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CHAPTER 8-4
TROPICS: EPIPHYTE ECOLOGY, PART 2

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Figure 1. Mossy forest in rainy season on Reunion Island. Bryophytes surround the branches like a muff. Photo Courtesy of Min Chuah-Petiot.

Adaptations

Living on trees often puts the bryophytes at the mercy of rainfall (where there is no fog), either as throughfall or stemflow. Thus, special adaptations are necessary for those times when it is not raining, for the substrate is unlikely to do much to maintain the humidity (Frahm & Kürschner 1989). Gradstein and Pócs (1989) suggest a number of adaptations that permit these taxa to be so successful in this living habitat:

1. **Green, multicellular spores** with **endosporous** development (Figure 2) [*e.g.* **Dicnemonaceae** (Figure 3), **Lejeuneaceae** (Figure 6, Figure 8-Figure 9)] (Nehira 1983), permitting the protonema to get a quick start. **Anisomorphic** spores in ***Macromitrium erythrocomum*** (Figure 4) (Ramsay *et al*. 2017) could increase chances of dispersal at different times.
2. **Sexual dimorphism** and **phyllodioicy** (having dwarf males that live on leaves or tomentum of females; Figure 5), possibly increasing gene flow by ensuring that males are close to females. [*e.g.* dwarf males in ***Macromitrium erythrocomum*** (Ramsay *et al*. 2017)].
3. Numerous means of **asexual reproduction**, **monoicous** condition, and **neoteny** (sexual maturity at early developmental stage; Figure 6), permitting movement from place to place among **ephemeral** (short-lived) substrata [*e.g.* **Lejeuneaceae** (Figure 6, Figure 8-Figure 9)] (Schuster 1984; Richards 1984).
4. **Rhizoid discs** (Figure 7) for anchorage and adhesion (Winkler 1967).
5. **Lobules** [**Frullaniaceae** (Figure 70), **Lejeuneaceae** (Figure 6, Figure 8-Figure 9)] and **hyaline leaf**

margins for absorption and retention of water; ***Colura*** (Figure 8-Figure 9) even has a closing apparatus at the entrance of its lobule (Jovet-Ast 1953). Many **Calymperaceae** (Figure 10) have **hyaline cells** (Figure 11) in their leaves (Richards 1984).

6. **Cushion** life form (Figure 28) on branches of open montane forests (Pócs 1982).

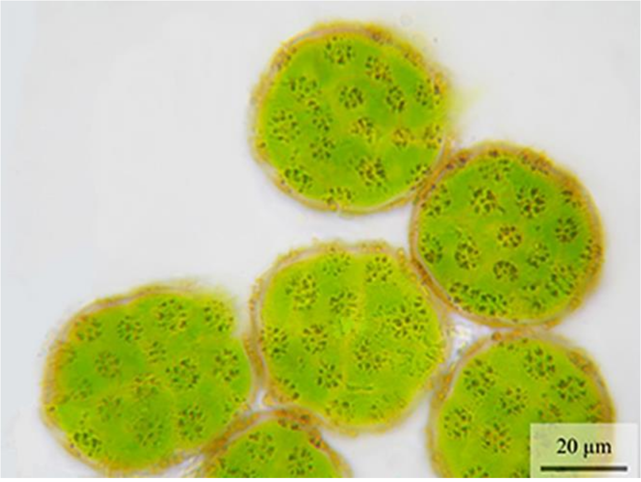

Figure 2. ***Frullania ericoides*** multicellular green endospores, demonstrating their germination within the spore. Photo modified from Silva-e-Costa *et al*. 2017, through Creative Commons.

Figure 3. ***Dicnemon*** sp., a genus with endosporic development. Photo by Vita Plášek, with permission.

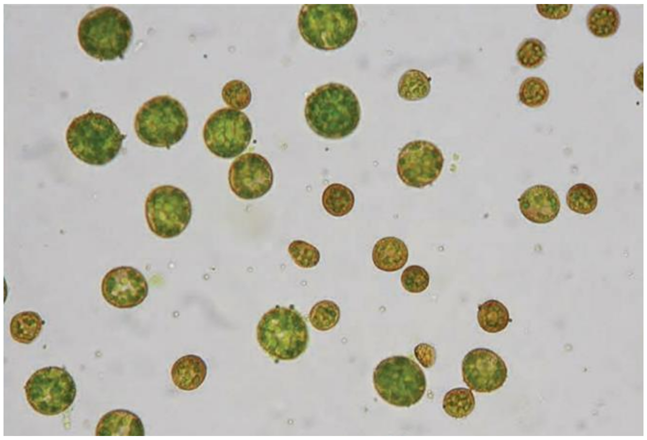

Figure 4. ***Macromitrium erythrocomum*** anisomorphic spores. Photo from Ramsay *et al.* 2017, with permission.

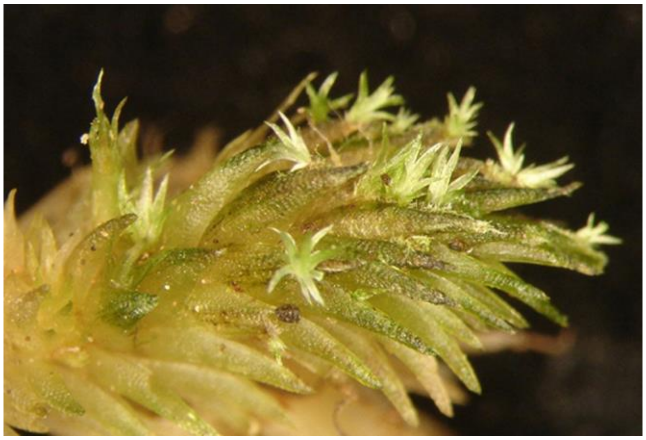

Figure 5. ***Leucobryum candidum*** with dwarf males, showing **phyllodioicy**. Photo by Paddy Dalton, with permission.

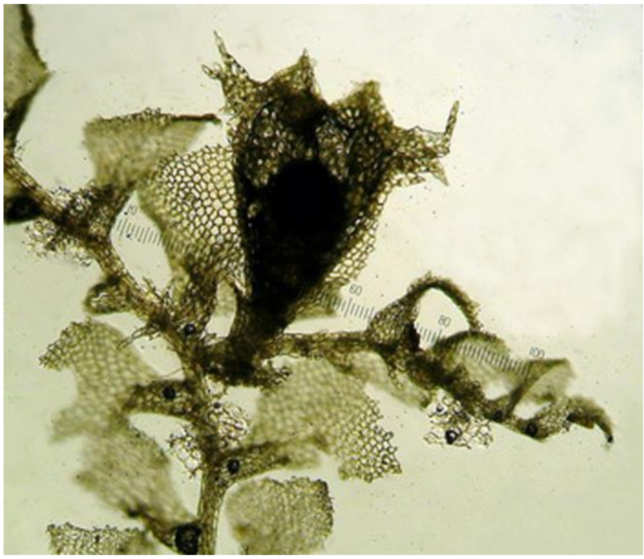

Figure 6. ***Drepanolejeunea inchoata*** with perianth, an example of **neoteny** in the **Lejeuneaceae**. Photo by Michaela Sonnleitner, with permission.

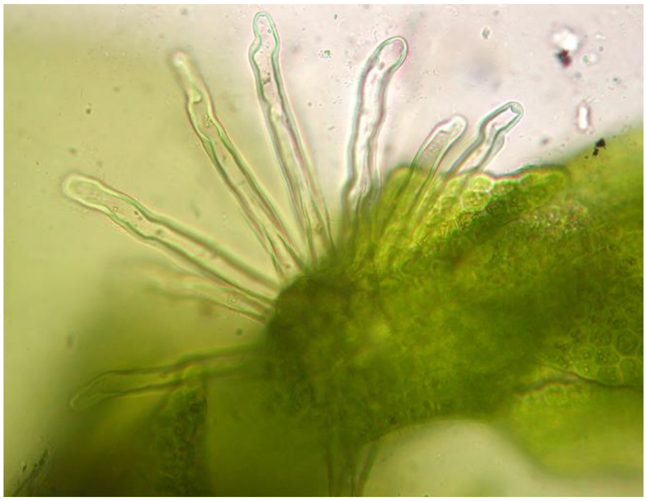

Figure 7. ***Frullania*** rhizoids. Photo courtesy of Andi Cairns.

Figure 8. ***Colura calyptrifolia*** on willow, with lobules showing. Photo by Stan Phillips, through public domain.

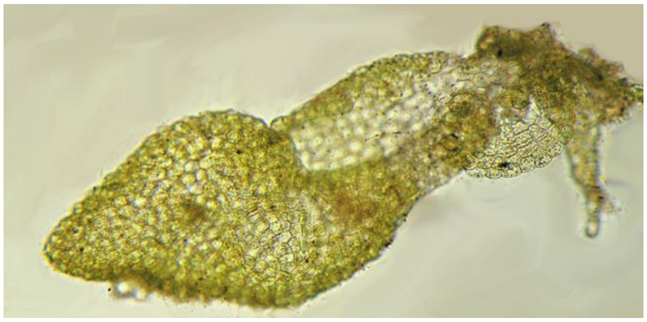

Figure 9. ***Colura*** leaf showing lobule. Photo courtesy of Jan-Peter Frahm.

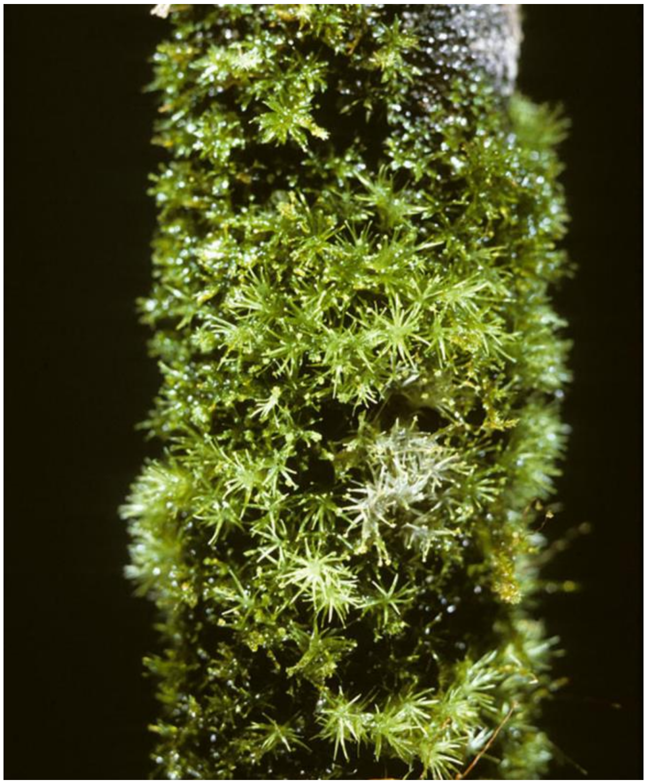

Figure 10. ***Leucophanes molleri*** (**Calymperaceae**). Some members of this family have hyaline cells in their leaves. Photo courtesy of Noris Salazar Allen.

Figure 11. ***Leucophanes molleri*** (**Calymperaceae**) leaf cross section showing hyaline cells surrounding photosynthetic cells. Photo courtesy of Noris Salazar Allen.

Frey *et al*. (1990) studied the epiphytes in Mt. Kinabalu (Figure 12) in North Borneo. They examined distribution patterns of life forms and the water-storing structures in epiphytes. They also looked at their role in water leaching, an important aspect in tropical forest nutrient cycling. Other useful studies on adaptations include those of Thiers (1988 – **Jungermanniales**, *i.e.* leafy liverworts; Figure 6, Figure 8) and Kürschner (2000 – adaptations in the tropical rainforest).

Figure 12. Mt. Kinabalu in Borneo. Photo through Creative Commons.

Pigmentation

In their study of ***Macromitrium*** in the Wet Tropics bioregion of Queensland, Australia, Ramsay *et al*. (2017) questioned the appearance of red species there. This was particularly striking in the epiphyte ***M. erythrocomum*** (Figure 13). Although some bryophyte species have been studied for their use of pigmentation as protection against high light (*e.g.*, Marshall & Proctor 2004), no tropical species has thus far been used in such experimentation. In ***Macromitrium*** species, red, orange, and yellow pigments are likewise most pronounced in species adapted for high light (Vitt 1994). In mosses, these accessory pigments occur mostly in cell walls. For ***M. erythrocomum***, the function of these pigments is elusive. These mosses grow in dense shade where protection from high light intensities is unnecessary. Ramsay *et al*. suggested that the pigmentation could be a genetic leftover from an ancestor adapted to high light.

Figure 13. ***Macromitrium erythrocomium*** from northern Queensland. Note young, green leaves at the bottom and mature yellow to reddish leaves on the mature plants with sporophytes. Photo from Ramsay *et al.* 2017, with permission.

This species also presents an interesting progression of leaf color in its life cycle (Ramsay *et al*. 2017). Young leaves are light green, having cells packed with chloroplasts and walls not colored (Figure 13). At this stage, the costa is already bright red. As the leaf ages, it loses its chloroplasts, making the cell lumen yellowish while retaining the red costa (Figure 13-Figure 14). It continues to develop red pigments, eventually filling the cells, and the walls also become colored, making the entire leaf red.

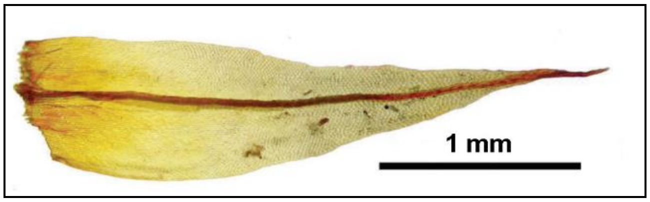

Figure 14. ***Macromitrium erythrocomum*** leaf with red costa. Photo from Ramsay *et al.* 2017, with permission.

Growth Forms and Life Forms

Growth forms, life forms, and life cycle strategies interact with other adaptations to provide the bryophytes with the best strategy for a particular environment. The main reference for growth or life forms of bryophytes is Mägdefrau 1982 and for life strategies During 1979. See also Volume 1, Chapter 4, of this series on Bryophyte Ecology for details on these.

Based on a number of pilot studies in the tropics (Frahm 1990; Frey *et al*. 1990, 1995; Frey & Kürschner 1991; Kürschner & Seifert 1995; Kürschner & Parolly 1998b; Kürschner *et al*. 1998), Kürschner *et al*. (1999) described generalizations of tropical growth forms, life forms, and life strategies for the epiphyte habitat. **Perennial stayers** and **perennial shuttle** species (see During 1979) are important life cycle strategies in most of the tropics. They dominate in the tropical lowland and submontane belt as well as in the cooler and more humid montane rainforest. However, in the former two they are **mat formers**, whereas in the montane rainforest they are mostly **fans** and **wefts** that rely on propagules and clonal growth. Some species have ciliate leaves that are able to collect water from fog. In the more xeric conditions of the open, upper montane forests, **short turfs**, **tall turfs**, and **cushions** predominate, but are also **perennial stayers** and **perennial shuttle** species. **Colonists**, by contrast, occur almost exclusively in secondary forests. Kürschner and coworkers considered these relationships to apply throughout the tropics.

In the Sulawesi rainforest (Figure 15) in Indonesia, the understory has a preponderance of **dendroid** and **fan-like** species of bryophytes, whereas the crowns of the trees have more **tuft** species than other types (Sporn *et al*. 2010). Like many other factors, this reflects the differences in microclimate between the upper canopy and the understory, but it also reflects differences in substrate provided by understory trees vs canopy trees.

Figure 15. Mountains of South Sulawesi, Indonesia. Photo by Achmad Rabin Taim, through Creative Commons.

Kürschner and Seifert (1995) described epiphytic communities in the eastern Congo basin (Figure 16) and nearby mountain ranges. These included consideration of life forms and water storage.

Figure 16. Forests in the Democratic Republic of the Congo. Photo from Bobulix, through Creative Commons.

Bryophyte life forms in flooded and non-flooded habitats in the Colombian Amazon (Figure 17-Figure 18) reflect the differences in humidity (Benavides *et al*. (2004). In the floodplains, the **fan** and **mat** forms predominate, whereas more epiphytic liverworts occur in the non-flooded forest.

