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Canopy Forum

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With this issue, *Selbyana* introduces a Canopy Forum column to encourage dialogue on the evolving field of canopy biology. The literature on the subject is expanding rapidly. Take, for instance, Mark Moffett's article in this issue, which is a follow-up to his recent article on canopy terminology (Moffett 2000).

For this inaugural column, comments were solicited from colleagues around the world regarding their perspectives on the emerging and promising field of canopy studies, two of which are printed here. Authors were asked to frame their comments, in part, in reaction to Moffett's article on terminology. All *Selbyana* readers are invited to submit comments as reactions to these two Moffett articles and on other canopy topics.

Canopy Forum will appear occasionally in *Selbyana,* to promote discussion on canopy perspectives. Reader comments and statements of opinion, in essay form, will be edited for style and length but will not undergo peer review. Contributions should be prepared according to Guidelines for Authors (see Information for Contributors on inside back cover and visit www.selby.org/research/pubs.htm). The Center for Canopy Ecology logo, making its inaugural appearance here, was designed by Jason LeFrock of Studio 217 in Sarasota, Florida. It is based on an Aztec name glyph from a codex compiled after the Conquest of Mesoamerica (see Berdan & Anawalt 1992).

What Is Canopy Biology? A Microbial Perspective

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The canopy at Tiputini, tributary of the Napo River in Ecuador, is accessed by a magnificent three-tiered tower connected to three sets of hanging bridges constructed by Bart Bouricius some 40 m above the ground. I am especially proud because Bart, biologist and carpenter, is a neighbor and former student of mine in the graduate section of our Environmental Evolution course. I have more than once verified his reputation as the world's premiere designer-builder of canopy walkways, both temperate and tropical.

In addition to the walkways at the Tiputini Biological Diversity Station, two towers of similar height permit views of the treetops. Emergent species are what first strike the eye. The viewer is drawn to a mental tracing of the curving river far below. Greenery of different shades topped by blue sky delight the walkway-climber as far as her view can fathom the recognizable.

After a flight from Quito to Coca and a 2-hour bus ride to the "canoa" (open-to-the-rain motor-powered river boat), the visitor realizes that all evidence of people has receded. Roofed huts of fishing folk have given way to sunning birds, turtles, and palms on riverbanks profuse with a tangle of the unknown and unknowable liana, shrub, and tree. Experiencing the river, one wonders how any canopy could be, in principle, even more mysterious. For the next 7 hours, downriver noise abounds—clacking, flapping, croaking, splashing, cawing, buzzing—but no human sounds other than the motor and murmurs of fellow boat people are heard. Speeding downstream, we marvel at the rapid currents and total absence of the 21st century—not even an airplane penetrates the wilderness. In this timeless land beside the river, the lush green appears nameless.

Since 1977 in field studies and back in the campus laboratory, my students and I have studied a thriving ecological community of intertidal marine microbes, beholden to photosynthesizers of various types. At Laguna Figueroa in Baja California Norte, Mexico (FIGURE 1), oxygenic *Microcoleus, Lyngbya,* and *Gloeothece* are underlain by the anoxygenic purple *Thiocapsa* and *Chromatium.* Certain hardy organisms, the resistant forms of *Paratetramitus,* in among the green and purple, are known to survive freezing and desiccation for more than 5 years. These *Paratetramitus* forms are difficult to distinguish from another hardy similar-looking organism called *Mychonastes desiccatus.* These two kinds of life are the same size, the same spherical shape, and probably present in many populations at the same abundance. Distinguishing them in the community requires fluorescence for the chlorophyll wavelength. Both fluoresce when placed in the ultraviolet spotlight but give off different colors. *Mychonaste*s glows red, as chlorophylls enable it to photosynthesize, unlike *Paratetramitus,* whose fluorescent image reveals a green-glowing cyst wall. Beneath these two 8-micron spheres, greenish chlorobia of various types abound. Globules of sulfur give rise to hydrogen sulfide and other sulfurous gases, as we descend into the microbial community. Still further down in this vertically laminated ecological wilderness, at the low-tide level, *Desulfovibrio* and presumably *Desulfobacter* thrive. So, too, dwell *Spirochaeta* and the viviparous giant serpentine swimmer *Spirosyplokos.* That is the "canopy," in terms of Moffett (2000). The emergent photosynthesizers, those above the vertically laminated strata, tend to be brown and boat-shaped. Some 60 genera (perhaps 100 species) of these delicate-filigreed emergents at our field site have been identified by talented taxonomists.

