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Colonization of Stripped Branch Surfaces by Epiphytes in a Lower Montane Cloud Forest, Monteverde, Costa Rica[1]

Key words: *cloud forest; colonization; Costa Rica; epiphyte; Monteverde; secondary succession.*

EPIPHYTES GROW ON SUBSTRATES THAT ARE DIVERSE AND EPHEMERAL. Canopy-dwelling plant communities are subject to disturbances such as wind, animal movements, waterlogging and subsequent sloughing, branch breakage, and treefalls. These perturbations result in their ultimate death and decomposition on the forest floor (Matelson *et al.* 1993). The rate of loss and replacement for epiphyte communities in forest canopies is unknown because the length of most studies has been short relative to the timescale needed to monitor epiphyte colonization and growth.

Some forest management practices (*e.g.*, epiphytic-moss harvesting for the floral trade in the Pacific Northwest of North America) and research activities (*e.g.*, climbing into trees and knocking epiphytes off) cause apparent short- and long-term changes in epiphyte communities. Although moss collectors and researchers often try to minimize damage to the communities they are harvesting or studying, the potential for their activities to affect canopy plant communities has not been investigated quantitatively. Little has been documented on the amount of time and conditions required for epiphyte communities to regenerate following disturbances. Understanding epiphyte community dynamics under natural con-

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ditions may help mitigate potential negative effects of human activities and contribute to our understanding of community succession.

Although the community composition and abundance of epiphyte communities at single points in time have been documented in numerous tropical and temperate forests (Oliver 1930, McCarthy *et al.* 1986, Peck *et al.* 1995), the dynamics of epiphyte communities has been studied only rarely and indirectly. Successional patterns of epiphyte communities in temperate forests have been inferred by using chronosequences of forest stands (Dudgeon 1923), toposequences of tree branches (Stone 1989), or by aging the underlying branches in temperate forests through counting annual rings (Pike 1978). The general pattern of epiphyte succession on temperate trees is that early colonizers are poikilohydric mosses and crustose or fruticose lichens. These die in place and a layer of dead organic matter accumulates, which serves as substrate for the few vascular epiphytes that occur in temperate forests (Benzing 1995).

The dynamics of epiphyte communities in tropical forest ecosystems, however, is largely unknown due to the high diversity of epiphytes and the inability to determine reliably the age of epiphyte substrates. Studies have been based either on communities existing at a single point in time (Yeaton & Gladstone 1982) or anecdotal data. Observations from tropical dry forests, for example, indicate that lichen colonization of vertical tree trunks is extremely slow, with areas scrubbed clean remaining virtually bare 15 years later (D. Janzen, pers. comm.).

In vegetation such as tropical montane cloud forests, in which epiphytes are highly diverse and abundant, recovery from small-scale disturbance would be expected to be very rapid. With nearly every available branch and bole covered with diverse epiphytes, one would expect that canopy communities on exposed branch surfaces resulting from within-canopy disturbances in these forests would be recolonized within a very short period. In this note, I report on a decade of monitoring the amount, composition, and location of epiphyte cover following experimental stripping of large branches on mature trees in Monteverde, Costa Rica. This is part of a landscape-level study on the ecological roles of epiphytes in tropical cloud forests (Nadkarni *et al.* 1995, 2000).

Fieldwork was conducted from May 1987 to March 1997 in the Monteverde Cloud Forest Reserve, a lower montane moist forest in Costa Rica (10°18′N, 84°48′W). Annual gross precipitation is *ca* 2200 mm, but actual wet deposition is much higher because of frequent wind-driven mist and fog (Clark 1994). The study area is in tropical lower montane wet forest (1550 m elev.) in Leeward Cove Forest (Lawton & Dryer 1980), with a broken canopy 12–25 m in height and a density of *ca* 150 trees/ha (>10 cm DBH; Nadkarni *et al.* 1995).