Leerdam *et al*. (1990) described the epiphytes of a Colombian cloud forest (Figure 19). Bryophytes comprise most of the biomass. They found a sequence of life forms along the canopy branches, creating two groups: inner canopy and outer canopy. These are mostly **tall turfs** and **smooth mats**, respectively. The life forms corresponded with microclimatological factors, water and nutrient availability, and substratum age. The phorophyte species also influence the type of growth and life forms that grow there.

Figure 17. Amazon rainforest. Photo by Phil Harris, through Creative Commons.

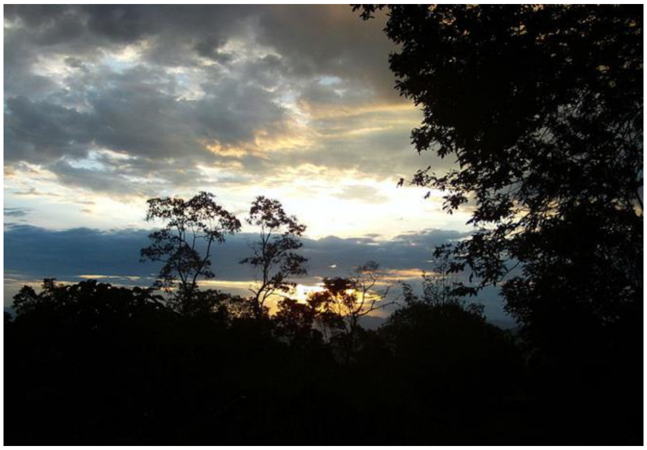

Figure 18. Colombian Amazon. Photo by Actorsuarez, through Creative Commons.

Figure 19. Colombian cloud forest with White Yarumo. Photo by Alejandro Bayer Tamayo, through Creative Commons.

Some striking life forms that are almost exclusively tropical are the **feather**, **bracket**, and **pendent** (Figure 20) forms. These seem to reflect the high atmospheric humidity around the first few meters of the tree bole, where little air stirs to carry away the moisture quickly.

Pendent (Figure 20) bryophytes are common in areas with high humidity. Proctor (2004) examined the light and desiccation responses of two of these **pendent** taxa [***Weymouthia mollis*** (Figure 21) and ***W. cochlearifolia*** (Figure 22)]. ***Weymouthia cochlearifolia*** is more typical forming patches on the trunk and branches, but it can grow as a **pendent** form. ***Weymouthia mollis*** typically grows as a **pendent** form. ***Weymouthia cochlearifolia*** reached 95% saturation at 160 µmol m^{-2} s^{-1} PPFD, whereas ***W. mollis*** ranged 176-307 µmol m^{-2} s^{-1} PPFD or even more. They demonstrated the primary needs of **pendent** forms: high levels and reasonably regular precipitation, shelter from wind, and moderate shade. From this they surmised that exposure and the high evaporation rate that accompanies it will favor **small cushions** or **smooth mat** life forms. Proctor reasoned that exposure would minimize the boundary-layer resistance to CO_2 uptake and maximize the mechanical effects of wind. **Tight cushions** and **smooth mats** can more easily resist these. On the other hand, the more open life forms are more exposed for efficient light interception and CO_2 uptake.

Figure 20. ***Cheilolejeunea jackii*** **pendent** liverwort on the Galapagos Islands. Photo courtesy of Robbert Gradstein.

Figure 21. ***Weymouthia mollis***, a species that is typically **pendent**, in Chile. Photo by Juan Larrain, with permission.

Figure 22. ***Weymouthia cochlearifolia***, a species that can form both **mats** and **pendent** forms. Photo by Niels Klazenga, with permission.

Some bryophyte species develop different life forms based on their habitat (Ford 1994). For example in Queensland ***Papillaria*** (Figure 23) spp. on ***Sloanea woollsii*** (Figure 25) exhibit forms ranging from **long pendent** forms in the canopy branches to **creeping mats** on lower branches and the upper trunk. **Dendroid** forms are especially common on tree trunks. Stumps have mosses such as the dominant ***Camptochaete vaga*** (see Figure 24), but also can have ***Dicranum*** spp. (see Figure 26)

Figure 23. ***Papillaria crocea***, a species of the Wet Tropics in Australia. Photo courtesy of Andi Cairns.

Figure 24. ***Camptochaete*** sp. from New Zealand. Photo by Jan-Peter Frahm, with permission.

Figure 25. ***Sloanea woollsii*** with epiphytes on the base and trunk. Photo by Peter Woodard, through public domain.

Figure 26. ***Dicranum*** sp., a cushion former from the Neotropics. Photo by Michael Lüth, with permission.

Additional references on tropical bryophyte life forms include those of Kürschner and Parolly (1998a, 2005, 2007).

Life Cycle Strategies

One of the most important adaptations to tropical climates is that of life cycle strategies. These must be timed to coordinate with wet and dry periods. Sperm require at least some water for transfer. Spores are dispersed best by dry winds.

Furthermore, life strategies of epiphytic bryophytes change with altitude. Frey *et al*. (1995) compared these strategies in the eastern Congo basin (Figure 27), a tropical lowland. In the primary rainforests of the tropical lowland and lower montane, the epiphytes were generally **perennial shuttle** species and **perennial stayers**. These had low to moderate sexual and asexual reproduction. This strategy combination is well suited for the high temperature and humidity regime, particularly for the leafy liverworts that dominate these communities. In the montane rainforests and cloud forests the perennial shuttle species have high asexual reproduction, with both propagules and clonal growth contributing. In **secondary woodlands** (areas of regrowth), ericaceous woodlands, and subpáramo of African volcanoes, the perennial shuttle and perennial stayers with high levels of sexual reproduction reach their greatest numbers. This is facilitated by the regular production of sporophytes in the **xeric** (dry) conditions with a strong **diurnal** (daily) climate. This reproductive strategy is typical of epiphytes in xeric woodlands.

Figure 27. Lowland rainforest, Congo Basin, Cameroon. Photo by Mauri Rautkari, through Creative Commons.

Kürschner (2003) described the life strategies of two epiphytic bryophyte associations in southwestern Arabia. The species are mostly drought tolerant. Their life strategies are distinctly correlated with their ecological site conditions. The ***Orthotricho*** (Figure 28)-***Fabronietum socotranae*** (Figure 29) is a drought-tolerant association dominated by **cushions**, **short turf**, and **mats** – **perennial stayers** with regular sporophyte formation. By contrast, in the sub-humid ***Leptodonto*** (Figure 30)-***Leucodontetum schweinfurthii*** (Figure 31) association, the typical life forms are **tails** and **fans**. These are **pleurocarpous perennial shuttle** species that have large spores. These large spores limit them to short-range dispersal, relatively low reproductive rates, and generative reproduction. This association has a much higher diversity of life forms and life strategies, including liverworts.

Figure 28. ***Orthotrichum tasmanicum*** with capsules. Photo by David Tng, with permission.

Figure 29. ***Fabronia pusilla***; in Arabia ***Orthotricho-Fabronietum socotranae*** is a common association. Photo by Michael Lüth, with permission.

Figure 30. ***Leptodon longisetus*** from Tenerife; this genus forms the ***Leptodonto-Leucodontetum schweinfurthii*** association in humid Arabia. Photo by Jonathan Sleath, with permission.

Figure 31. ***Leucodon julaceus***; this genus forms the ***Leptodonto-Leucodontetum schweinfurthii*** association in humid Arabia. Photo by Bob Klips, with permission.

Spore size is an adaptive trait wherein small spores have a good chance for long-distance dispersal and large spores do not, but have a greater chance for successful germination and establishment (Kürschner & Parolly 1998a). Few bryophytes are able to use both strategies. However, one notable exception is an epiphytic **heterosporous** (having two sizes of spores) moss of the Andes of northern Peru – ***Leptodontium viticulosoides*** (Figure 32). More recently, this was reported in ***Macromitrium erythrocomum*** (Figure 4, Figure 13) from the Australian Wet Tropics (Ramsay *et al*. 2017).

Figure 32. ***Leptodontium viticulosoides***, a heterosporous species that uses both long-distance dispersal of small spores and more successful establishment of large spores. Photo by Claudio Delgadillo Moya, with permission.

Having similar adaptive traits in similar conditions is common among bryophytic epiphytes (Kürschner 2003, 2004a) – a product of convergent evolution. This convergence is common among life strategies of tropical bryophytes.

Additional studies on life strategies include Egunyomi and Olarinmoye (1983), Kürschner (2004b), Kürschner and Parolly (2005, 2007), and Kürschner *et al*. (2006, 2007).

Dispersal and Colonization

Colonization must be preceded by dispersal. Thus, to examine colonization rates, we must necessarily understand the limitations to dispersal.

Yeaton and Gladstone (1982) examined colonization patterns of epiphytic orchids on calabash trees (***Crescentia alata***; Figure 33) in Costa Rica. They hypothesized that the number of propagules produced by the species determined the colonization pattern. The same hypothesis can be considered for bryophytes.

Figure 33. ***Crescentia alata*** in Guanacaste dry forest. Photo by Daniel H. Janzen, through Creative Commons.

Wolf (1994) examined the factors that control the distribution of bryophytes and lichens in the northern Andes (Figure 34). He concluded that randomness of propagule supply appears to be the most important factor in determining the epiphyte composition on branch and trunk segments.

Figure 34. Northern Andes in Colombia. Photo by Conocer, through public domain.

But Mari *et al*. (2016) reached a somewhat different conclusion. They avoided the differences among **phorophytes** (plants on which epiphytes grow) by sampling only one tree species, ***Aldina heterophylla*** (a legume). This is a dominant species in the Amazonian white-sand habitats and sports heavy loads of epiphytes. Mari and coworkers attempted to quantify the importance of the tree zone in colonization by comparing geographic distances at scales of 100 m^2 and 2,500 km^2. At the larger, regional scale, the tree zone explained approximately two-thirds of the primary compositional gradient – a factor more than double that accounted for by site differences.

On the other hand, spatial effects were absent at the fine scale of 100 m^2, with more dissimilarity than expected by chance when compared to communities on neighboring phorophytes. The researchers concluded that microsite availability, not dispersal limitation, is the most important factor in structuring the epiphytic communities of this forest type.

The **phorophyte** itself can play a role in the colonization (Olarinmoye 1977). Such factors as bark roughness and smoothness determine whether a propagule is able to adhere once it arrives. Leachates from the host leaves could inhibit growth, but for the leafy liverwort ***Radula flaccida*** (Figure 35), it was only extracts, not leachates, that inhibited growth (Olarinmoye 1981, 1982).

Figure 35. ***Radula flaccida*** habit with gemmae. Extracts, but not leachates, from tree leaves inhibited growth on the phorophyte host. Photo by Michaela Sonnleitner, with permission.

Oliveira *et al*. (2009) noted the gradient of bryophyte species communities from the base of the tree to the top of the canopy in the Guianas (Figure 36), highlighting the role of niche assembly in defining these communities. They set out to test whether niche assembly, rather than dispersal limitation, drives species composition of epiphytic bryophyte communities on a large spatial scale. Using three lowland forests, they sampled six different height zones of several trees in each. They tested whether specialists maintain a preferred height zone across the Guianas. They found that 57% of the species had a preferred height zone throughout the localities. In fact, the communities were more similar across 640 km at the same height zone than they were among the heights on any single tree. Hence, they concluded that niche assembly was a stronger determinant of the communities than were dispersal factors on both local and regional scales.

While the similarity within a zone is greater even at 640 km than among height zones of a tree, the similarity within the same locality is greater than that with greater distances (Oliveira & ter Steege 2015). Using nine localities across 2800 km from east to west in the Amazon forest (Figure 17), these researchers again demonstrated that height zone explains most of the variation among communities. The outer canopy communities exhibit the greatest similarity between trees and localities. The variation at the geographic scale could be explained primarily by elevation and temperature.

Figure 36. French Guiana tropical forest. Photo by Cayambe, through Creative Commons.

Oliveira and ter Steege (2015) furthermore found that establishment limitation is strongest at the extremes of the vertical gradient. Communities of the tree base and the outer canopy draw individuals from outside the habitat species pool at a rate of 0.28 and 0.22, respectively, in contrast with values between 0.55 and 0.76 of other height zones, contrasting with the hypothesis that species inhabiting the canopy have higher chances of engaging in long-distance dispersal events (see *e.g.* Gradstein 2006, p. 17). Whereas the canopy may have a greater exposure to propagules that are in the air currents, they are also subject to winds that can dislodge the propagules. They might also be limited by propagule availability as those propagules might be constrained by their canopy of origin, preventing them from entering the air currents. Oliveira and ter Steege suggested that bryophytes in these two extreme zones (outer canopy and tree base) might be, through time, subjected to stronger selection.

Hietz (1997) studied the population dynamics of epiphytes in a Mexican humid montane forest. He used repeated photographs to follow 5,124 individuals (44 species) for more than two years. This study demonstrated the importance of branch loss as a contributor to the mortality of epiphytic flowering plants and ferns.

Nadkarni (2000) performed one of the few experimental studies on colonization by epiphytes. She stripped branch surfaces of their epiphytes in a lower montane cloud forest, then tracked what landed where and whether it was able to remain where it landed. Epiphytes are lost from the canopy due to sloughing, branch breakage, and treefalls, typically caused by wind or heavy rainfall. Most of our understanding of colonization patterns has been from studying forests of a series of ages and comparing their floras. In the temperate forest, colonization is rapid, with up to 6 cm elongation in the first year. Furthermore, the composition is similar to that of the original community. But in the tropical forest, colonization is very slow, exhibiting no colonization in the first five years! The new colonization furthermore differs markedly from the original communities. Instead of the dead organic matter, bryophytes, and tracheophytes of the mature branch community, the new community begins with crustose and foliose lichens. Even more surprising is that instead of encroachment from the sides, the colonizers enter the bare areas from the bottom up. In the sixth year, algae and bryophytes begin to colonize the lower sides of branches. This appears to be related to the greater moisture on that side of the branch.

Nadkarni (2000) concluded that bare branches, typically with smooth bark, retain little moisture and are unsuitable for the developing epiphytes. Once early lichens become established, more water is retained, permitting growth of species adapted to frequent drying. As colonization increases, nutrients as well as water are retained, permitting larger and less xerophytic species to survive. She further surmised that at the branch tips, where colonization is much more rapid, the small branches are more able to trap and hold propagules, and they are more exposed to fog and mist, thus having more available moisture. In both cases, once the bryophytes become established, the better retention of water and nutrients facilitates a more rapid continuation of the colonization.

In a separate study, Nadkarni *et al*. (2000) experimented with artificially dispersing bryophyte fragments in a tropical montane cloud forest of Costa Rica, using quadrats above branches of saplings and mature trees of ***Ocotea tonduzii*** (see Figure 37). Only 1% of the dispersed fragments were retained by the sapling crowns for the six months of the study. On the other hand, branches in the forest canopy, already possessing intact epiphyte communities, retained 24% of the dropped bryophytes. Branches that had been stripped of their epiphytes retained only 5%.

Figure 37. *Ocotea minarum*; ***Ocotea tonduzii*** was used to study adherence of bryophyte fragments in Costa Rica. Photo by Denise Sasaki, through Creative Commons.

Colonization of bryophytes can be important to establish a suitable habitat for larger epiphytes such as orchids. Zotz and Vollrath (2003) found that epiphytes on the palm ***Socratea exorrhiza*** (Figure 38-Figure 39) become established in bryophyte clumps (Figure 39) more often than could be expected from randomness, but they nevertheless do not seem to depend on them 100%. This enhancement of the habitat by bryophytes most likely accounts for the delay in tracheophyte colonization until the trees are at least 20 years old.

Figure 38. ***Socratea exorrhiza*** in Brazil. Photo by Andrew J. Henderson, Palmweb, through Creative Commons.

Figure 39. ***Socratea exorrhiza*** with various tracheophyte epiphytes established in bryophytic epiphytes. Photo by David J. Stang, through Creative Commons.

A number of ant species live in the trees in the tropics and some even build nests using tracheophytes (Longino & Nadkarni 1990; Blüthgen *et al*. 2001). In Costa Rica, these ants often make nests in arboreal litter, mosses, and humus that accumulate under the canopy epiphytic tracheophytes. The species in the canopy are rarely found on the ground and their travels among the canopy branches are likely to contribute to the dispersal of bryophyte fragments, gemmae, and spores. Their role in dispersal needs to be explored quantitatively.