More than 200 species (distinguishable species documented in the literature) repeatedly present forms of life at our Mexican field site and at comparable, cosmopolitan locales. Like the canopy seen from the swinging bridge built with plastic footholds by Bouricius, the vast majority of life in our field samples is unknown. We have an inkling of only those beings that survive mistreatment in the laboratory or greenhouse. The real number of the kinds of inhabitants in our samples is far more likely to be 1000 than the 210 or so that we and our colleagues have tabulated.

A sample containing a thousand life forms cut from a marine microbial mat on the Pacific shore is but a single cubic millimeter in size. Similar samples from the delta of the Ebro River (Spain) or the beach at Matanzas (Cuba) are roughly one millimeter high by one millimeter deep by one

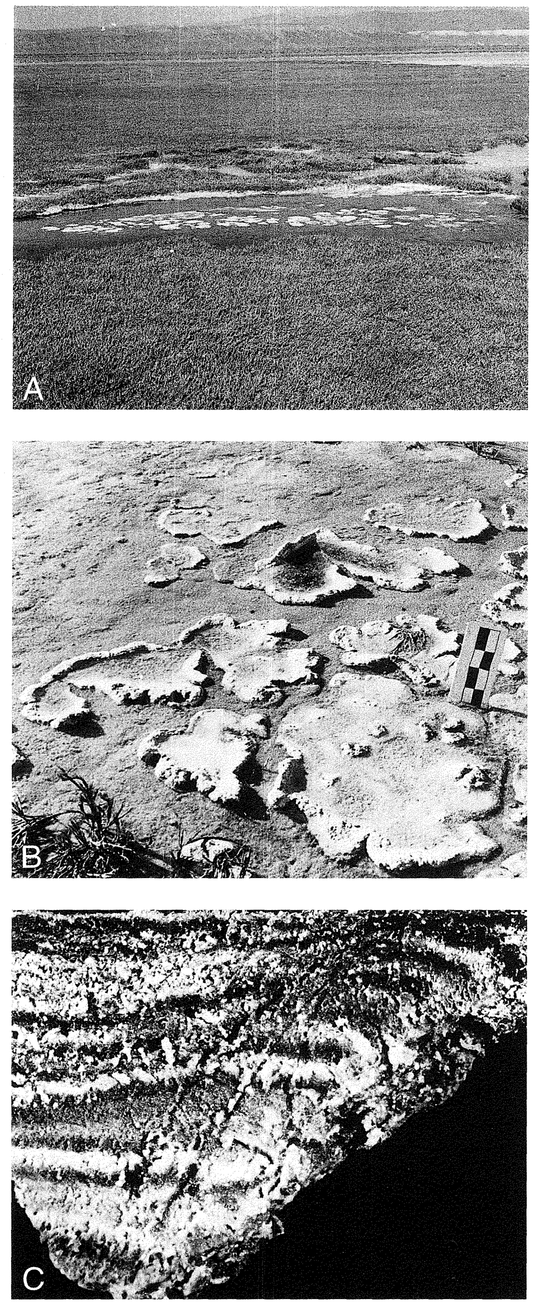

FIGURE 1. Microbial mat communities. **A.** An aerial view of Laguna Figueroa in Baja California Norte, Mexico. **B.** *Microcoleus* in microbial mats in situ; units are 10 cm. **C.** A hand sample (ca. 15 cm wide) of a microbial mat community dominated by *Microcoleus chthonoplastes* (cyanobacterium).