The Monteverde epiphyte flora is extremely diverse and abundant (Nadkarni 1984, Ingram & Nadkarni 1993). Branch surfaces in the crown interior of nearly all mature trees support epiphytes (bryophytes, herbs, woody shrubs, and hemi-epiphytes) in interwoven root-humus mats up to 25 cm thick. The greatest accumulations of humus are found on junctions of large branches. Outer branches and branch tips are partially to completely covered with bryophytes and small xerophytic herbaceous plants, with very little or no accumulated humus (Nadkarni *et al.* 2000). Relative to the forest floor, the upper tree canopy experiences more wind (Lawton 1982), more frequent mist deposition (Clark, Nadkarni, Schaeffer, and Ghulz 1998), higher air temperature maxima, and more frequent wetting/drying cycles (Bohlman *et al.* 1995).

At this site, epiphytes fall from the canopy throughout the year at a mean rate of 50-g dry wt/m^2/yr in a variety of forms, from individual plant parts to large mats that cover whole branches (Nadkarni & Matelson 1992). When climbing in the canopy, one frequently encounters patches of exposed bark resulting from individual plants and whole mats sloughing off branches. These "epislides" are apparent in all areas of the canopy. Exposed areas on branch tips and branch locations in the outer canopy appear to be related to bird foraging and movement; exposed areas on inner branch locations appear to be related to large, mature epiphyte mats falling off due to their own weight, or due to large arboreal mammals unintentionally knocking them off (*e.g.*, howler monkeys, tayras) or pulling them off as they forage for invertebrates in bromeliads (white-faced capuchins).

In April 1987, my research team established a 4-ha intensive research plot. We rigged *ca* 35 trees from the most common families of trees in this forest with mountain-climbing equipment, following Perry (1978). To sample the original epiphyte community, we chose a random subset of all accessible branches in five of the trees we climbed (Table 1). All live and dead epiphytic material was cut and

TABLE 1. *Identity of host tree and number of cylindrats sampled for which original and recolonizing epiphyte communities were monitored from 1987 to 1997 in Monteverde, Costa Rica. NS = not sampled due to tree or branch loss during the 10 years of the monitoring period.*

Tree Number	Family	Genus species	Number of cylindrats for original community	Number of cylindrats for recolonizing community
1	Moraceae	*Ficus tuerckheimii*	9	5
2	Moraceae	*Ficus velutina*	12	3
3	Moraceae	*Ficus velutina*	9	NS
4	Sapotaceae	*Pouteria viride*	12	5
5	Lauraceae	*Beilschmedia pendula*	12	NS

removed from cylindrats *ca* 75 cm in length around inner branches (within 5 m of the central trunk). Cylindrats were marked with small aluminum tags tied to the distal and proximal ends of the plot. The samples were separated in the laboratory into three categories (vascular plants [leaves, stems, roots], bryophytes, and dead organic matter [DOM]), the latter of which consisted of intercepted host tree and epiphyte litter, crown humus, and invertebrate frass. There was virtually no lichen cover or any exposed bare branch. All materials were dried at 105°C for 48 h and weighed.

To quantify the colonizing epiphyte communities, I visited all of the cylindrats and noted and photographed the colonization of epiphytic plants at least one time per year for a decade following the stripping. In the course of the monitoring period, some of the cylindrats were lost due to branch- and treefall. In June 1997, I measured cover of colonizing epiphytes by wrapping a clear acetate sheet around the branch and then placing another clear acetate sheet marked with a matrix of 100 dots (10 × 10 cm) at five random locations around the branch segment. I counted the number of dots that touched epiphytic plants and characterized each "hit" into one of five categories: bryophyte, vascular plant, crustose lichen, foliose lichen, and bare bark. The measurements were tallied and converted to percent cover. Tree and branch effects for the original and colonizing plant communities were tested with nested ANOVA. The plots were ranked by abundance (total biomass for original communities, total percent cover for colonizing communities) and tested for correlation.

First, I expected the epiphytes to grow back rapidly, since this forest was replete with abundant and diverse canopy plants on nearly all tree surfaces. Also, "primary succession" of branch substrates (*i.e.,* young branch tips in the canopy and stems of saplings in the understory) rapidly accumulated epiphytes within two or three years of growth. Second, I expected the incoming community composition to closely reflect the original community (*i.e.,* the community would rapidly replace itself). Third, I expected epiphytes to colonize primarily through encroachment from the sides of the cleared plots (*i.e.,* grow out from the edges of the exposed branch segments). These expectations were based on the literature (*e.g.,* Rhoades 1995) and supported by data on colonizing epiphytic bryophytes in a 50-yr-old temperate forest in the Pacific Northwest, (A. Cobb and G. Ramsey, pers. comm.; N. Nadkarni, pers obs.). Our observations of early colonization following branch-stripping in that forest indicated that colonization of branches is relatively rapid (up to 6 cm of elongation in the first year following removal of the original community), and that the composition of the colonizing bryophyte community is very similar to the original community. The source of nearly all temperate forest colonization is due to encroachment from the sides of cleared cylindrats.