In contrast with the experimental colonization study by Nadkarni (2000), Frahm *et al*. (2000) observed that crustose lichens seemed to inhibit epiphytic bryophyte growth. They tested extracts of these lichens and bark samples on spore germination of the soil bryophytes ***Ceratodon purpureus*** (Figure 40) and ***Funaria hygrometrica*** (Figure 41). These extracts inhibit spore germination of these two species. They also tested the extracts on seeds of the bromeliad *Vriesea splendens* (Figure 42) and the soil-dwelling mustard *Lepidium sativum* (Figure 43). The extracts reduce the germination of seeds of *Vriesea*, but they actually promote germination of *Lepidium*. Thus we cannot conclude from this study of soil species whether the crustose lichens actually inhibit growth of bryophytes that are normally epiphytes, but the results suggest that such interaction needs to be tested.

Figure 40. ***Ceratodon purpureus*** with young sporophytes, a soil-dwelling species whose spore germination is inhibited by at least some lichen extracts. Photo by Hermann Schachner, through Creative Commons.

Barkman (1958) and Pócs (1980) suggested that bryophytes may cause their own displacement by retaining water that makes tracheophytic epiphyte presence possible. They furthermore form humus, accelerate bark decay (Barkman 1958), and facilitate anchorage of seeds and other propagules.

Figure 41. ***Funaria hygrometrica*** with young sporophytes, a soil-dwelling species whose spore germination is inhibited by some lichen extracts. Photo by Hermann Schachner, through Creative Commons.

Figure 42. *Vriesea splendens*; germination of seeds in this species are inhibited by lichen extracts. Photo by Bernard Dupont, through Creative Commons.

Figure 43. *Lepidium sativum*, a species in which seed germination is enhanced by lichen extracts. Photo by Dinesh Valke, through Creative Commons.

Host Trees

Specific bryophyte-host relationships have been reported a number of times in temperate regions where tree species richness is very low, as for example those found by Slack (1976). As is often the case, she found strong preferences among eastern North American trees, but none of the bryophytes occurred exclusively on one tree sp.

Wolf (1995) summarized the forces leading to presence and abundance of species in epiphytic bryophyte communities in the canopy of an Upper Montane Rain Forest, Central Cordillera, Colombia. He considered two ways to look at these communities: emphasis on quality or quantity of preceding propagule supply; within community interactions such as competition. For the first of these, researchers have placed great importance on observed distribution patterns and high variability between epiphyte communities in seemingly identical habitats. But the great cover and biomass in these tropical montane rainforests suggests that competitive interactions may also be important. In his own study, Wolf found 120 bryophyte taxa (and 61 macrolichens). He recognized four community types from outer to inner canopy. Nevertheless, these four communities share many species and exhibit a species richness of about 100 taxa each. The inner canopy, with thick branches (21-80 cm diameter) had significantly fewer taxa per unit surface area, with an average of 1.72 taxa per dm^2 compared to 3.2 from the thinner middle canopy branches. Richness was even higher in the outer canopy, with 7.8 taxa per dm^2. If time were the most important factor, then the inner crown should have the highest number of species. Instead, one finds that the thick inner branches and trunks carry large patches of individual clones, suggesting competition through horizontal growth.

In the subtropical Tenerife, Canary Islands, González-Mancebo *et al*. (2003) described epiphytic bryophyte communities from five tree species in a laurel forest (Figure 44). Most of these bryophytes (37 species total) are **facultative epiphytes**, living on other substrates as well. And many are found on several tree species, with five being found on all five tree species. They further supported the observations that the species composition varies with bark characteristics, leeward vs windward exposure, height on tree, tree size, and degree of uprightness. Growth and life forms also relate to the moisture conditions of the bark.

Figure 44. Laurel forest on Tenerife, Canary Islands. Photo by Inkaroad, through Creative Commons

In tropical forests that have high tree species richness, such host-tree relationships are absent; at the same height, one can expect to find mostly the same bryophytes in the same forest. However, in tropical forests with low tree species diversity, clear host-tree relationships may be observed. The best example is demonstrated by Cornelissen and ter Steege (1989; ter Steege and Cornelissen 1989) on dry evergreen forest in Guyana dominated by two tree species (***Eperua grandiflora*** (rough-barked) or ***E. falcata***) (wallaba, smooth-barked; Figure 45-Figure 46). Not surprisingly, the two tree species host different epiphytic bryophyte assemblages, with the rough bark of ***E. grandiflora*** supporting more epiphytes.

Figure 45. ***Eperua falcata***, Guyana, showing smooth bark. Photo by Bernard Dupont, through Creative Commons.

Figure 46. ***Eperua falcata***, a species that has smooth bark and inhabits dry sites. Photo by Hiobson, through Creative Commons.

Rudolph *et al.* (1998) examined host tree characteristics in a western Andean rainforest in Ecuador (Figure 47). Müller and Frahm (1998) elaborated on the epiphytic mosses in an Ecuadorian montane rainforest in the Andes. They found 65 species (24 mosses, 41 liverworts) on the ten trees they examined. They found no significant correlation between species number and branch diameter, branch exposure, or elevation. However, as bark *p*H increased, the number of epiphytic bryophyte species decreased.

Figure 47. Ecuador tropical rainforest in middle of Rio Tiguiono at Bataburo Lodge. Photo by Andreas and Christel Nöllert, with permission.

Thus, even in cases where host specificity is absent, certain characteristics seem to encourage or discourage bryophytes. As noted earlier, bark differences in the tropics can be important for some bryophyte species, but have little effect on bryophyte communities or species richness.

Host "trees" can also include tree ferns. Jaag (1943) examined the foliage renewal rate, leaf life, and epiphyte "involvement" on tropical tree ferns. Frahm (2003) described the meager studies on epiphytes on tree ferns. In Southeastern Brazil, he identified 142 species on ***Cyathea*** (Figure 48-Figure 49) and ***Dicksonia*** (Figure 50) trunks. Most of these seem to be chance occurrences, with only 20 species occurring on more than 10% of the fern trunks in the study. Vital and Prado (2006) found a species new to Brazil (***Ceratolejeunea dentatocornuta***; see genus in Figure 51) occurring on ***Cyathea delgadii*** (Figure 52-Figure 53). These were in a fragment of the Atlantic forest in the state of Sao Paulo. In total, the researchers found 35 bryophyte species, 12 of mosses and 23 of liverworts. Medeiros *et al*. (1993) reported epiphytes on ***Cibotium*** species (Figure 54) and ***Sphaeropteris cooperi*** (=***Cyathea cooperi***; Figure 55), both tree ferns, in a Hawaiian rainforest (Figure 56).

Figure 48. ***Cyathea arborea*** in Guadeloupe. In Brazil and elsewhere, this genus serves as substrate for epiphytic bryophytes. Photo by Patrice, through Creative Commons.

Figure 49. ***Cyathea arborea***. In Brazil, trunks of this genus serve as substrates for epiphytic bryophytes. Photo by Xemenendura, through Creative Commons.

Figure 50. ***Dicksonia antarctica***. In Brazil, this genus serves as substrate for epiphytic bryophytes. Photo by Fir0002-Flagstaffotos, with online permission.

Figure 51. ***Ceratolejeunea cubensis***; ***C. dentacornuta*** was found as a new species on ***Cyathea delgadii*** in Brazil. Photo by Scott Zona, with permission.

Figure 52. ***Cyathea delgadii***, host of the new species of liverwort ***Ceratolejeunea dentacornuta***. Photo by Alcatron, through Creative Commons.

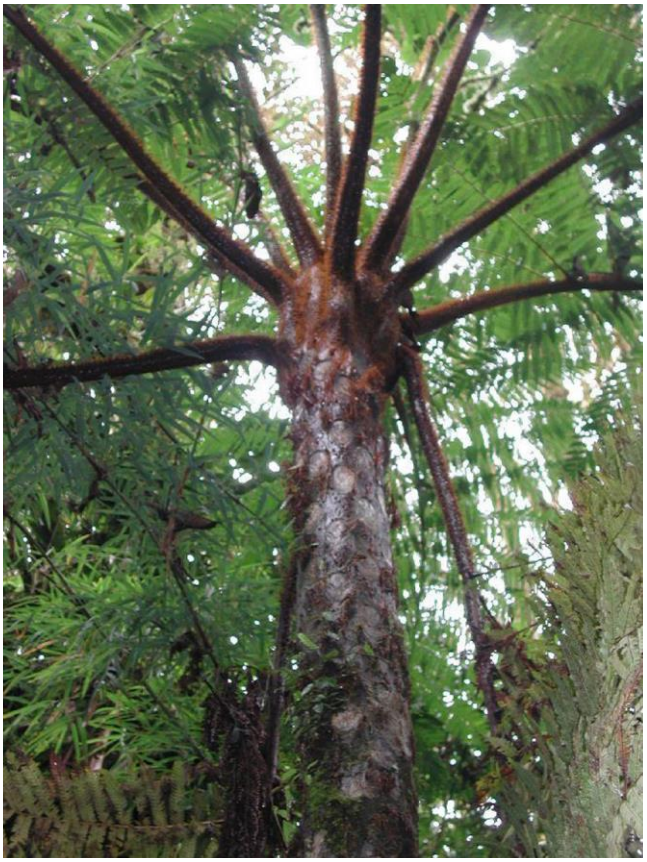

Figure 53. ***Cyathea delgadii***, host of the new species of liverwort ***Ceratolejeunea dentacornuta***. Photo by Alcatron, through Creative Commons.

Figure 54. ***Cibotium menziesii***; some members of this genus host bryophytic epiphytes in Hawaii. Photo by Forest and Kim Starr, through Creative Commons.

Figure 55. ***Sphaeropteris cooperi***, host of bryophytic epiphytes in Hawaii. Photo through Creative Commons.

Figure 56. Spring rainforest stream with mosses, Hawaii. Photo by Jcklyn Baltazar, through Creative Commons.

Using a line-intercept method, Batista and Santos (2016) studied the epiphytic bryophytes in the Atlantic Forest of southeastern Brazil (Figure 57). They identified 71 taxa. The mean coverage did not vary significantly among the various phytophysiognomies. Nevertheless, the species compositions were distinct among these phytophysiognomies, but no cohesive or isolated groups emerged. There was, however, a correlation between bryophyte cover and tree DBH. Bark *p*H of the palm ***Euterpe edulis*** (Figure 58) and bark roughness of members of the tree fern family **Cyatheaceae** (Figure 52-Figure 53, Figure 55) also affected species composition.

Figure 57. Atlantic forest, Pernambuco coastal habitat, Camarigibe, Brazil. Photo by Leonardo Brito Uniemelk, through Creative Commons.

Figure 58. ***Euterpe edulis*** in Brazil. Bark *p*H of this species affects species composition of bryophytic epiphytes. Photo by Alex Popovkin, through Creative Commons.

In areas with many plantations and more than one host species, more specificity may present itself. For example, in Nigeria over 60% of ***Octoblepharum albidum*** (Figure 59) collections were from ***Elaeis guineensis*** (Egunyomi 1975, 1978), whereas ***Calymperes palisotii*** (Figure 60) prefers ***Albizia saman*** (Figure 61-Figure 62) over the relatively smooth, non-fissured bark of ***Lagerstroemia*** sp. (Figure 63-Figure 64) (Egunyomi & Olarinmonye 1983). Different agroforests [mango (Figure 65) and *Citrus* (Figure 66)] house unique bryophyte communities. Ezukanma *et al*. (2019) found that each of these two communities had 12 bryophyte species, but only five were common to both.

Figure 59. ***Octoblepharum albidum***, one of the eight most common bryophytic epiphytes in the Amazon basin. Photo by Portioid, through Creative Commons.

Figure 60. ***Calymperes palisotii*** showing gemmae on leaf tips. Photo from Wilding *et al.* 2016, with permission.

Figure 61. ***Albizia saman***, substrate for ***Calymperes palisotii***. Photo by A. Gentry, MBG, through Creative Commons.

Figure 62. ***Albizia saman*** rough bark suitable for ***Calymperes palisotii***. Photo by David Stang, through Creative Commons.

Figure 63. ***Lagerstroemia speciosa*** from India. The smooth bark of species of ***Lagerstroemia*** in Nigeria is not suitable for the moss ***Calymperes palisotii***. Photo by Raju Kasambe, through Creative Commons.

Figure 64. ***Lagerstroemia speciosa*** bark from Hawaii, USA; smooth bark in this genus is not a preferred substrate for the moss ***Calymperes palisotii*** in Nigeria. Photo by Kim and Forest Starr, through Creative Commons.

Figure 65. Mango agroforest in India, a forest type that supports unique bryophyte communities in Nigeria. Photo from Bioversity International, through Creative Commons.

Figure 66, ***Citrus*** (orange plantation), a forest type that supports unique bryophyte communities in Nigeria. Photo by Hans Braxmeier, through Creative Commons.

Height on Tree

Andersohn (2004), working in central Guatemala, asked the question "Does tree height determine epiphyte diversity?" He listed the epiphytes, including the bryophytes. Many other studies have provided insight into this question.

Like epiphytes in other parts of the world, communities at the base, trunk, and crown differ due to light, moisture, and nutrients [Cornelissen & ter Steege 1986; Montfoort & Ek 1990; Kürschner 1990 (studied only base and trunk)]. In some forests, the tree bases receive so little light that even bryophytes are unable to grow there. The branches, on the other hand, can have complex, dense growths that sometimes surround the entire branch like a winter muff (Figure 1) for warming one's hands. In the crown, high light intensity and dryness become limiting. For example, in the dry evergreen (wallaba – ***Eperua falcata***; Figure 45-Figure 46) forest of Guyana, bryophytes and lichens on the canopy twigs of mature ***Eperua*** trees are predominantly of two types, the sun-tolerants and the pioneers (facultative epiphylls) (Cornelissen & ter Steege 1989). Many researchers follow the zones as described by Johansson (1974) (Figure 67-Figure 68).

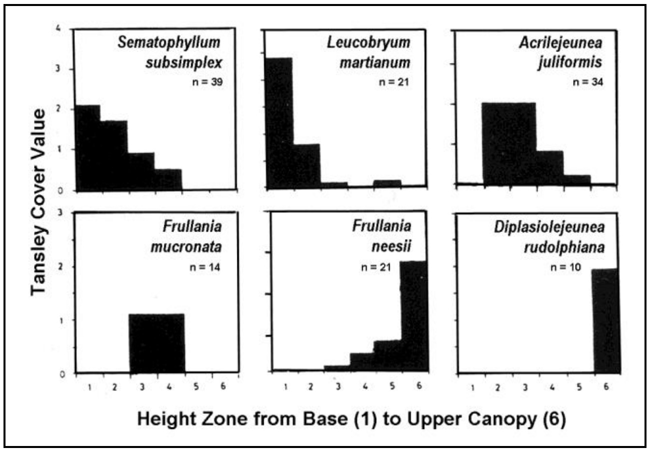

Figure 67. Vertical distribution (see Figure 68) of four moss and two leafy liverwort species in Guyana. Height zones are in Figure 68. Modified from Cornelissen & ter Steege 1989.

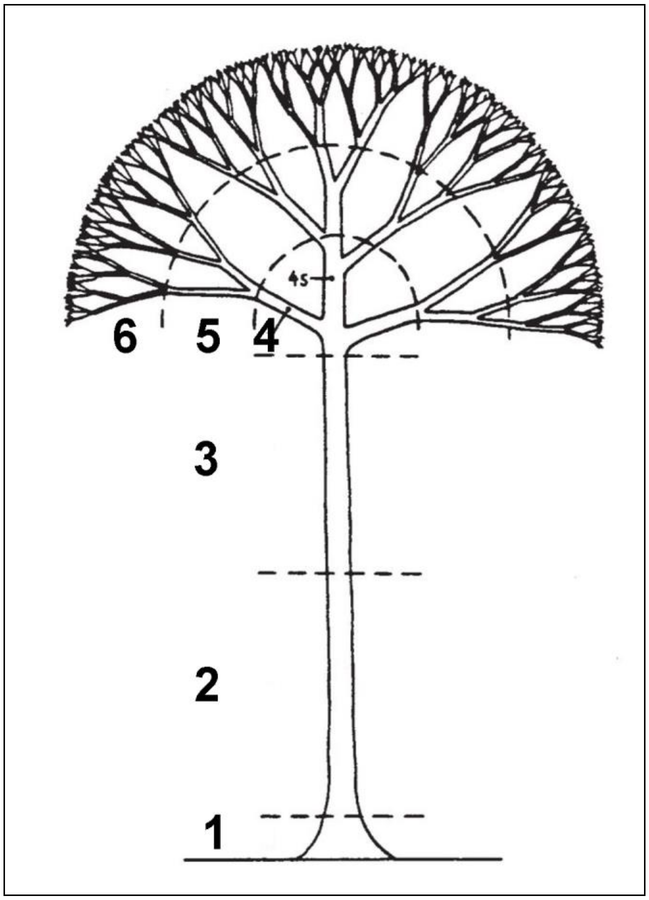

Figure 68. Epiphyte zones on a tree. Modified from Johansson 1974.