FIGURE 2. At the Tiputini Biodiversity Station, this area under the canopy walkway may contain several hundred stable microbial communities that await study. Here we see the lower portion of a tree about 100 feet tall.

millimeter long. How can the glorious canopy sample of Amazonia (say 100 × 100 × 50 kilometers so vastly larger than the microbial sample) possibly be analyzed by the amateurs who love her or even by the professionals who make her their life's work? Scientists admit to an extremely deficient view of our tiny microbial mat samples after more than two decades of study of this particular microcosm (FIGURE 2). We hardly know its major components and how the populations change in the most dramatic of temperature, salt concentration, and precipitation swings with the seasons. If so little is known of a cubic millimeter, imagine my awe at the view from the tower of the Amazonian macrocosm.

"Life," sang John Lennon, "is what happens when you're making other plans." "Life" is what you see, smell, hear, and feel at the canopy tower. Words and numbers hardly make an organizational dent when attempting to describe the prodigiosity. Moffett (2000) makes a valiant attempt to regulate the unruly by delineating terms of canopy biology. At least he has ignored the pernicious financial jargon so detrimental to scientific analysis: benefit, cost, fitness, reciprocal altruism, and the like. Here I have an opportunity for a single suggestion, as I applaud his effort to stay as close as he can to the observations themselves.

My suggestion regards terms for physical associations between organisms that are members of different taxa. First abandon the words and the use of these words in definitions that contain "host," "parasite," and other implied taxonomic categories in them (such as "epiphyte," "endophyte") and replace them with words that convey what precisely is meant. Why? Because the ambiguity intrinsic to these terms is unavoidable and obfuscating. Topological, nutritional, and ecological concepts are not distinguished. Identificational, positional, metabolic, genetic, and temporal information becomes so conflated that these terms entirely lack meaning.

All intertaxonomic physical associations that last for most of the life history of at least one of the partners are, by definition, symbioses. Such associations should never be classified by ecological outcome (beneficial, pathogenic, mutualistic, parasitic, etc.) because outcome always depends on particulars of environment and timing. Rather symbioses (whether strangler fig, vesicular-arbuscular zygomycotous fungi in the tissues of dicotyledonous plants, or bromeliads perched on palms) require analysis by level of association. By "levels," I mean whether or not the association is at the behavioral level (such as the topological relation of the bromeliad with the branch) or metabolic level (such as the fungus that derives photosynthate from the dicot) or at the level of shared gene product (such as the nitrogen-fixing rhizobium of the *Acacia* or *Mimosa* root nodule) or even integration at the most intimate genic level (such as the *Agrobacterium* that sends its plasmid-borne genes to be incorporated into the plant cell's chromosomes in the crown gall). Often in interspecific physical associations (symbioses by definition), the levels of partner association are simply not known, which needs to be explicitly stated. The topological and temporal bases of associations should be reflected in any permanent or casual physical association—at the canopy or below. Does the physical presence of one partner persist during the entire life history of both, as is the case for chloroplasts, mitochondria, and many fungi of plant roots? If impermanent for both, then, by definition, the association must be cyclical for at least one partner as, for example, the fungi that induce germination of orchid seeds. Terms like "endophyte" are particularly egregious since the "phyte" often refers to the fungal partner (and the fungi are, of course, in no way plants, even though "-phyte" is a Greek legacy). This type of rampant confusion and taxonomic ignorance by ecologists has a single major consequence. The entire field (which, in principle, extends far beyond the restrictions of academic biology, for example, into climatology, geology, paleontology, stratigraphy, atmospheric and soil sciences) is maligned, disdained, or ignored—except when desperately needed for practical (including financial-aesthetic) purposes like Disneyland.

If our descriptors employ unambiguous taxonomic information (such as that found in the list of all taxa of all organisms classified from phylum to class (Gale Group 2001) or for the higher taxa of kingdoms and phyla (Margulis & Schwartz 1998), one serious problem is resolved immediately. When ambiguous terms like "parasite," "endophyte," and "protozoa" are replaced by the actual taxonic, metabolic, temporal, and spatial relationships that are actually meant, the canopy and its biology will remain a mystery but a somewhat less daunting one.