The results from Monteverde were surprising. First, the rate of colonization was extremely slow. For the first five years after stripping, no epiphytes had colonized the exposed branch sites; cylindrats were completely bare. Second, the returning communities differed strikingly from the original communities. Dead organic matter, bryophytes, and vascular plants, with no bare bark or lichens, dominated the original communities. Crustose and foliose lichens, with very little vascular plant colonization (Fig. 1), dominated the colonizing communities.

Third, the pattern of colonization contrasted with that of other studies. Instead of encroachment from the sides, epiphytes in the Monteverde cylindrats colonized the branches from the bottom up.

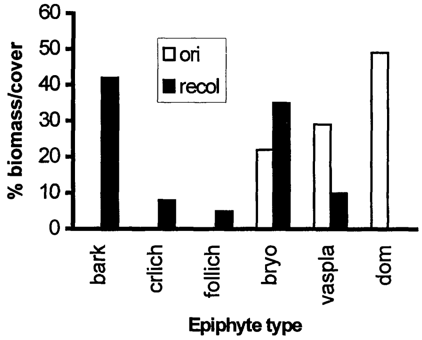

FIGURE 1. Abundance of components for the original (ori) community in percent total biomass and that of the colonizing (recol) community in percent total cover of epiphyte communities on inner branches of mature trees in Monteverde, Costa Rica. Crlich = crustose lichens; follich = foliose lichens; bryo = bryophytes; vaspla = vascular plants; dom = dead organic matter, including intercepted litterfall, detritus, and crown humus.

During the sixth year, I noted that some of the branches had algae and bryophytes growing on the underside of the branch. I also noted that following precipitation events, the bottom half of the branch dried out more slowly than the top half, due to the "shading" effect of the branch itself. After eight years, on some of the branches, the bryophyte cover from the underside of the branch had coalesced on the upper part. By the tenth year, small seedlings of vascular plants (tiny bromeliads and succulent-leafed *Peperomia* and orchid species) were rooted in the accumulated substrate.

For the original epiphyte mats, there was a strong tree effect on total epiphyte biomass ($P < 0.002$). There was a branch effect in the original communities for only one of the five trees (tree no. 4, Table 1). There was no tree or branch effect on the amount of total cover for the colonizing epiphyte communities ($P < 0.05$). There was a weak positive relationship ($r = 0.22$) between the abundance of the original community (total biomass) and the colonizing epiphyte community (total percent cover).

These results indicate that the branch substrate of large mature branches may be inimical to early secondary succession after stripping, even though the general environmental conditions and life histories of mature canopy communities foster luxuriant epiphyte growth. Why might colonization of the mature cloud forest epiphytes occur so slowly, and from the bottom of the branch up when epiphytes on young branch tips in the canopy and on saplings on the forest floor colonize rapidly around the entire circumference of the stem? Because they lack organic connection to the pool of water and nutrients on the forest floor, mature epiphytes may require substantial and constant moisture on their immediate substrate to survive; bare bark has very little water and nutrient retention capacity. Tree bark in tropical montane forests is generally smooth with few "safe spots" for propagules or rootlets to hang onto, especially in heavy rainstorms. The early colonizers, which are surface-adhering and poikilohydric cryptogams, are capable of withstanding substantial periods of desiccation; however, they themselves take time and require some moisture to develop into substrates useful for colonization by others, as suggested by their initial presence on the moister underside of the exposed branches. These colonizers provide a substrate for mineral accumulation from leaf leachate, water retention, and for physical attachment of more complex forms of epiphytic plants that constitute later successional communities.