Zonation patterns occur from branch tips to center of the crown as well. Freiberg and Freiberg (2000) found that in the two lowland and two montane forests they studied in Ecuador (Figure 69), the epiphytic biomass per branch surface decreases from the center of the crown to the periphery.

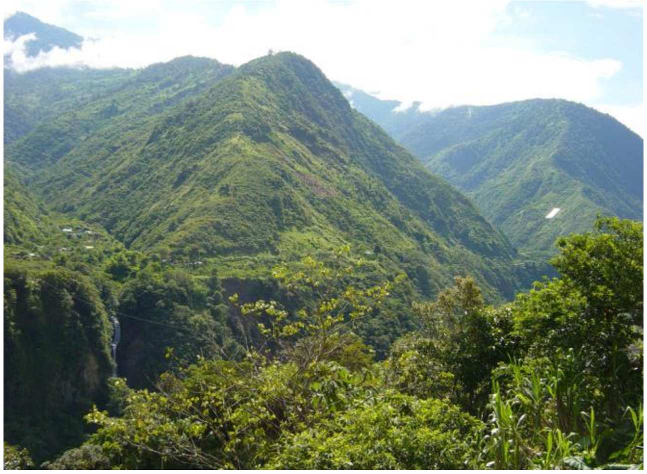

Figure 69. Montane forests, Ecuador. Photo by Martin Zeise, through Creative Commons.

Pócs (1982) found that mosses dominate the base of the trunk, but leafy liverworts, especially the ever-present ***Frullania*** (Figure 70) and **Lejeuneaceae** (Figure 6, Figure 8-Figure 9), dominate the branches.

Figure 70. ***Frullania*** sp., a genus that dominates branches of tropical trees. Photo by George Shepherd, through Creative Commons.

In French Guiana (Figure 37), Gehrig-Downie *et al*. (2013) compared the diversity and vertical distribution of epiphytic liverworts between the lowland rainforest and the lowland cloud forest. These lowland cloud forests occur in river valleys with high air humidity and morning fog. This combination creates ideal conditions for epiphytic leafy liverworts. The researchers found a significantly higher species richness of these liverworts in the cloud forest and the species composition differed (Figure 71) in all six height zones (Figure 68).

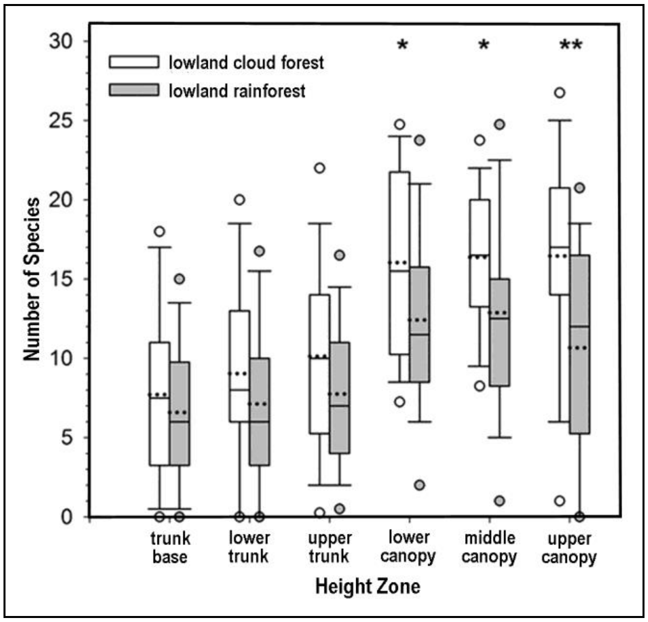

Figure 71. Number of epiphytic liverwort species in each tree height zone (see Figure 68) in the lowland cloud forest and lowland rainforest. n=24 trees per forest type. Boxes are upper and lower quartile, unbroken lines are medians, dotted lines are means, whiskers are 95 percentile, and circles are max and min. *$P<0.05$, **$P<0.01$ for t-test differences. Modified from Gehrig-Downie *et al*. 2013.

The lowland cloud forests included more indicator species, particularly shade epiphytes and generalists that also occur in the montane forests (Gehrig-Downie *et al*. 2013). The lowland rainforest exhibited sun epiphyte indicators that characterize dry, open sites. At least in this case, liverwort species richness differs more between forest types than it does among elevation types. Furthermore, the lowland cloud forest may be more species-rich than are the montane rainforests. As is typical throughout most tropical habitats, the **Lejeuneaceae** (Figure 6, Figure 9, Figure 20, Figure 51) represents the largest family, with 95 species. This was followed by **Plagiochilaceae** (9 spp.; Figure 72) and **Frullaniaceae** (7spp.; Figure 70). In the **Lejeuneaceae**, ***Lejeunea*** (Figure 73) had 14 species; ***Ceratolejeunea*** (Figure 51), ***Cololejeunea*** (Figure 74), and ***Plagiochila*** (Figure 72) each had nine species there.

Figure 72. ***Plagiochila*** sp. in the Neotropics. Photo by Michael Lüth, with permission.

Figure 73. Epiphyllous ***Lejeunea*** sp., a species-rich genus in the Neotropics. Photo by Bramadi Arya, through Creative Commons.

Figure 74. ***Cololejeunea gracilis*** var. ***linearifolia*** from Guadeloupe on leaf; ***Cololejeunea*** is a species-rich genus in the Neotropics. Photo by Tamás Pócs, with permission.

Jarman and Kantvilas (1995), working on epiphytes of an old Huon pine (***Lagarostrobos franklinii***; Figure 75) in Tasmania, found 76 species of lichens, 55 of bryophytes, and 16 tracheophytes on that single tree. One factor accounting for the high diversity is that there is little overlap in species between the base and canopy taxa. Bryophytes dominate at the base, but lichens dominate in the more exposed crown. The bryophytes and lichens on these older trees build sufficient biomass peat on the branches that terrestrial tracheophytes are able to become established in the peat.

Oliveira and ter Steege (2013) used a standardized sampling method across the Amazon Basin (Figure 76) to describe the epiphytic bryophytes in five height zones from the forest floor to the canopy. They sampled eight canopy trees per locality, generating 3,104 records. They were able to identify 222 species and 39 morphospecies. As expected, the leafy liverwort family **Lejeuneaceae** (Figure 6, Figure 9, Figure 20, Figure 51) was the most common (55%), followed by the moss families **Calymperaceae** (Figure 10) (8%), **Leucobryaceae** (Figure 5) (4%), and **Sematophyllaceae** (Figure 102) (4%). Among these, 155 species occur in more than one locality, with 57 species considered to be specialists. In the canopy they found 29 species that are exclusive to the canopy.

Figure 75. ***Lagarostrobos franklinii***, a species that hosts lots of bryophytic epiphytes in Tasmania. Photo by Krzysztof Ziarnek, through Creative Commons.

Sporn *et al*. (2010) reported a record number of 146 epiphytic bryophyte species on eight canopy trees and eight trees from the understory of a submontane rainforest in Central Sulawesi, Indonesia (Figure 77). The trunks of canopy trees have significantly different species composition from that of the understory trees. Furthermore, 45% of the species are restricted to canopy tree crowns, whereas only 12% are restricted to the understory. This study emphasized that inventories of epiphytic bryophytes in a tropical forest should not only focus on canopy trees but also include the small understory treelets and shrubs, which may add at least 10% more species. A similar conclusion was reached by Krömer *et al.* (2007) in a study on tracheophytic epiphyte diversity in tropical submontane and montane forests.

Krömer *et al*. (2007) found that 90% of the tracheophytic epiphytes in the submontane and montane forests of the Bolivian Andes were represented in tree zones Z1-Z2 in the Johansson tree zones (Figure 68). Canopy tracheophytes were primarily orchids and ferns that had special adaptations to the frequent drought conditions. This vertical distribution responds to microenvironmental gradients of the tree, including light intensity, wind speed, and air temperature that increase with height, and moisture that decreases with height. But just what role do bryophytes have in their success?

Figure 76. Amazon rainforest aerial view in Brazil. Photo by Lubasia, through Creative Commons.

Figure 77. Sulawesi forest. Photo by T. R. Shankar Raman, through Creative Commons.

In lowland rainforests around Mabura Hill (Figure 78), Guyana, South America, Cornelissen and Gradstein (1990) reported 134 (52 mosses, 82 liverworts) bryophytes species. Of these, ~30% are **Lejeuneaceae** (Figure 6,

Figure 9, Figure 20, Figure 51**)**. Mountaineering techniques permit study of the forest canopy. There, 50% of the bryophyte species are exclusive to the canopy. The mixed forest has more exclusive species than does the dry evergreen forest, largely because of the outer canopy effect where xerophytic species occur. The canopy species in the dry evergreen forest have wider vertical distributions than do those in the mixed forest, a difference the researchers attribute to the more open canopy foliage in the dry evergreen forest.

Wolf (1994) examined epiphytic vegetation in the northern Andes (Figure 34). He restricted the bark type and sampled four full-grown forest trees at altitudinal intervals of ca 200 m from 1,000 to 4,130 m asl. The variation he found did not seem to relate to any environmental factor. Rather, as noted above, it seemed to relate to randomness in propagule supply. Nevertheless, ordination indicates that distribution patterns relate to altitude and height within the host tree. Interestingly, Oliveira and ter Steege (2015) found the same relationship in Amazonian lowland rainforest (Figure 76). Unlike many other studies, Wolf also found a relationship between the epiphytic vegetation and the host species, particularly for the host ***Brunellia occidentalis*** (see Figure 79-Figure 80), a high altitude species with rapid growth. There is no indication of a relationship with chemical characteristics of suspended soil.

Figure 78. ***Eperua rubiginosa*** seedlings, Mabura Hill Forest Reserve, Guyana. Photo by Hans ter Steege, through Creative Commons.

Figure 79. *Brunellia comocladifolia*; ***B. occidentalis*** is an epiphyte host at high altitudes in the Andes. Photo by Yolanda Leon, through Creative Commons.

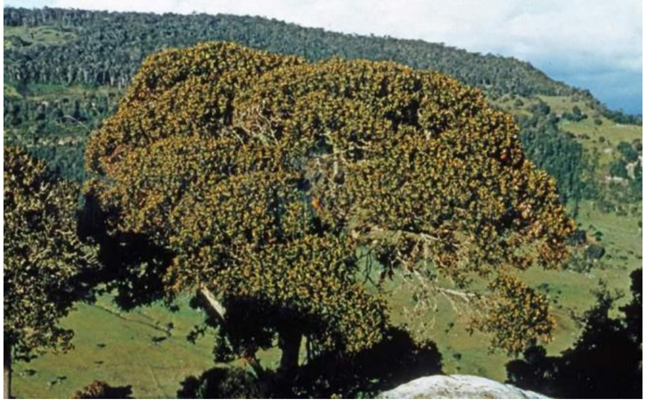

Figure 80. *Brunellia goudotii* in Colombia; ***B. occidentalis*** is an epiphyte host at high altitudes in the Andes. Photo by Alvaro Neira, through Creative Commons.

Oliveira *et al*. (2010) noted that, like tracheophytes, bryophytes demonstrate a species gradient from the base to the upper canopy of the host trees. They set out to test the role of niche assembly on a regional scale. They sampled six height zones on several trees in each of three lowland forests of the Guianas (Figure 37) and found that height zone was relatively consistent in the three localities, despite distances up to 640 km, and that that consistency was greater than among communities within the height zones of a single tree (30-50 m in height). More than half (57%) of the species exhibited a height zone preference.

Overall, Oliveira (2010) identified 225 species and 38 morphospecies of Amazonian basin epiphytic bryophytes. As we might expect, the leafy liverwort family **Lejeuneaceae** was the most species-rich family (55% of species). Among the mosses, the most common families were **Calymperaceae** (8%), **Leucobryaceae** (4%), and **Sematophyllaceae** (4%). All four of these families occurred in all 9 sampling locations. The most common species was the leafy liverwort ***Cheilolejeunea rigidulus*** (see Figure 81), followed by ***Ceratolejeunea cornuted*** (Figure 82), ***Octoblepharum pulvinatum*** (Figure 83), ***Octoblepharum albidum*** (Figure 59), ***Archilejeunea fuscescens*** (see Figure 84), ***Sematophyllum sub simplex*** (Figure 85), ***Lopholejeunea subfuscus*** (Figure 86), and ***Symbiezidium barbiflorum*** (see Figure 87). These eight species accounted for 21% of the known species in the study.

Figure 81. ***Cheilolejeunea*** sp. from the Neotropics; ***C. rigidula*** is the most common epiphytic bryophyte in the Amazon basin. Photo by Michael Lüth, with permission.

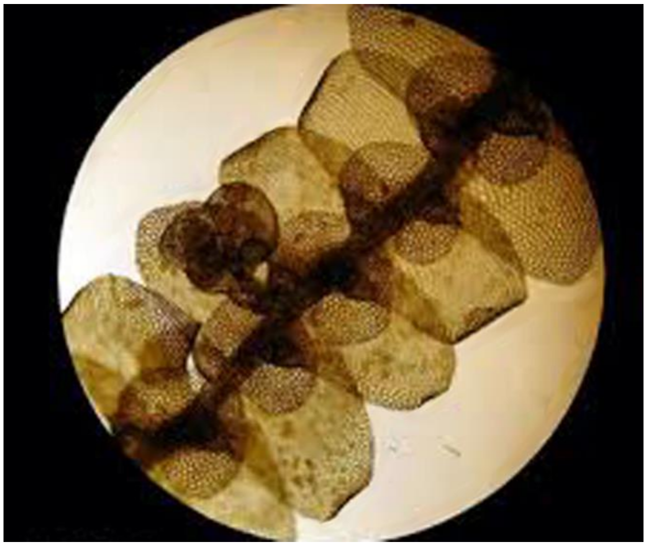

Figure 82. ***Ceratolejeunea cornuta***, one of the eight most common bryophytic epiphytes in the Amazon Basin. Photo by Michaela Sonnleitner, with permission.

Figure 83. ***Octoblepharum pulvinatum*** (light green), one of the eight most common bryophytic epiphytes in the Amazon basin, and ***Syrropodon*** on tree bark in the Luquillo Mountains, Puerto Rico. Photo by Janice Glime.

Figure 84. ***Archilejeunea olivacea***; ***A. fuscescens*** is one of the eight most common bryophytic epiphytes in the Amazon Basin. Photo by John Braggins, through Creative Commons.

Figure 85. ***Sematophyllum subsimplex***, one of the eight most common bryophytic epiphytes in the Amazon Basin. Photo by Yelitza Leon, through Creative Commons.

Figure 86. ***Lopholejeunea subfusca***, one of the eight most common bryophytic epiphytes in the Amazon Basin. Photo by Yang Jiadong, through Creative Commons.

Figure 87. ***Symbiezidium*** sp.; ***S. barbiflorum*** is one of the eight most common bryophytic epiphytes in the Amazon Basin. Photo by Hermann Schachner, through Creative Commons.

Oliveira (2010) found that a total of 155 species occurred in more than one locality, and of these 57 were considered to be specialists (37%), whereas 98 (63%) were considered generalists. The specialists were typically found at the extremes of the gradient, either in zone 1 or zone 6. Only 8 seemed to be specialists in other tree zones. Oliveira concluded that the structure of the communities fit the Neutral Model of Biodiversity and Biogeography, *i.e.*, being there by random recruitment from the local environment. The distribution of the species appears to be influenced by two processes. On a local scale, the interaction between the environment and local abundance provide the greatest influence. Within the Amazon basin, the abundance of the species in the **metacommunity** (sum of all communities sampled in localities and linked by dispersal) are the primary influence. Furthermore, the frequency of long-distance dispersal increased with the height of the zone in the tree. What seems strange is that the greatest genetic distance occurs between the canopy and subcanopy.