Canopies in Canopies in Canopies

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Canopy biology rests on two premises. First, a canopy is the upper interface between a living system and its environment. Second, biological interfaces are fuzzy, thick layers. Such interfaces cannot be mathematical surfaces without thickness: dimension 1 is a mathematical line; d2 is a surface; and d3 is a volume. A fuzzy surface with a fractal dimension between 2 (surface) and 3 (volume), for instance, dimension 2.145, has thickness and hence biological reality (Lorimer et al. 1994). This must be regarded within a scaled biological systems hierarchy (Oldeman 1990, Rossignol et al. 1998).

Basic Patterns

Zooming in from space, Terra shows a green sheen, its thickness invisible at that scale. This green line is vegetation (Figure 3A), the biological interface between the planet and the air much like a sandwich with a bottom layer of bread (soil), a thin layer of sandwich-spread (biosphere), and a top layer of bread (troposphere). Moffett (2000) implicitly used two slices only. This engenders the following widespread concept: in any vegetation, everything above the ground can be seen as canopy. A three-slice analysis, however, combined with fuzzy set principles (e.g., Kosko 1994) provides a clearer picture, on condition that its scale level is explicit.

Zooming in to a "kilometric" scale (Figure 3B), the biosphere appears as a sandwich, with green canopy above, a complex of sap-conducting stems in the middle, and the rhizosphere below. Vegetation canopies of all sorts—from steppes or agricultural fields to rain forests—form fuzzy interfaces between ecosystem and atmosphere. Their fuzzy thickness is at the scale of the biosphere at that spot, from millimeters in lichen vegetations to decameters (10 m) in forests.

At a "hectometric" (100 m) scale, vegetation canopies also show sandwich architecture (Figure 3C, specific example of a forest). A working definition of a forest canopy is the greenish layer in between the lowest living tree branch and the upper level of the crowns (Oldeman 1974). Canopies have a wavy nature (hence canopy rafts!). The green surface above 1 m^2 of soil exceeds 1 m^2 and is folded. (Oldeman 1992, 1994; the folded forest). Most biological exchange interfaces are folded to fit a high surface in or around a reduced volume, from lichens to lungs. At wider scales too, folding occurs in ever-different configurations.

The canopy of a big tree crown at a "decametric" scale (Figure 3D) constitutes a fold of the forest canopy, folded itself by crownlets, each originally an architectural model *sensu* Hallé et al. (1978). Crownlets form the crown canopy in the sandwich above sets of branches (transport, middle layer) and a trunk (below, sap-source). At the "metric" scale (Figure 3E), the leaf canopy is a quite homogeneous fuzzy set of small, mostly unbranched, leaf-bearing twigs (Blanc 1991). The branches below, as a middle layer, are mainly the remaining parts of crownlets. The lowest layer of heavy branches supports and feeds both layers above. The metric-scale level is useful in mapping biotopes of smaller organisms. Such biotypes originate from an intricate folding of layers, structuring a dynamic, complex milieu. A typical neotropical

