fundamentally to canopy biology as a discipline.

A broadened outlook on canopies also helps us achieve our research goals. Forest canopies have proven labor intensive or intractable for researching community change in time and space (e.g., Nychka & Nadkarni 1990, Parker & Brown 2000). No matter the research area under study, researchers should consider the advantages of using a plant community shorter than forests. Even the understanding of organisms specific to tree crowns (e.g., many bromeliads or primates) could be enhanced by focus on surrogate organisms in a meadow (for example, the stratification of microbes or the orientation of insects, mice, or frogs). As yet relatively little effort has been made in using non-forest habitats to investigate how such characteristics as plant architecture, stratification, and microclimate influence the lives of plant-dwelling species. As a result, the non-forest literature bearing on our interests is small and scattered. Many of the questions with a strong research tradition in forest canopy biology could be profitably pursued by other ecologists.

Table 1.

Core questions of canopy biology, ordered largely by decreasing scale. For non-forest systems, replace the word "trees" with the structurally dominant organism (e.g., herbs in prairies).

Canopy data on ...	**helps us to investigate such questions about canopy life as:**	**Current overall availability of such data:**
1) Community Ecospace	How many moths live in the community, say, per unit of bark surface?	Poor
2) Aggregate Properties of the Community	Do moth communities differ with humidity levels, as determined by height?	Good
3) Tree distributions	Do moth communities differ with tree species and their distributions?	Good
4) Tree architectures	How do caterpillars navigate through tree crowns to find fresh foliage?	Fair
5) Open spaces	How do airborne moths disperse through the forest labyrinth?	Poor to fair
6) Properties of structural elements-	Can resting moths detect wood-borne vibrations of approaching predators?	Fair

1) Community ecospace.

The space available to organisms is greatly enhanced by the vertical structuring of their substrates. How much so is a matter of conjecture. Any small nimble bird or agile climbing animal like a gibbon seems to experience canopies as a volume (even here not all points in the volume may be accessible, such as vegetation too dense to be entered or spaces too wide for a gibbon to cross). At the other extreme, and despite models to the contrary (Hölldobler & Lumsden 1980), an ant is unlikely to register community ecospace as a volume. Ants are restricted to within millimeters of every surface within their territories and thus experience canopies at between two and three dimensions. In essence a canopy represents for them a highly warped surface. Like science fiction ships using a "worm hole" to bridge points normally experienced as distant from each other, paleotropical Oecophylla weaver ants create shortcuts through this space by linking up their bodies into chains to access new branches, bridging whole trees this way (personal observation). The spatial difficulties of orientation and communication of canopy ants is wide open for investigation. The same is true for the spatial problems in the dispersal of mites, earthworms, and other small flightless canopy organisms.

2) Aggregate properties of the community.

Here I include the vertical distribution of canopy structural elements, as well as the concomitant stratification of the microclimate and other factors. Parker & Brown (2000) rightfully criticize studies of stratification for their methods, reproducibility, inconsistent terminology, and other weaknesses. Because the vertical dimension adds fascination to tree climbing and relates to dramatic changes in microclimate and associated communities, interest in these questions will continue. Nevertheless, it is a basic fact that defining strata or gradients requires averaging across space. Explaining any patterns that emerge necessitates research at finer spatial scales. For example, bark pH can vary with height on trees (e.g. Hyvärinen et al. 1992). If we find the height distribution of an epiphyte corresponds to that of bark pH, we might propose these plants prefer particular pH conditions. Testing this hypothesis would require checking the detailed distributions of bark pH's (e.g., Gauslaa 1995), especially at the actual locations occupied by the plants, followed by manipulations of pH in field or laboratory conditions (e.g. Hallingbäck 1990).

3) Plant distribution.