In the constant clouds of the dense montane **ombrophilous** (capable of withstanding or thriving in presence of high rainfall) forest (1,000 to 1,500 m asl) in southern Brazil (Figure 88), Santos *et al*. (2018) characterized six vertical zones on 28 trees and identified 96 species of bryophytes in 31 families. The leafy liverwort family **Lejeuneaceae** (Figure 6, Figure 8-Figure 9) was the most species-rich family, followed by **Frullaniaceae** (Figure 70). Liverworts predominated. Species diversity was high, ranging from H'=2.6 to H'=4.1, with high abundances. Of the 28 trees sampled, across this elevation range, the species composition was similar, with only two differing by more than 50%. Bryophyte cover ranged from 3.04% (2 m high to first branches; epiphylls) to 8.97% (0.0-0.5m) in the six phorophyte zones.

Tree Base

In the rainforests, the least light reaches the bases of the great trees (Pócs 1982). At the same time, the bases have the highest humidity in the forest. The bole height of dense bryophyte growth is limited by humidity and the physical condition of the bark, but where it is extremely wet it can reach as high as the first main branches, which may reach 8-10 m high (Richards 1954; Pócs 1982). More typically, it reaches up to 1-3 m, being limited by humidity that sinks to 60% during dry periods (Pócs 1974).

Figure 88. Brazilian southern highlands. Photo by Cecicilio, through Creative Commons.

On tropical tree bases one is likely to find **mats** and **wefts** of various ***Thuidium*** (Figure 89) species, intermixed ***Fissidens*** (Figure 90), and the leafy liverworts in **Lejeuneaceae** (Figure 6, Figure 9, Figure 20, Figure 51) and small turfs of mosses in **Orthotrichaceae** (Figure 28) (Gradstein & Pócs 1989). More suitable, porous bark often supports growths of the mosses ***Leucobryum*** (Figure 5), ***Leucophanes*** (Figure 10), and ***Calymperes*** (Figure 91). Farther up one might find **turfs** of the mosses **Dicranaceae** such as ***Leucoloma*** (Figure 92). As the **wefts** and **turfs** grade away from the base, one can find the **feather** type forming horizontal shelves on the bole (Figure 93) (Gradstein & Pócs 1989). The **dendroid**, **feather**, and **bracket** forms are specialists on the more narrow stems of small trees and branches of shrubs in this low-light zone, but they can also be found at the base (Pócs 1982). These include the mosses ***Lopidium*** (Figure 94) and ***Pinnatella*** (Figure 95) on all continents with tropical forests.

Figure 89. ***Thuidium cymbifolium*** with capsules, in a genus that can be found on some tree bases in tropical rainforests. Photo by Li Zhang, with permission.

Figure 90. ***Fissidens serratulus***, in a genus that occurs on tree bases in tropical rainforests. Photo by Jonathan Sleath, with permission.

Figure 91. ***Calymperes tenerum***, in a genus that occurs on porous bark of tree bases. Photo from the Auckland Museum, through Creative Commons.

Figure 92. ***Leucoloma*** sp. in the Neotropics, a genus that occurs above the tree base in tropical rainforests. Photo by Michael Lüth, with permission.

Figure 93. ***Neckera pennata***, demonstrating shelf formation. Photo by Janice Glime.

Figure 94. ***Lopidium concinnum***. Photo by David Tng, with permission.

Figure 95. ***Pinnatella*** sp. in Bhutan. Photo by David Long, with permission.

In the lowland rainforest of Guyana (Figure 96), Cornelissen and ter Steege (1989) found that the tree base community is characterized by the abundance of pleurocarpous mosses. In the wet, very shady habitats of tree bases these pleurocarpous species include **pendent** and **dendroid** mosses in the **Neckeraceae** (Figure 97-Figure 98) and **Pterobryaceae** (Figure 116) (Pócs 1982). In Asia and northern Australia, these include the mosses ***Homaliodendron*** (Figure 99) and ***Neckeropsis*** (Figure 97-Figure 98), both in **Neckeraceae**; in Africa one finds the mosses ***Renauldia*** and ***Hildebrandtiella*** (Figure 100) in the **Pterobryaceae** and ***Porotrichum*** (**Neckeraceae**; Figure 101). In the Neotropics, ***Neckeropsis disticha*** (Figure 97) and ***N. undulata*** (Figure 98) are ubiquitous. The mosses ***Sematophyllum*** (Figure 102) and ***Taxithelium*** (Figure 117) are likewise common in this zone. The number of species seems to vary in this synusia, with ~100 species in Vietnam, 60 in East Africa, and 50 in Cuba.

Figure 96. Forest at Angoulême, French Guiana (Guyana). Photo by M. Wilkinson, E. Sherratt, F. Starace, and D. J. Gower, through Creative Commons.

Figure 97. ***Neckeropsis disticha***, a species that occurs on tree bases of wet, shady Neotropical habitats. Photo by Piers Majestyk, through Creative Commons.

Figure 98. ***Neckeropsis undulata***, a species that occurs on tree bases of wet, shady Neotropical habitats. Photo by Scott Zona, with permission.

Figure 99. ***Homaliodendron flabellatum***, in a genus that occurs on tree bases of wet, shady tropical habitats in Asia and in tropical Australia, in densely shaded, lowland to montane habitats, epiphytic or on boulders. Photo by Yao, through Creative Commons

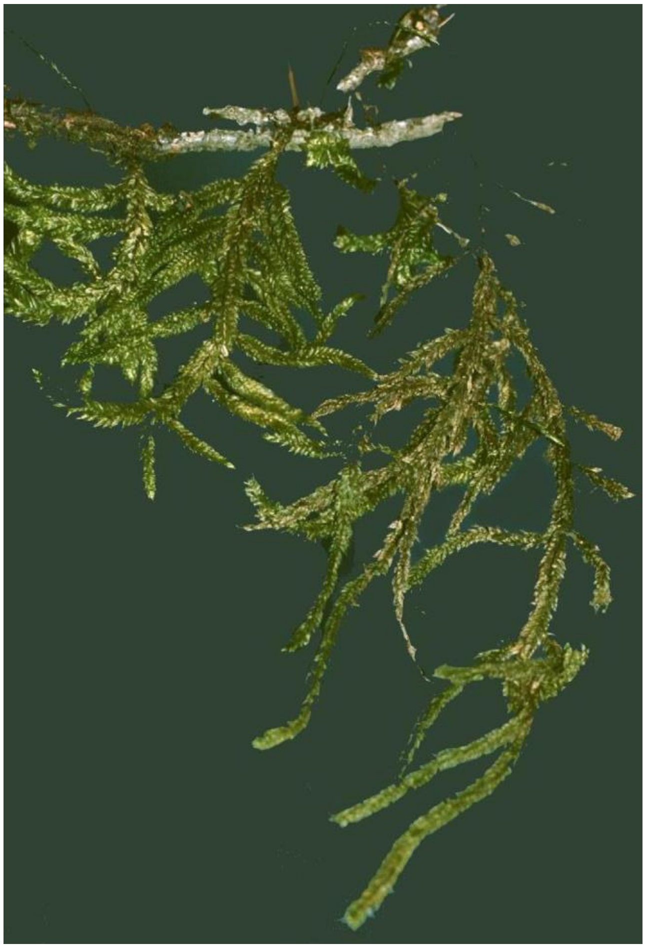

Figure 100. ***Hildebrandtiella guyanensis***, in a genus that occurs on tree bases of wet, shady tropical habitats in Africa. Photo by Claudio Delgadillo Moya, with permission.

Figure 101. ***Porotrichum bigelovii***, in a genus that occurs on tree bases of wet, shady tropical habitats in Africa. Photo from Calbryos, with permission through Paul Wilson.

Figure 102. ***Sematophyllum substrumulosum***, in a genus that occurs on tree bases of wet, shady Neotropical habitats. Photo by James K. Lindsey, with permission.

In Costa Rica, Holz *et al*. (2002) documented the diversity, microhabitat differentiation, and distribution of life forms in the tropical upper montane ***Quercus*** forest [***Q. copeyensis*** (Figure 103), ***Q. costaricensis*** (Figure 104)], using seven freshly fallen trees. They were surprised to find that not only is the tree base bryophyte community distinct from that of the rest of the tree, it is fundamentally the same as that of the forest floor! They also noted the importance of the understory as bryophyte habitat. On **lianas** (vines), poles, twigs on shrubs, ferns, and palms they found 65 species. More details of the Holz *et al*. study are in the subchapter Tropics – Altitude.

Figure 103. ***Quercus copeyensis***, a species whose tree base bryophytes match those of the forest floor. Photo through Creative Commons.

Figure 104. ***Quercus costaricensis***, a species whose tree base bryophytes match those of the forest floor. Photo by Stan Shebs, through Creative Commons.

Further descriptions of the epiphyte bryophyte habitat can be found in Richards (1954) from Guiana (Figure 37), Iwatsuki (1960) from southern Japan, and Tixier (1966) from South Vietnam.

Equihua and Equihua (2007) examined spatial distributions of ***Bryopteris filicina*** (**Lejeuneaceae**; Figure 105) on tree trunks in Chiapas, Mexico (Figure 106). They found it to be over-represented on ***Ampelocera hottlei*** (Figure 107), ***Brosimum alicastrum*** (Figure 108), and ***Guarea glabra*** (Figure 109), all species with smooth bark. Its distribution was determined by height on the tree, bark texture, and orientation, preferring smooth texture and a north-facing orientation.

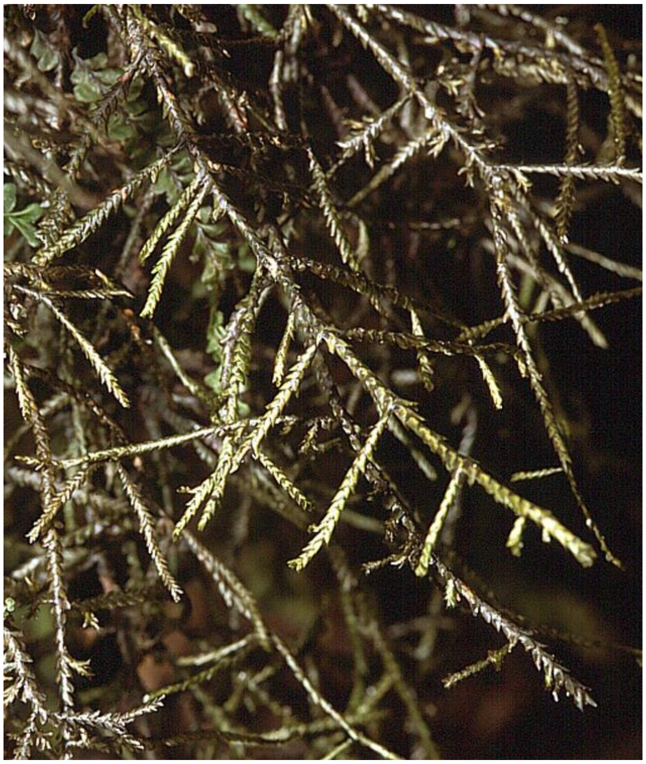

Figure 105. ***Bryopteris filicina*** in the Neotropics. Photo by Michael Lüth, with permission.

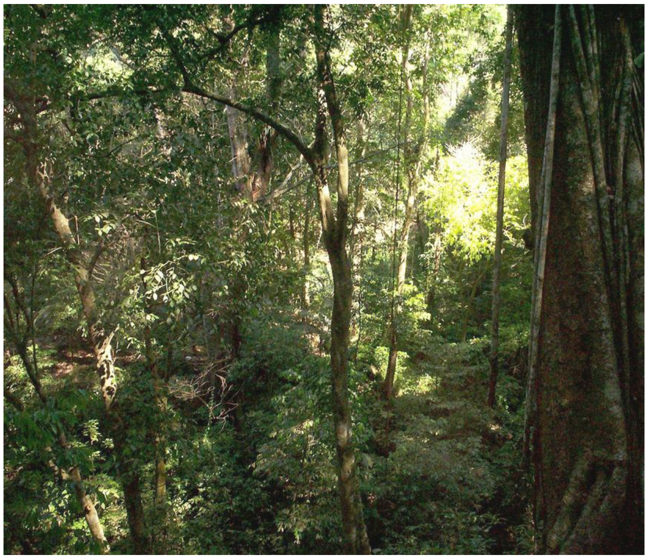

Figure 106. Selva Lacandona in Chiapas, Mexico. Photo by Marrovi, modified, through Creative Commons.

Figure 107. ***Ampelocera hottlei*** bole showing smooth bark, a tree preferred by bryophytes. Photo by Indiana Coronado, through Creative Commons.

Figure 108. ***Brosimum alicastrum*** tree base showing smooth bark, a tree preferred by bryophytes. Photo by David Stang, through Creative Commons.

Figure 109. ***Guarea glabra*** showing smooth bark, a tree preferred by bryophytes. Photo from Smithsonian Institution, through public domain.

Upper Trunk

The upper trunks have mostly appressed species (Schofield 1985, pp. 313-314). These are most commonly leafy liverworts such as ***Frullania*** (Figure 70) and **Lejeuneaceae** (Figure 6, Figure 9, Figure 20, Figure 51) (Pócs 1982). Among the mosses one can find **smooth mats** and thread-like **Sematophyllaceae** (Figure 102) again, as well as **Hypnaceae** (Figure 110) and ***Mitthyridium*** (Figure 111), again being appressed.

Figure 110. ***Hypnum cupressiforme*** var. ***heseleri***, a smooth mat former. Photo by Robin Stevenson, with permission.

Kürschner and Parolly (1998c) used the **Braun-Blanquet method** (system using cover-abundance classes; Poore 1955) to describe the various associations on tropical rainforest tree boles. The distribution patterns of the trunk-epiphytic vegetation can be generalized pantropically. Three alliances fall into two orders. Their distribution is correlated to structural parameters of the phorophyte stands and to **isothermic** (equal temperature) intervals: tropical lowland and submontane alliances (20-27°C mean annual temperature); subtropical and montane alliances of the montane rain- and cloud forests (12-20°C); temperate, boreal to subalpine alliances of elfin forests and ericaceous woodlands ((5)8-12°C). A fourth unit (<8°C) includes the Afro-subalpine ***Syntrichion cavallii*** (see Figure 112), mostly known outside the moist tropics and typical of the subpáramo vegetation.

Figure 111. ***Mitthyridium micro-undulatum***, among the genera one can find on the upper trunks. Photo by Jan-Peter Frahm, with permission.

Figure 112. ***Syntrichia*** sp., ***Syntrichia cavallii*** is part of an Afro-subalpine association that lives in elfin forests with low temperatures. Photo by J. C. Schou, with permission.

Lower Branches

The lower, thick canopy branches are typically inhabited by large **mats** of robust epiphytic bryophytes such as ***Plagiochila*** (Figure 72), ***Bazzania*** (Figure 105, Figure 113), ***Macromitrium*** (Figure 114), and others (Cornelissen & ter Steege 1989). Using mountaineering techniques, Cornelissen and ter Steege sampled the ***Eperua*** trees [***Eperua grandiflora*** and ***E. falcata*** (Figure 45-Figure 46)] in the dry evergreen forest of Guyana (Figure 45) from the base to the highest canopy twigs. This revealed a clear vertical distribution pattern of species and life forms for bryophytes. The upper canopy twigs are particularly species rich with both sun epiphytes and pioneers (facultative epiphylls).

Figure 113. ***Bazzania*** from the Neotropics. Photo by Michael Lüth, with permission.

Figure 114. ***Macromitrium*** sp. from the Neotropics. Photo by Michael Lüth, with permission.

Epiphyllous bryophytes, predominantly leafy liverworts in the **Lejeuneaceae** (Figure 6, Figure 9, Figure 20, Figure 51), abound in this lower branch zone, but also occur in abundance in the forest understory (Gradstein & Pócs 1989), in both cases living out of the damaging and desiccating reaches of the sun. The general trend observed for epiphylls is a reduction of species richness from the understory to the canopy (see Montfoort & Ek 1990), while species richness of epiphytes usually increases. These epiphyllous communities are discussed in the subchapter Tropics: Epiphylls.