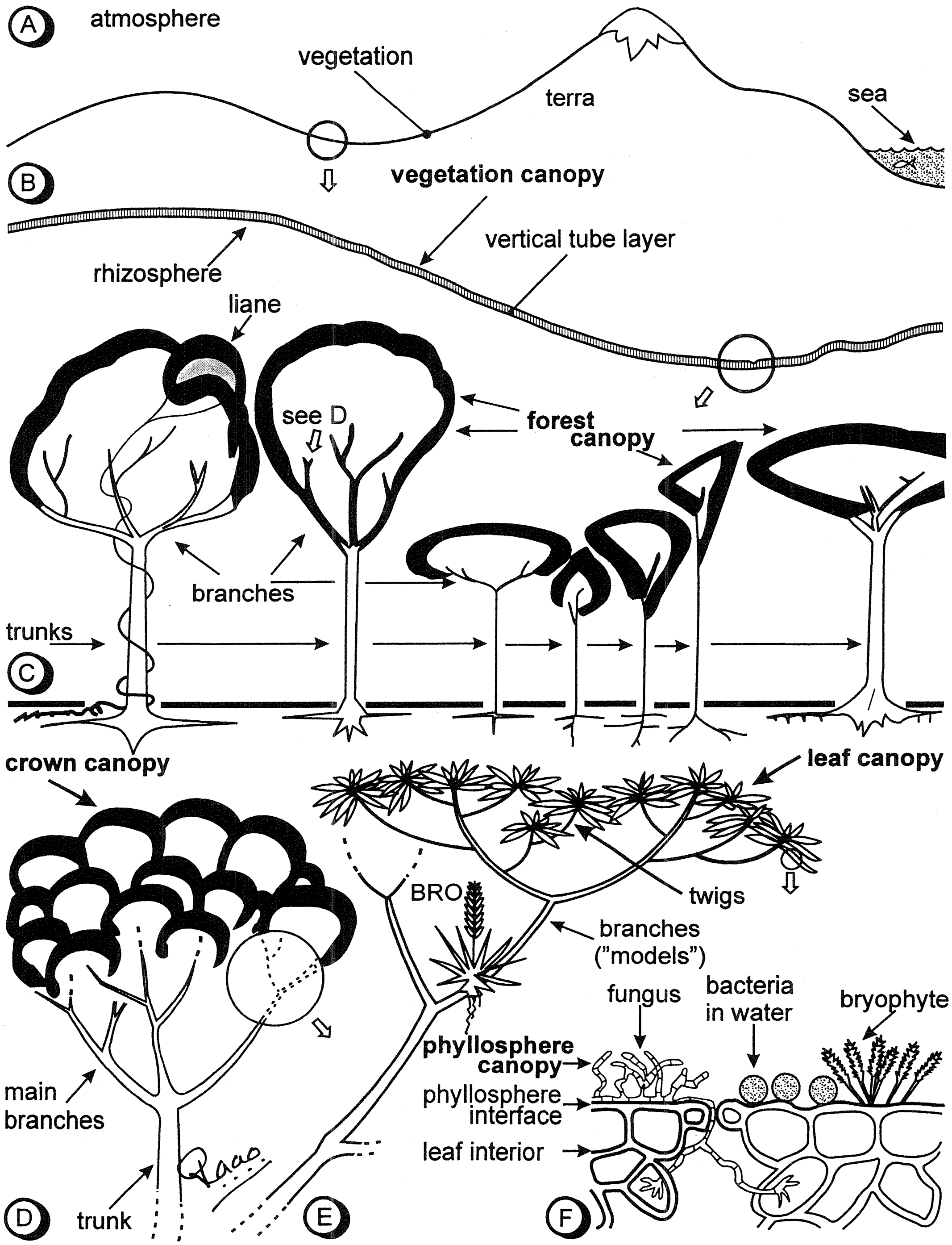

FIGURE 3. Canopies in canopies in canopies. At each scale level, the canopy is folded, increasing the biological exchange interface above a unit soil surface (Oldeman 1992).

A. Global scale. Vegetation as interface between air and land. Note fish (far right), inconsistent at this scale. **B.** Regional, "kilometric" scale. Vegetation, from lichen film to forest, shows three-layer sandwich architecture with two interfaces. This contrasts with the often-used two-layer image. At both sides, vegetation canopy and rhizosphere border on a middle, vertical transport tube layer (vegetation thickness exaggerated to make architecture visible). **C.** Local, "hectometric" scale. Forest shows three-layered sandwich architecture with two in-example is the bromeliad mini-ecosystem (FIGURE 3E) with dry and wet parts, bryophytes, insects, amphibians, and snakes.