Why does secondary succession of mature branches after stripping proceed so slowly compared to the rapid primary succession that takes place at canopy-level branch tips and on understory saplings? Canopy-level twigs are very small in girth; they may be able to "capture" and retain wind-borne vegetative strands of bryophytes, like spaghetti on the tines of a fork. Also, their direct exposure to blowing mist, which occurs most abundantly at the outer edge of the canopy, provides a more constant supply of moisture and atmospheric-borne nutrients than branches in the crown interior and on the forest floor, where mist coalesces into larger drops and is leached of much of its nutrient content (especially nitrogen; Clark, Nadkarni, and Gholz 1998; Clark, Nadkarni, Schaefer, and Gholz 1998).

In the understory, saplings present small-diameter branch substrates on which, as with canopy branch tips, strands of falling cryptogams can be snagged and retained. The understory environment is much moister than that of the upper canopy, especially in the dry season (Bohlman *et al.* 1995); thus water availability may not be as limiting as it is for mature branches and branch tips in the canopy. This is supported by the absence of lichens on saplings, whereas crustose, foliose, and fruticose lichens were common on canopy branch tips.

One scenario for the development of undisturbed epiphyte communities on the inner branches of mature trees is a sequence that may take the generation time of the tree. Rapid colonization of branchlets by cryptogams that are snagged and retained occurs when the trees are understory saplings, and during subsequent primary succession of canopy-level branch tips. As the trees age, these colonizers grow along with the increase in branch diameter and the concomitant changes in light and precipitation regimes and the increasing depth of accumulated dead organic matter. The high biomass and diversity of the mature epiphyte communities may be due largely to the positive feedback that follows their establishment; once they are established through the canopy tip and understory sampling sequence, they continue to accumulate water and allochthonous nutrients (Nadkarni & Matelson 1991).

This sequence of autogenic succession, in which the biotic community fosters the perpetuation of suitable habitat, would be broken when the positive feedback mechanisms are cut off by removal of the biotic community (as mimicked by these experimental manipulations). Following disturbance on large branches within the canopy, a very different habitat is created—bare bark, a broad, slippery surface that is unlikely to snag threads of bryophytes, and one subject to rapid drying. Thus, "recolonization" in this case is not really recolonization, but rather colonization of a very different habitat into which propagules normally fall and germinate. The high spatial variability of within-canopy substrates requires large numbers of samples to characterize these processes. Recovery may occur only after a very long time, if ever. Thus, mature epiphyte communities effectively may be as old and as potentially nonrenewable as their host trees.

Once the bryophytes have grown up and around the circumference of the branch, however, colonization of the textured, water-retentive and nutrient-richer substrate may be much more rapid than the initial stages observed in this study. My results indicate that this phenomenon must be monitored for longer than a decade to document the next stages of succession and to ultimately understand how vulnerable these mature epiphyte communities are to disturbance.

The weak positive relationship between the relative abundance of the original community biomass and the amount of cover of the colonizing epiphyte community indicates a faint "ecological footprint" of the original community on the colonizing epiphytes (*i.e.,* the abundance of the original community helps determine the abundance of the colonizing community). One mechanism for this pattern could be those original communities with the greatest abundance of epiphytes providing more available propagules directly adjacent to the site of colonization. Alternatively, the pattern could be attributed to the response of both original and colonizing communities to the conditions at a particular site; *i.e.,* certain branch locations may be good sites for both the original and colonizing communities due to their physical characteristics (*e.g.,* exposure to mist and wind, branch diameter, horizontal angle) or substrate characteristics (*e.g.,* rugose bark). If either of these explanations is true, the ecological footprint may become more pronounced when more time elapses. The strong between-tree effects observed in mature, but not colonizing, epiphyte communities support this idea.

Studies of succession in arboreal plant communities relate in interesting ways to studies of succession in terrestrial plants. For example, the colonization of landslides, which constitutes primary succession, is analogous to colonization of a new twig or the stems of an understory sapling. The post-landslide community undergoes succession to mature forest with a concomitant change in environmental conditions (*e.g.,* attenuation of light in the understory, accumulation of soil organic matter). If the understory is stripped or damaged (*e.g.,* the "socolado" treatment of tropical lowland forests), it may take decades for the understory to regrow in the very low light intensity, as compared to the rapid development of vegetation on the newly cleared landslide. Long-term studies on the dynamics of epiphytic plant communities in the canopy—on the order of several decades—will provide insights on ecological succession and restoration of arboreal and terrestrial root plant communities.

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