Twigs

Wolf (1993a, b, c, 1995) described the changes in epiphytic bryophyte community structure of the montane forest, from the canopy twigs to the thickest lower canopy branches, in admirable detail. The lower branches and terminal twigs (Figure 115) of lowland forests support the **pendent Meteoriaceae** (Figure 115) and **Pterobryaceae** (Figure 116), provided it is sufficiently humid, and also the ever-present leafy liverworts ***Frullania*** (Figure 70) and **Lejeuneaceae** (Figure 6, Figure 9, Figure 20, Figure 51) (Pócs 1989). Here one finds **Neckeraceae** (Figure 97-Figure 98) and **Pterobryaceae** such as ***Lopidium*** (Figure 94) or ***Pinnatella*** (Figure 95), or others that are more specific to certain continents (Pócs 1982). ***Sematophyllum*** (Figure 102) and ***Taxithelium*** (Figure 117) reach their peak here. Farther up on the main branches, bryophytes must withstand high light and desiccation. There, dense mats occur, including the mosses **Cryphaeaceae** (Figure 118), **Erpodiaceae** (Figure 119-Figure 120), **Orthotrichaceae** (Figure 28), and **Sematophyllaceae** (Figure 102), as well as the liverworts ***Frullania*** and **Lejeuneaceae** (Figure 6, Figure 9, Figure 20, Figure 51). For those of us from the north temperate and boreal zones, only **Orthotrichaceae** and a few ***Frullania*** and **Lejeuneaceae** taxa are familiar.

Figure 115. ***Pseudobarbella mollissima***, a **pendent** moss in Japan. Photo by Janice Glime.

Figure 116. ***Hildebrandtiella guyanensis*** (**Pterobryaceae**) in the Neotropics. Photo by Michael Lüth, with permission.

Figure 117. ***Taxithelium planum***. Photo by Scott Zona, with permission.

Figure 118. ***Cryphaea jamesonii*** (**Cryphaeaceae**) from the Neotropics. Photo by Michael Lüth, with permission.

Figure 119. ***Aulacopilum abbreviatum*** forming **mats** on a tree in Bareilly India. Photo by Michael Lüth, with permission.

Figure 120. ***Aulacopilum abbreviatum*** forming a dense **mat** in Bareilly India. Photo by Michael Lüth, with permission.

Several species found on the fine canopy twigs are not restricted to this habitat but also occur lower down in the forest on the upper trunks or on living leaves in the forest understory (Cornelissen & ter Steege 1989). These species are considered pioneer species of the rainforest, well adapted to growth on open, unstable substrates. Most of them are small **Lejeuneaceae** (Figure 6, Figure 9, Figure 20, Figure 51) and copiously reproduce by vegetative propagules.

Romero (1999) found the most abundant **pendent** bryophytes on the thin branches (<1 cm diameter). The highest biomass per unit substrate occurred on branches of shade-tolerant species.

Canopy

The canopy, especially the outer canopy, can be a very different and stressful habitat in the forest. It is exposed to the full force of the wind. But based on turbulence analysis of two Amazon rainforest canopies (Figure 17, Figure 76), Kruijt *et al*. (2000) reported a sharp daytime attenuation of turbulence in the top third of the canopies. Thus, within the canopy there is very little air movement. Their hypothesis is that "the upper canopy air behaves as a plane mixing layer." This suggests that tropical rainforest canopies differ from other forests where there are rapid, coherent downward sweeps that penetrate the lower canopy. This penetration does not occur in these Amazonian rainforests. Rather, there is strong heat absorption by the canopy leaves near the top. The weak turbulence is unable to destroy the temperature gradient that is present through the large canopy depth. The inversion is likely to be maintained by strong heat absorption in the leaves concentrated near the canopy top, with the generally weak turbulence being unable to destroy the temperature gradients over the large canopy depth.

Sillett (1991) studied canopy bryophyte communities of six mature ***Ficus aurea*** (Figure 121-Figure 122) trees to elucidate the canopy bryophyte community and compare microhabitats. He divided these into three intact cloud forest and three isolated trees in Costa Rica. He used hemispherical canopy photography to compare light in the crowns, determining that the interior crowns of isolated trees were twice as bright as those in the intact forest. Isolated trees had lower species richness and life-form diversity. He found 41 species of mosses on the intact forest trees compared to only 29 on the isolated trees, with 50 species in total. The bryophytes on the forest trees are dominated by **pendants**, **fans**, **wefts**, and **tall turfs**, whereas the isolated trees have more **short turfs**. As in other studies, variation of bryophyte communities is greater within a single tree than among trees. Furthermore, the among-tree variation is greater in the forest than among isolated trees.

Figure 121. ***Ficus aurea***, a species that supports many more epiphytes when in the forest than when isolated in the open. Photo by Forest and Kim Starr, through Creative Commons.

Gradstein (2006) described the lowland cloud forest of French Guiana (Figure 123) (in moist river valleys below 400 m asl) where the climate differs from that of the mixed lowland rainforest, but differs by the frequent presence of fog and a large presence of epiphytes, especially liverworts. This forest has species richness of epiphytic liverworts that is similar to that at 2,000 m asl in the Andes and exhibits three times the richness of the Amazonian lowland forest (Figure 17, Figure 76). The moisture counterbalances the high temperatures, permitting the large diversity. The taxonomic composition and abundance differ from those in the tropical montane cloud forest. In the lowland cloud forest, asexual reproduction and dispersal are significantly more common in the canopy than in the forest understory. These canopy species have significantly wider ranges than that found among understory species. Gradstein suggested that these wider ranges are due to long-range dispersal by spores.

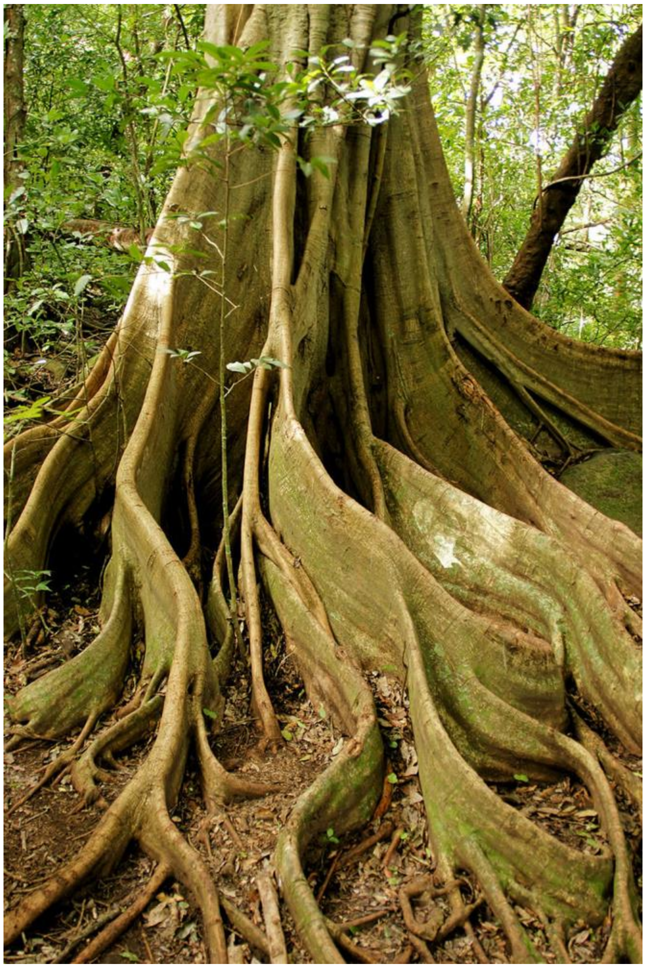

Figure 122. ***Ficus aurea*** in Costa Rica, showing epiphytes on the buttresses. Photo by Has Hillewaert, through Creative Commons.

Figure 123. Canopy in a lowland cloud forest of French Guiana. Photo by Renske Ek, courtesy of Robbert Gradstein.

Logs and Rotten Wood

Where lumbering or wind and hurricane disturbances occur, logs become a visible feature of the landscape (Figure 124). They also result from the normal aging and death of a tree. These logs provide a different habitat, especially in the **epixylic stage** (after bark is lost; Figure 125), than that of tree trunks.

Figure 124. Illegal export of rosewood logs from Madagascar. Photo by Erik Patel, through Creative Commons.

Figure 125. Decorticated log with epixylic bryophytes. Photo from UuMUfQ, through Creative Commons.

Winkler (1976) conducted some of the earliest studies of tropical bryophytes on rotten wood. Frahm (2003) compared the taxa on rotten wood in the tropics. This is the primary available substrate in lowland forests due to the heavy cover of leaf litter elsewhere on the forest floor. Logs usually are inhabited by **Sematophyllaceae** (Figure 102), **Hookeriaceae** (Figure 134), and **Leucobryaceae** (Figure 5) among the mosses. At Monteverde, one can also find ***Pyrrhobryum spiniforme*** (Figure 126) (Gradstein *et al*. 2001). In the cloud forest of Monteverde, Costa Rica (Figure 127), one can find the bryophytes on logs that can differ from these (see subchapter Tropics: Altitude, part 2).

Figure 126. ***Pyrrhobryum spiniforme*** in Hawaii. Photo by Alan Cressler, with permission.

Figure 127. Monteverde cloud forest, Costa Rica. Photo by Haakon S. Krohn, through Creative Commons.

The rotten wood of moist tropical montane forests supports a rich bryophyte flora. Such logs on Mt. Meru and the Usambara Mountains in Tanzania (Figure 128) supported 102 taxa of bryophytes on logs (86 mosses, 16 liverworts), including 71 taxa in 51 20x20 cm plots. (Mattila & Koponen 1999). Cornelissen and Karssemeijer (1987) presented a scale to determine the decomposition stage of the wood: 1 – knife does not penetrate, 2 – penetrates one centimeter, 3 – penetrates several centimeters, 4 – penetrates to the handle. (See also Frahm 2003 for its use in the tropics.)

In Neotropical Puerto Rico, Sastre-de Jesús (1992) found that **Lejeuneaceae** (Figure 6, Figure 8-Figure 9) and **Calymperaceae** (Figure 10, Figure 91) dominated the logs with bark intact. Softwood logs frequently had ***Taxithelium planum*** (Figure 117) and ***Isopterygium tenerum*** (Figure 129). Bryophytes on heavily decayed logs tended to have species with higher water requirements, presumably due to the relatively constant water content of these logs.

Figure 128. Western Usambara Mountains, Tanzania. Photo by David Ashby, through Creative Commons.

Figure 129. ***Isopterygium tenerum***, a species that occupies softwood logs in Puerto Rico. Photo by Scott Zona, through Creative Commons.

Rotten logs and rotting wood with bryophytes are able to retain good moisture (Laman 1995). This in turn provides a suitable and important substrate for the germination of seeds such as ***Ficus crassiramea* subsp. *stupenda*** (Figure 130-Figure 131).

Figure 130. ***Ficus crassiramea*** subsp. ***stupenda***, a species that germinates on bryophyte-covered logs in the tropics. Photo by Pia Tan, through Creative Commons.

Figure 131. ***Ficus crassiramea*** subsp. ***stupenda***, a species that germinates on bryophyte-covered logs in the tropical rainforest. Photo by Reuben C. J. Lim, through Creative Commons.

Parolly and Kürschner (2005) reported that under the relatively stable climatic conditions of tropical montane forests, the decay process is predictable. These conditions favor the **weft** and **mat** life form, following **perennial stayers**, a succession similar to that of the trunk epiphytic communities. Flood disturbance is more likely to favor species that are **dendroid** and **mat**-forming **shuttle species** that utilize a diaspore bank to return after flooding. In dry conditions, species are more likely to be **short-turf**-forming colonists. Shady sites are most suitable for **wefts**, giving them greater exposed surface area to take advantage of the low light conditions.

In the remnant Atlantic forest (seasonal coastal deciduous forest; Figure 132) of Brazil, Germano and Pôrto (1996, 1997) found 35 epixylic species of bryophytes. These comprised 11 families of mosses [**Calymperaceae** (Figure 10, Figure 91), **Pilotrichaceae** (Figure 133), **Fissidentaceae** (Figure 90), **Hookeriaceae** (Figure 134), **Hypnaceae** (Figure 135), **Leucobryaceae** (Figure 5), **Leucomiaceae** (Figure 136), **Orthotrichaceae** (Figure 28), **Plagiotheciaceae** (Figure 137), **Sematophyllaceae** (Figure 102), **Thuidiaceae** (Figure 138)] and 5 families of liverworts [**Aneuraceae** (Figure 139), **Frullaniaceae** (Figure 70), **Geocalycaceae** (Figure 140), **Plagiochilaceae** (Figure 72), **Radulaceae** (Figure 35)]. Note the absence of **Lejeuneaceae**. They related the species composition to the decomposition stage of the substrate (Germano & Pôrto 1997).

Figure 132. Remnant Atlantic forest, Brazil. Photo by Leandro Pereira Chagas, through Creative Commons.

Figure 133. ***Pilotrichella ampullacea*** (**Pilotrichaceae**), in a family that occurs on logs in the Atlantic forest of Brazil. Photo by Jan-Peter Frahm, with permission.

Figure 134. ***Cyathophorum bulbosum*** (**Hookeriaceae**), in a family that occurs on logs in the Atlantic forest of Brazil. Photo by Peter Woodard, through Creative Commons.

Figure 135. ***Hypnum curvifolium*** (**Hypnaceae**) with capsules on rock, in a family that occurs on logs in the Atlantic forest of Brazil. Photo by Bob Klips, with permission.

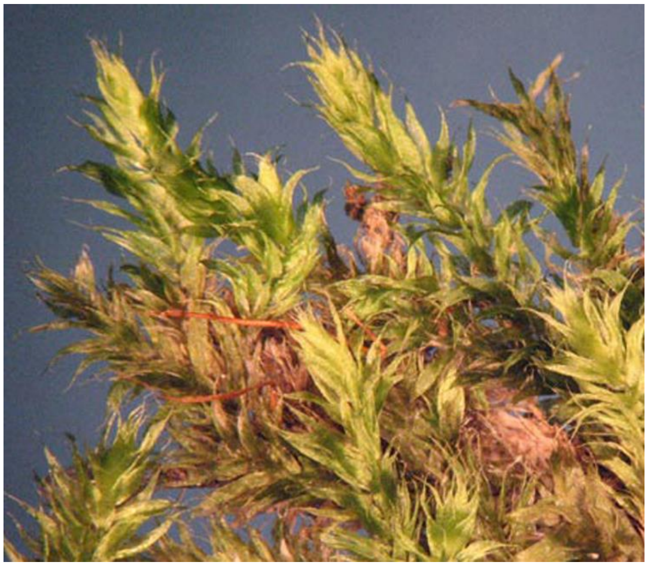

Figure 136. ***Leucomium strumosum*** (**Leucomiaceae**), in a family that occurs on logs in the Atlantic forest of Brazil. Photo by Claudio Delgadillo Moya, with permission.

Figure 137. ***Plagiothecium undulatum***; the **Plagiotheciaceae**, a family represented in a remnant of the Atlantic Forest. Photo by J. C. Schou, with permission.

Figure 138. ***Pelekium*** *cf.* ***gratum***. Photo by Shyamal L., through Creative Commons.

Figure 139. ***Riccardia multifida*** (**Aneuraceae**), in a family that occurs on logs in the Atlantic forest of Brazil. Photo by Hermann Schachner, through Creative Commons.

Figure 140. ***Geocalyx graveolens*** (**Geocalycaceae**), in a family that occurs on logs in the Atlantic forest of Brazil. Photo by Michael Lüth, with permission.

In forest fragments in the Atlantic forest (Figure 132) of northeastern Brazil, Silva and Pôrto (2009) used 100 m transects and small (<100 ha), medium (100-500 ha), and large (>500 ha) fragments to examine fragmentation and edge effects on bryophytes growing on decaying wood. They identified 99 species of epixylic bryophytes (52 liverworts, 47 mosses); liverworts barely predominated here. They found that fragment size was important in determining composition, richness, diversity, and abundance on epixylic substrata. Furthermore, species richness, coverage, and shade tolerance did not correlate with the distance from forest edge. Rather, edge effects seemed to be non-linear, extending beyond 100 m from the forest edge.