Since Erwin (1982), much of the research on canopy arthropods has concerned their communities at the level of whole trees. The possibility that many arthropods may be specialists on one or more tree species suggests the potential importance of viewing plants as islands over evolutionary time (Janzen 1968, 1973) – both in explaining levels of biodiversity within and between trees, and potentially even in modelling the processes that generate such bounty. Instead of viewing individual plants of a species as islands in a uniform ocean, to conform to the classic biogeographic perspective (MacArthur & Wilson 1967), "patchwork biogeography" models could treat communities as a continuum of plant islands. Each plant is assigned a longevity and set of growth rules; a likelihood that a given organism will survive either long enough to disperse through it, exploit it for resources and leave or stay and reproduce; and parameters to indicate the accessibility of the plant to the organism (based on a plant's size, density, boundary layers, et cetera, e.g., its "permeability": Wiens et al. 1985 Mauremooto et al. 1995). In addition to host-plant-centric treatments of communities, it is clear that forest diversity is highly structured at scales both smaller and larger than that of whole trees. These scales range from forest types (which are more numerous than ecologists once imagined: Tuomisto et al. 1995) to other relatively stable canopy elements that qualify as islands sensu Haila (1990), such as flowers, phytotelmata, and leaves (to a microbe) (e.g., Seifert 1975, Andrews et al. 1987, Jenkins & Kitching 1990, Richardson 1999). Even microclimatic features more subtle than canopy gaps may generate an island-like landscape within canopies (consider Herwitz & Slye 1992). Moreover, Dawkins (1982) argues that the definition of phenotype should be extended to include the effects genes have on the environment. With this consideration, I propose that the colonies of ant species maintaining wide-ranging, relatively stable, long-lasting territories represent significant "islands" within tropical canopies. Ant territories exist as "mosaics" within and between crowns in the tropics (Dejean et al. 1999), mosaics that overlay but are partially independent of the mosaic of the trees themselves. As small, pugnacious social organisms, workers thoroughly scour these territories to drive off intruders and kill prey while promoting the survival of species-specific assemblages of mutualistic, commensalistic, and parasitic

associates. Like other island-like features of canopies, then, ants may add significantly to the potential for a diversity of species to pack into vegetable space.

4) Plant architecture.

There is a burgeoning literature on this topic, that is, the size, angles, distributions, development, and spatial relationships of aerial plant parts (I include here also the presence of vines and other interconnections). Classically architecture is described for trees by the models of Hallé et al. (1978). The "Hallé-Oldeman architectural model" classification is suggested by one key practitioner to be "comparable to the development of the binary system of nomenclature by Linnaeus" (Tomlinson 1983). However, the system has been little used by non-morphologists, arguably due in part to the overall neglect of the potential importance (e.g., Hallé 1990) of substrate architecture on canopy organisms. There have been a few studies of the effects of branch spacing, angle, and width on the growth of epiphytes and the locomotion of vertebrates, but no broad studies of how architecture constrains canopy life. Consider the presence of well-beaten vertebrate highways at some tropical canopies sites (Perry 1978, Sillett et al. 1995), demarcated by epiphytes spread to either side of a branch, like hair from a part. Perry (1978) found evidence of multispecies use and active pruning, but to date no one has mapped such a trail in relation to available tree architecture, nor seen how it originates, or how its usage relates to the dynamics of canopy structure.

5) Open space.

Open space within vegetation merits special consideration because of its potential effect on microclimate and on locomotion or dispersal of organisms, and because many aspects of the subject remain virtually ignored. Open spaces can include the intervals between stems and leaves within plants, crown shyness, airways between forest strata, and gaps, large and small, caused by plant death. Gaps are commonly studied to the detriment of research on other kinds of spacings, because of their role in forest succession and diversity (Lieberman & Lieberman 1989). There is a growing literature (mostly on primates, bats, birds, and diaspores) showing that spaces represent barriers to some species and pathways ("flyways") to others. But as yet little information exists on how open space might structure resident populations and species distributions. A common problem is that researchers tend to think of the structures themselves (the plants) whereas in some cases the space between objects may be the "resource" being used. For example, the high frequency of gliding species in tropical Asia has been attributed to structural features like the height of trees and the scarcity of vines linking up them in many forests of that region (Emmons & Gentry 1983, Dudley & DeVries 1990). It may be more accurate to ascribe the success of gliding in Asia to the wider spaces within the forests that result from such structural features, given that substantial height per se is not required by most gliders, and that gliding should be more efficient than scrambling along vines between trees (Moffett 2000).

6) Properties of structural elements.

How do the structural and chemical properties of plant substrates, such as wood and leaves -- their insolation, efficiency at transmitting vibration, surface texture and stability, density, hardness, compliance, stiffness, strength, pH, capacity for water absorption and retention, tendency to leach nutrients, among many other attributes – how do these variables effect life on or in plants? One of the largest and oldest areas of investigation in all canopy biology is the question of substrate choice by epiphytes, especially cryptogams (e.g., Barkman 1958). Another area of intensive study has been herbivory as it relates to secondary compounds, nutrient content and the mechanical difficulties of feeding (Scholwalter 2000). Outside these research focal points, the literature is widely scattered, with many potential research avenues of enormous prospects.

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