The outer interface at a "centimetric" 1:1 scale (not illustrated) is the phyllosphere in the large sense (Ruinen 1956, 1961, 1974; FIGURE 3D). It tops a very fine sandwich structure with the leaf tissues in the middle and the twigs below. This sandwich system seemingly shows true two-dimensional surfaces, but their lack of thickness is an optical illusion. Ruinen (1953) showed the nature of this interface with microscopic biological thickness at the "millimetric" scale. Whole micro-ecosystems live half in and half outside the leaves (FIGURE 3F). Ruinen (1974) demonstrated crucial ecological functions of forest and grassland phyllosphere communities in nitrogen and sugar recycling. At this scale, bacteria, yeasts, fungi, algae, lichens, and bryophytes build diverse compartments.

Some intermediate biological scale levels, such as bryophyte communities on branches (Wolf 1993), are left unmentioned here. An orderly, logical, biological canopy theory must demand definition, identification, and description of all levels; and it must weigh their biological importance. They form a more important baseline than species richness and frequency. Species are carriers of ecological functions, but many redundant species or species webs each ensure one and the same ecological function. Species counts hence are not false, but they are impractical as a foundation for canopy theory.

QUANTITATIVE CANOPY BIOLOGY?

Canopy biology often lacks consistency because of a lack of definition of geometrical, temporal, and organizational scales. The fish in FIGURE 3A (far right) cannot exist at that superwhale scale! Adding to the confusion is the inherent absence of sharp limits and the general presence of gradients (Van Rompaey 1993) characterizing many-scaled, nested, highly complex living systems, including all canopies. Hence artificial, pixel-like limits, meaningless in themselves, often are substituted. Precision of measures and counts decreases because, even without flaws inherent in counting (Hayes 2001), researchers cannot know the exact onset and end of objects. Canopy data should be scrutinized closely, because the nature of the data themselves can open wide chasms between biological theory and reality, between model and living system. Are our scientific portraits of canopy reality in fact surrealistic?

Data processing is also less straightforward than assumed. Maps and drawings are indispensable to see the meaning of sizes, weights, and numbers. Map codes must separate the ephemeral from the permanent, averting indiscriminate comparison of quick and slow processes. Shifty limits cannot be made honest by the use of average values. Average precision is artificial; rather let us adopt mathematical methods based from the outset on fuzzy sets and fractal dimensions, fuzzy logic and fractal geometry (Oldeman 2001a, 2001b). Many cases, however, need no math at all. A time sequence of maps often suffices to explain canopies biologically. Scale drawings are quantitative documents, liable to be digitized if so required (Koop 1989, Oldeman 1990).

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terfaces. Forest canopy built by crowns above; root zone below; in the middle, transport layer of vertical trunks and stems. **D.** Large organismic, "decametric" scale. Tree crown shows three-layered, rounded sandwich architecture. Crown canopy above, built by crownlets; trunk below as sap source; in the middle, vertical main branches for transport. Omitted is the organismic, "decimetric" scale (cf. Wolf 1993). **E.** Sub-organismic, "metric," 1:1 scale (drawn smaller, "naked eye scale"). Crownlet with asymmetric sandwich architecture. Leaf canopy above, built by homogeneous unbranched leaf-bearing twigs; main branch below as sap source; in the middle, remaining branches of small "tree models" (Hallé et al. 1978), transporting sap. BRO = Bromeliad mini-ecosystem. **F.** Phyllosphere, "millimetric" scale (drawn larger, "loupe scale"). This scale is finer than sandwiches formed by organs and tissues. Populations once more build biological architecture. Phyllosphere zone with a flat sandwich structure, inverted on the lower leaf face. Phyllosphere canopy outside, built by micro-organisms with the "haustorial" zone inside, and parts of micro-organisms exploiting the older leaf. Leaf surface in the middle, phyllosphere in the strict sense of an interface (Ruinen 1956), with selective transport function. Fungi enter leaf through stomata. Biological exchange surfaces greatly increase by microscopic "green folds." Micro-folding explains huge quantity of nutrients and assimilates recycled by phyllosphere organisms as well as in the rhizosphere (cf. Ruinen 1974). Canopies and folds are built very differently per scale level but ensure very similar basic biological exchange functions.

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