In Pernambuco, Brazil, Germano and Pôrto (1996) described the dominant bryophytes in several community types. They found that ***Cololejeunea sicaefolia*** (see Figure 141), ***Lejeunea quinque-umbonata*** (Figure 142), both in the **Lejeuneaceae**, and ***Riccardia*** spp. (Figure 139) are exclusively **epixylic** in their study area.

Figure 141. ***Cololejeunea subcristata***; ***C. sicaefolia***, a leafy liverwort that occurs exclusively on decaying wood in the Pernambuco, Brazil, study area. Photo by Scott Zona, through Creative Commons.

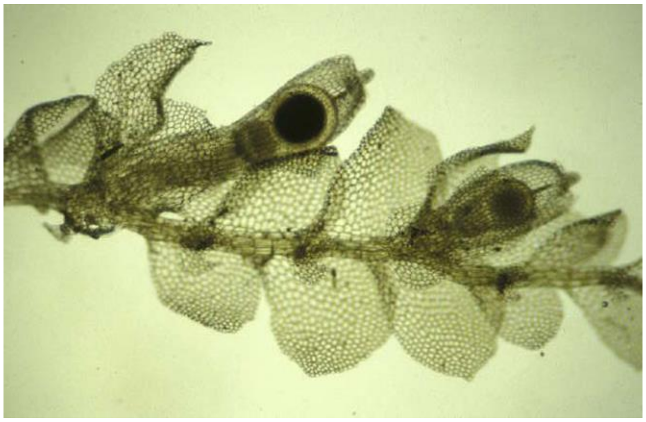

Figure 142. ***Lejeunea quinque-umbonata***, a leafy liverwort that occurs exclusively on decaying wood in the Pernambuco, Brazil, study area. Photo by Elena Reiner-Drehwald.

Sampling

Many bryophytes grow high in the canopy and this provides a particular challenge for collection. Popular recent methods include rope-climbing (Figure 143) (Perry 1978; Whitacre 1981; Cornelissen & ter Steege 1986) and bow-and-arrow techniques (Dial & Tobin 1994). These methods can even be used to collect the tiny leafy liverworts that hide among the larger bryophytes and tracheophytes. Tweedie and Bergstrom (1995) developed a hierarchical approach for bryophytic epiphytes that could handle their spatially complex ecosystems.

Figure 143. Rope-climbing to sample the canopy of a lowland rainforest in the Colombian Amazon. Photo by Laura Campos, courtesy of Robbert Gradstein.

Pardow *et al.* (2012) concluded that bryophyte life-form analysis of the canopy can be accomplished from the ground in the lowland rainforest of French Guiana (Figure 37). When this is the case, life forms could be used easily to indicate functional diversity.

Several sampling techniques for estimating abundance of non-vascular epiphytes, including bryophytes, have been developed over the past decade. The efficacy of those techniques, however, has never been investigated. Lovai *et al.* (2012) compared three protocols for sampling epiphytic bryophytes in tropical montane rainforests. They examined ladder quadrats, 10 x 10 cm quadrats at intervals of 40 cm, and a 10-cm-wide strip around the stem. The use of 10 x 10 cm quadrats at intervals of 40 cm proved to be the most effective and efficient sampling method for quantifying bryophyte cover and demonstrated a typical species-area curve (Figure 144).

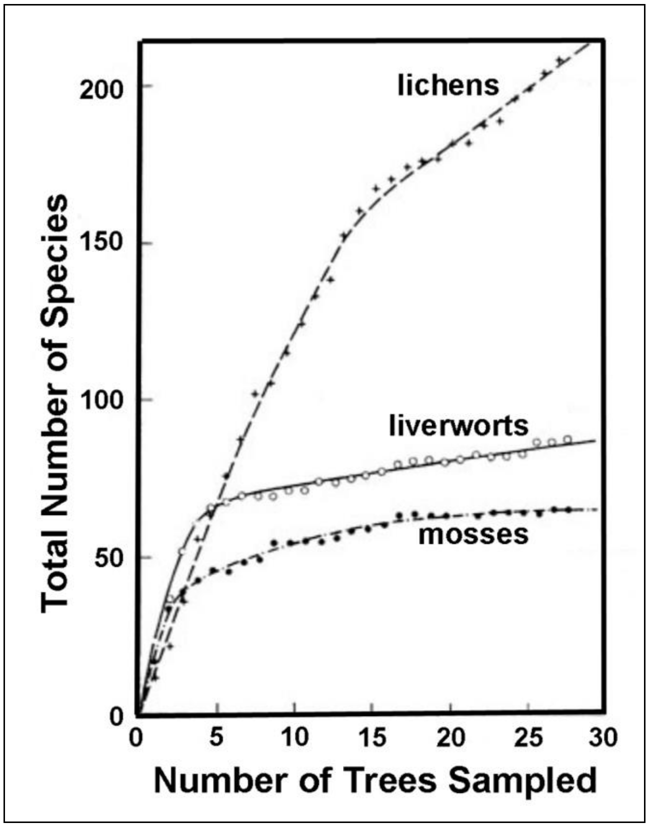

Figure 144. Species-area curve for epiphytic bryophytes and lichens in a lowland rainforest of French Guiana, based on Montfoort & Ek 1990.

Bryant *et al.* (1973) used **R-mode analysis** (species x species) and **Q-mode analysis** (principal component analysis for linear discriminant analysis) (Lee *et al.* 2017) of area x area to compare the distributional patterns of 155 species of leafy liverworts in the Luquillo Mountains of Puerto Rico (Figure 145. They compared high altitude with low-altitude areas, shaded, moist habitats with open, more exposed habitats, and disturbed, low-elevation habitats with less disturbed habitats at all elevations. R-mode and Q-mode produced nearly identical distribution patterns. Therefore, either method can be used to determine which species are the best indicators of habitat differences.

Figure 145. El Yunque National Forest, Luquillo Mountains, Puerto Rico. Photo by Kai Griebenow, through Creative Commons.

A technique that has been used in ecological studies in several ecosystems is that of recording **morphospecies** (species forms). This permits the researchers to use a team of novices and accomplish a wide survey in a short time (Gradstein *et al.* 2003). Using the technique for bryophytes, lichens, and tracheophytes, but not epiphylls, they estimated that they could inventory one hectare of tropical rainforest in two weeks. No identifications were attempted, enabling a team of six with three specialists (bryophytes, lichens, tracheophytes) and three assistants to accomplish the survey.

Gradstein *et al.* (2003) developed a standard protocol of recording morphospecies (species forms) for rapid and representative sampling of epiphyte diversity of one hectare of tropical rainforest. Based on species-accumulation curves they found that inventories of 5 whole trees, using standard plots in all height zones, may be sufficient to sample 70-80% of the diversity of the epiphytic bryophytes of the forest. For vascular epiphytes and epiphytic lichens, however, more trees must be sampled. Using the protocol, the bryophyte inventory of one hectare can be accomplished in two weeks by a team of one specialist and one field assistant. The results obtained by means of the standard protocol have been used for making comparisons of bryophyte species richness along elevational gradients (Gehrig-Downie *et al.* 2013) and along disturbance gradients (Gradstein & Sporn 2010). A standardized technique also permits comparisons between locations (countries) and hopefully even among researchers.

Quadrats

Nadkarni (2000) established "cylindrats" that she used to track colonization. In a lower montane cloud forest, Monteverde, Costa Rica, she used photography to track the colonization in these epiphytic plots. She also wrapped a clear acetate sheet around the branch, then placed a second clear sheet with a matrix of 100 dots (10x10). Using five random locations around the branch segment she counted the number of dots that touched epiphytes. These counts were converted to percent cover.

Affeld *et al*. (2008) used single samples (30 x 25 cm) from 96 epiphyte assemblages located on inner branches of 40 northern rata (***Metrosideros robusta***; Figure 146-Figure 147) trees to show that epiphytes are important in determining community structure on South Island, NZ.

Figure 146. ***Metrosideros robusta*** with epiphytes. Photo by Phil Bendle, through Creative Commons.

Wolf (1993d) used **relevés** (visual descriptions of vegetation of area plus habit and habitat data) to study epiphytes in the tropical montane rainforest in the northern Andes (Figure 34). This usually involves examining all the microhabitats and niches to find all possible species. They used rope-climbing techniques to reach the bryophytes.

Figure 147. ***Metrosideros robusta*** showing inner branches. Photo by Phil Bendle, through Creative Commons.

Rope Climbing

Early tropical researchers, in an attempt to get better representation of the canopy bryophytes, frequently used ropes to help them climb the trees (Wolf 1993a, b, c, 1995; Gradstein *et al*. 1996; Nadkarni 2000).

Sillett (1991) set out to develop a quantitative method for sampling tropical canopy bryophytes. He used hemispherical canopy photography to learn that interior crowns of isolated trees (Figure 148) are twice as bright as the interior crowns of intact forest trees of the same species (***Ficus tuerckheimii***; Figure 149). He climbed the trees to sample them. Sillett used a cost-benefit analysis that indicated more branches per tree and fewer plots per branch minimizes time but provides similar information.

Figure 148. Tree climbing on tropical montane isolated tree, showing the brightness of the canopy. Photo by F. Werner, courtesy of Robbert Gradstein.

Figure 149. ***Ficus tuerckheimii***, a species used by Sillett to develop methods for sampling the canopy. Photo by Dick Culbert, with online permission.

Older techniques such as tree climbing for collecting canopy bryophytes can present several problems. Many twigs and small branches cannot be reached from those branches that are strong enough to support the climber. Pole-climbing techniques require using a harness and the climbing spikes used can dislodge bryophytes and other epiphytes and put holes in the tree trunks, providing entry sites for pathogenic fungi and insects (Perry 1978). Inspired by Perry (1978), Cornelissen and ter Steege (1989) developed a rope-climbing technique that has been used by many researchers, including Dimitri Montfoort, Renske Ek, Jan Wolf, Ingo Holz, Nicole Nöske, Simone Sporn, Sylvia Mota de Oliveira, Laura Campos, and Angel Benitez, among others.

Using this method, Lücking *et al*. (1996) and Gradstein *et al*. (1996) reported that trees can be prepared for rope climbing in an hour, permitting the researcher to climb to 30 m in 5-10 minutes. Unfortunately, the outer branches are too fragile for climbing and must be sawed off.

Non-bryologists who collect may be fascinated by the epiphyllous species and usually do not provide representative sampling of the branch species. They furthermore often fail to provide the necessary data, such as substrate, that helps the taxonomist to identify the samples. While their collections are valuable to increase our knowledge of the species in an area, they can miss whole groups of taxa and should be used with caution for quantitative conclusions or ecological inferences.

Bow and Arrow

Perry (1978) modified the pole climbing techniques by adding ropes to the equipment. Once the rope is thrown over a sturdy branch, it can be used to help hoist the climber to the level of the branches. The placement of the rope is facilitated by use of an 80-pound pull crossbow and weighted arrow tied to 30-pound test monofilament. The weight of the arrow insures that the arrow will fall to the ground. A spool can be wrapped around the line to prevent tangling.

This is only the first step. Next, a 120-240 pound test braided line is attached to the first, smaller line (Perry 1978). The line that can support the climber is too heavy for the bow and arrow. The heavier (240 pound test) line is needed if there are many large branches because abrasion by the branches can break the lighter-weight line. Safety is a foremost concern.

Ter Steege and Cornelissen (1988) described rope techniques (Figure 150-Figure 153) to climb trees to capture epiphytic bryophytes. These were based on previous use by Day (1962), Pike *et al*. (1975), Perry (1978), Perry and Williams (1981), Whitacre (1981), Hoi (1984). Ter Steege and Cornelissen (1986) used a rope technique in Guyana (Figure 96), Wolf (1986) in Colombia, Montfoort & Ek (1990) in French Guiana (Figure 143).

Ter Steege and Cornelissen (1988) emphasized safety aspects: making sure the branch is strong enough and has an angle of less than 45º; using a proper, strong knot; avoiding branches infected by parasites and hemiparasites. The technique requires shooting an arrow over the selected branch (Figure 150), carrying with it a strong nylon fishing line (50-60/100). Tangles are prevented by keeping the line on a fishing reel, preferably a sea-fishing reel, attached to the bow. The arrow head is weighted with lead to help it return to the ground through the branches. The arrow is then removed and a 3-mm cord is tied to the fishing line using a double sheet bend knot (Figure 150). Winding the reel helps to pull the line and attached cord over the branch. An 11-mm speleocord is attached to the 3-mm cord using a double sheet bend knot (see Figure 150 for knots). This 11-mm cord is hauled over the limb by hand power. Construct a lasso with a figure of eight knot and pull it against the limb. The 3-mm cord is attached to the free end of the knot to facilitate pulling the knot down after use. Test the strength of the branch by having **two** people hang onto it with their full weight. Be prepared to get out of the way if the branch breaks! Hang two ascenders or jumars (Figure 151) on the rope to facilitate ascent. Attach one ascender to a seat belt and the other to the climber's feet (Figure 151). Always use locking karabiners to link the ascenders (Figure 152-Figure 153). Another rope can be tossed over desired branches higher up, using a load attached to a 3-mm cord. The procedure of hanging a rope is then repeated. I recommend reading the original article for details. And if this vocabulary is unfamiliar to you, you might not have enough experience to use this method safely.

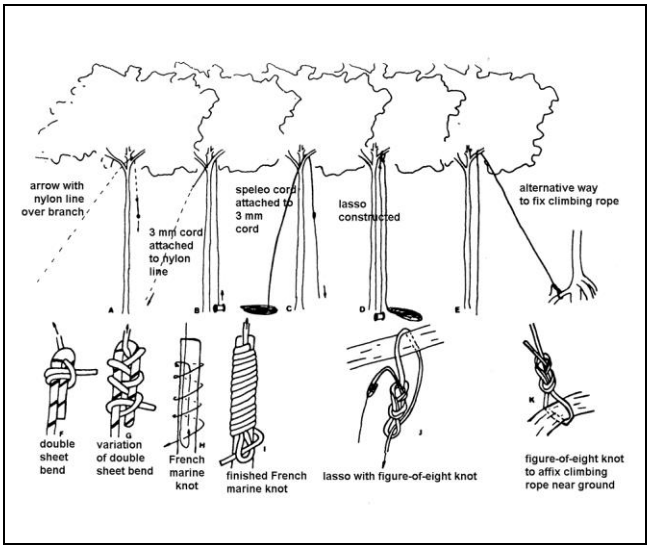

Figure 150. Knots used for rope climbing of trees. Modified from ter Steege & Cornelissen 1988.

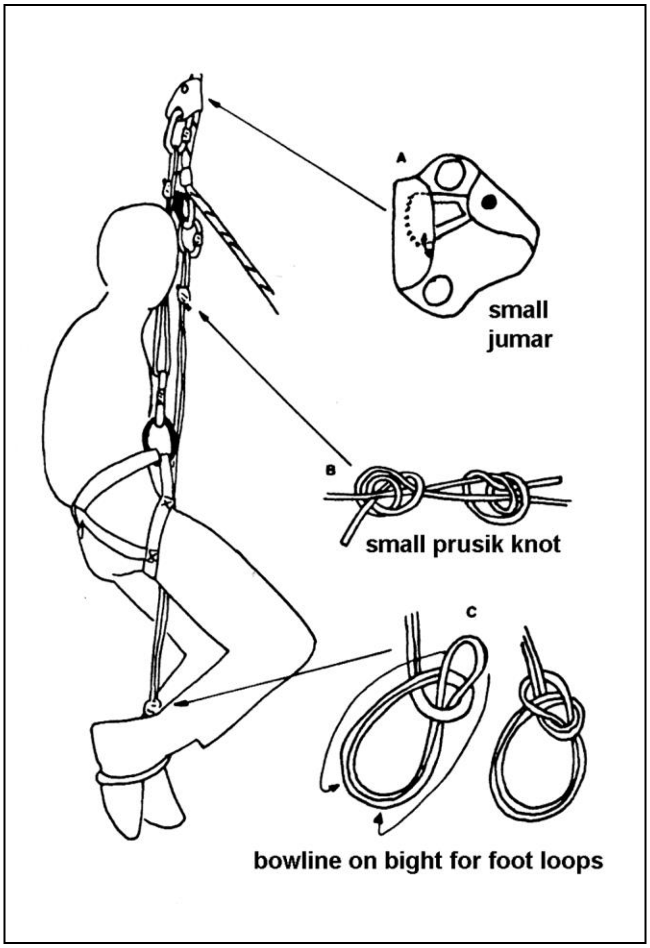

Figure 151. Climbing gear. Modified from ter Steege & Cornelissen 1988.

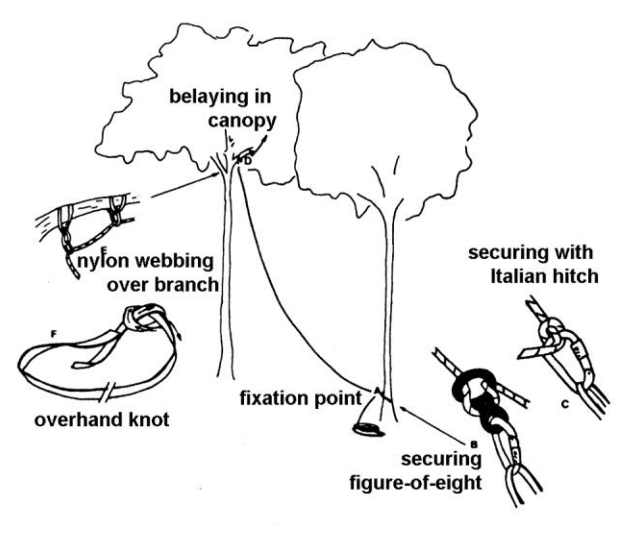

Figure 152. Free-climbing technique. Modified from ter Steege & Cornelissen 1988.

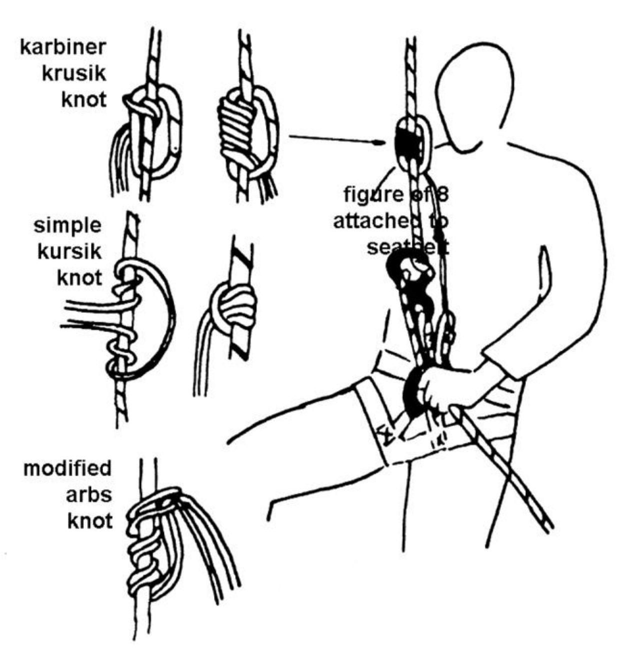

Figure 153. Rappelling knots. Modified from ter Steege & Cornelissen 1988.

Other Canopy Access

Hallé (1990) used an inflatable raft carried by a hot-air dirigible to gain access to canopy epiphytes. Other methods include the use of cranes (Figure 154-Figure 155) (Parker *et al*. 1992; Zotz & Vollrath 2003) and special platforms and walkways (Figure 156) (McClure 1966; Grison 1978; Perry 1978). Lowman *et al*. (2012) provide the standard modern reference on canopy research methods.

Figure 154. Canopy crane at Surumoni, Venezuela. Photo courtesy of Robbert Gradstein.

Figure 155. Canopy crane with gondola in Panama. Photo courtesy of Robbert Gradstein.

Figure 156. Costa Rica skywalk. Photo by Dirk van der Made, through Creative Commons.

Role

Gotsch *et al*. (2016) emphasized the importance of epiphytic material in tropical montane cloud forests (Figure 156). As noted earlier, they intercept both nutrients and moisture from the atmosphere and contribute these over an extended period of time to the forest floor. The amounts of these contributions vary with stand age and microclimate. This epiphytic biomass provides food sources for both birds and mammals, and birds use bryophytic biomass for nest building. Gotsch and coworkers state that more than 200 species of birds use the epiphytes. Wilding *et al*. (2016) cited a number of pendent genera of mosses and liverworts that are used in nest building. These included the mosses ***Papillaria***, ***Floribundaria***, ***Meteorium***, and ***Squamidium*** and the liverworts ***Frullania*** and ***Plagiochila***.

Barkman (1958) and Pócs (1980) suggested that bryophytes may cause their own displacement by retaining water that makes tracheophytic epiphyte presence possible. They furthermore form humus, accelerate bark decay (Barkman 1958), and facilitate anchorage of seeds and other propagules.

Adventitious Roots

Herwitz (1991) found that adventitious roots of the montane tropical rainforest canopy tree species ***Ceratopetalum virchowii*** (see Figure 157) take advantage of the nutrient-rich stemflow, whereas the stemflow of other canopy tree species is nutrient-poor. Such observations as this raise the question of the role of bryophytes in the development of adventitious roots.

Figure 157. *Ceratopetalum apetalum*; ***Ceratopetalum virchowii*** is a canopy tree in the tropical montane rainforest and uses adventitious roots to gain nutrients from stemflow. Photo by John Tann, through Creative Commons.

Nadkarni (1994) found that epiphytic bryophytes do provide a rooting medium for adventitious roots of trees. In fact, a dynamic interaction may occur in which the bryophytes help the tree, and the tree roots likewise help the establishment of the epiphytic community. The bryophyte mat traps inorganic nutrients (Nadkarni 1986) and organic nutrients (Coxson *et al*. 1992) that are leached from members of the epiphyte community. These nutrients nourish the roots of the tree (Nadkarni & Primack 1989). The two appear to grow in mutual benefit, with the roots benefitting from the nutrients and providing a larger anchoring system for the epiphytes as they grow (Nadkarni 1994). As the bryophytes and organic matter increase, they provide more leachates, causing the tree roots to increase.

Leary *et al*. (2004) found that nodulation of the legume ***Acacia koa*** (Figure 158) occurred in the canopy in Hawaii. These nodules contain the bacterium ***Bradyrhizobium*** (Figure 159) in pockets within the canopy. These pockets provide organic soils with trapped nutrients and often form among bryophytes. They even have lower aluminum levels than the terrestrial soils.

Figure 158. ***Acacia koa***, Maui, Hawaii, a species that forms nodules in epiphytic organic soils, including among bryophytes. Photo by Forest and Kim Starr, through Creative Commons.

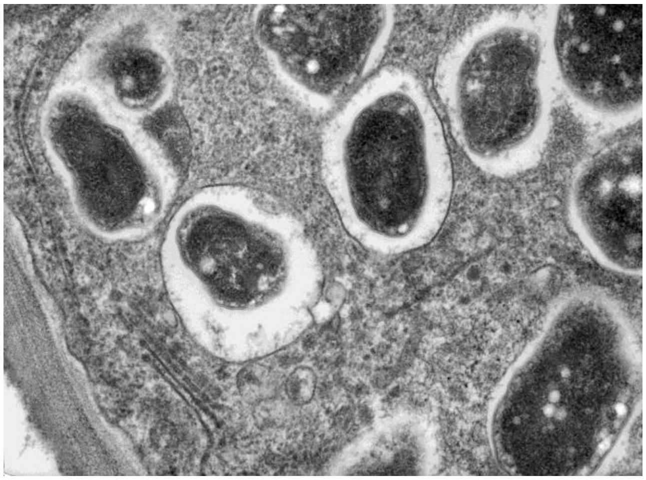

Figure 159. ***Bradyrhizobium japonicum*** from soybean root nodule. A species of ***Bradyrhizobium*** occurs in nodules among mosses on ***Acacia koa***. Photo by Louisa Howard, through public domain.

Substrata for Tracheophytes

Zotz and Vollrath (2003) used a canopy crane (Figure 154-Figure 155) to explore the epiphyte flora of the palm ***Socratea exorrhiza*** (Figure 38-Figure 39) in a primary lowland rainforest of Panama. They examined each palm in a 0.9 hectare and identified 701 tracheophyte epiphytes and hemi-epiphytes on 118 palm trees, identifying 66 species. The tracheophytes usually do not colonize trees less than 20 years old. These tracheophytic epiphytes are significantly associated with bryophytes, but the researchers could find no species that seemed to depend on the bryophytes. On the other hand, one must wonder if the bryophytes are important in maintaining moisture for the roots and storing nutrients trapped during precipitation events, as well as providing a suitable anchor for germinating seeds.

In Madagascar, orchids commonly grow in beds of ***Leucoloma*** (Figure 160) on tree trunks (Pócs 1982; Catherine La Farge, Bryonet September 2004). The bryophytes trap nutrients that make them a suitable substrate for epiphytes.

Figure 160. ***Leucoloma*** sp, India, common substrate for orchids on tree trunks. Photo by Shyamal L., through Creative Commons.

But finding orchids among bryophytes does not indicate any necessary role for the bryophytes. Tremblay (2008) relocated a rare epiphytic orchid after its dislocation from Hurricane Georges. He found that the orchid population size did not correlate with the percent of moss cover on the standing trees. Nevertheless, the orchids seemed to be more frequent when the tree bole had 40-90% moss cover. We need studies to determine the role in bryophytes in trapping and holding seeds and seedlings until the orchids and other plants are able to attach to the tree.

Probably the best example of a moss-dwelling epiphyte is the neotropical fern genus ***Melpomene*** (Figure 161). Almost all species in this genus grow in dense epiphytic bryophyte mats (Lehnert 2007). Sylvester *et al*. (2014) noted that the highest epiphyte elevation known for a tracheophyte was from the southern Peruvian Andes. They reported three species of the fern ***Melpomene*** from ***Polylepis pepei*** (see Figure 162) forests above 4,250 m, with ***Melpomene peruviana*** reaching close to 4,550 m asl. Could it be that bryophytes contribute in some way to their ability to live at these high elevations?

Figure 161. ***Melpomene firma*** and ***M. monoliformis*** – grammitid ferns, both species that grow in dense bryophyte mats in trees. Photo by Marcus Lehnert, courtesy of Robbert Gradstein.

Figure 162. ***Polylepis rugulosa*** in the Andes; ***Polylepis pepei*** is host to ***Melpomene*** species in the Andes. Photo by Alexander Yates, through Creative Commons.

Ferns often inhabit bryophyte mats, where the bryophytes may support the heavy weight of the rhizome on vertical surfaces. Kelly *et al*. (2004) reported that ***Elaphoglossum hoffmannii*** was typically associated with mosses, specifically with ***Syrrhopodon gaudichaudii*** (Figure 163). ***Elaphoglossum wawrae*** (Figure 164) is a Hawaiian epiphytic endemic that occurs in moss mats, and is among the tracheophyte species that characterize the montane zone (Higashino *et al*. 1988; Kitayama and Mueller-Dombois 1992). ***Elaphoglossum glabellum*** growing on ***Epeura falcata*** (Figure 45-Figure 46) is restricted to small moss mats that occur around forks and knots found only in the lower canopy in the lowland rainforest of Guyana (Figure 96) (ter Steege & Cornelissen 1989). On ***Epeura grandiflora***, this species occurs on bryophyte mats from the lower trunk to the middle canopy. The bryophyte mats provide a longer supply of water. But bark differences may account for the differences in bryophyte cover, with ***E. grandiflora*** having rougher bark than that of ***E. falcata***. They may also provide a chemical buffer against toxins in the bark (Frei 1973).

Figure 163. ***Syrrhopodon gaudichaudii***, a species that typically is found with ***Elaphoglossum hoffmannii***. Photo by Michael Lüth, with permission.

Figure 164. ***Elaphoglossum wawrae*** among mosses, a fern endemic to Hawaii that seems to benefit from an association with bryophytes. Photo from USDA, through public domain.

On the other hand, Werner and Gradstein (2008) studied the factors important for seedling establishment of tracheophytic epiphytes in the Andes and found no relationship to bryophyte cover. Rather, isolated trees closer to the forest had significantly greater colonization by these plants, but colonization did not correlate with greater canopy or bryophyte cover.

Friend or Foe?

Cacao plantation owners had concerns over the epiphytes on the leaves, removing them in an effort to improve productivity of the fruit crop (Sporn *et al*. 2007). Removal of epiphytes from cacao had no notable effect on the harvest size of the cacao trees.

But sometimes the bryophytes seem to have negative effects on these trees. Akinfenwa (1989) reported that the epiphytic moss ***Erythrodontium barteri*** (Figure 165) reduced yield of the ***Theobroma cacao*** (Figure 166) trees. They cause a "dressing" effect on palms wherein the leaf bases collect soil in the leaf axils. This soil supports an epiphytic community with microbial activities in the soil. The result is decay of leaf bases, causing the joints to weaken. They can no longer support the epiphytic community, causing it to fall gradually along with the remains of the leaf bases. This process continues as the trees age and grow taller, resulting in smooth boles and consequently fewer leaves for photosynthesis.

Figure 165. ***Erythrodontium squarrosum*** from the Neotropics; ***E. barteri*** is known to reduce yield in the cocoa tree, ***Theobroma cacao***. Photo by Michael Lüth, with permission.

Faunal Habitat

The epiphytes provide a suitable habitat for a number of arthropods in the Neotropical cloud forest (Yanoviak *et al*. 2004). The arthropod morphospecies are similar between green and brown portions of the epiphyte mats, but relative abundances often differ. The most common of these arthropods was an oribatid mite; these preferred the brown portion in laboratory trials.

Bryophytes are home to a variety of frogs and salamanders and are even used by chimpanzees to gather water. Birds use them for nesting material. These interesting interactions are discussed in the volume on Interactions.

Figure 166. ***Theobroma cacao*** in the Dominican Republic, host of epiphytic bryophytes. Photo by C. T. Cooper, through public domain.

Summary

Bryophytes exhibit a number of adaptations to the epiphyte living style. Many of these relate to the usually dry habitat and short duration of available water. The adaptations include green, multicellular spores, sexual dimorphism, asexual reproduction, monoicous condition, rhizoid discs, hyaline leaf margins, and cushion life forms. Their life strategies are typically **perennial stayers** and **perennial shuttle species**. In humid lowland areas **mats** are typical, contrasting with the **fans** and **wefts** that rely on propagules and clonal growth in the montane rainforest. Ciliate leaves collect water. In the xeric open, upper montane forests, **short turfs**, **tall turfs**, and **cushions** predominate. The understory often has **dendroids** and fans while the crowns have more **tufts**. In other cases, the inner branches have **tall turfs** and the outer ones have **smooth mats**. **Fans** and **mats** predominate in floodplains. **Colonists** occur almost exclusively in secondary forests.

The large spores facilitate short-distance dispersal and rapid development when water is available. Arrival on the tree bark appears to be a random event. Succession begins with crustose and foliose lichens and typically proceeds from the underside of the branch upward, although some observers conclude that the lichens inhibit the bryophytes. Ants may sometimes help in the dispersal. Rough bark is more easily colonized and holds more water for growth.

Host specificity is less important than tree characteristics. These relate to bark characteristics, leeward vs windward exposure, height on tree, tree size, and degree of uprightness. The inner canopy has thick branches and fewer bryophyte taxa compared to the thinner middle canopy branches, with greatest richness in the outer canopy. Many species are **facultative** epiphytes. Increasing bark *p*H seems to result in decreased bryophyte richness. Tree base, trunk, and crown differ due to light, moisture, and nutrients. Approximately 45-50% of the species occur in the crowns of rainforest trees.

Tropical forests have an array of vertical niches, but on a horizontal scale, 4-5 trees are adequate to find 95% of the diversity. The **Lejeuneaceae** are common in the canopy as branch epiphytes and as epiphylls. Tree bases often have **mats** and **wefts** of ***Thuidium*** spp., with ***Fissidens*** spp., **Lejeuneaceae**, and **Orthotrichaceae**. Farther up the trunk are **feather** types. **Dendroids**, **feathers**, and **brackets** occur on narrow stems of small trees and branches of shrubs in the understory. Species on the upper trunk are more appressed and correlate with structure of the phorophyte stands and to temperature zones. The lower branches and thick canopy branches typically have large **mats**; epiphyllous **Lejeuneaceae** abound. In moist forests, twigs support **pendent Meteoriaceae**, **Pterobryaceae**, ***Frullania***, and **Lejeuneaceae**. On drier twigs one can find **Cryphaeaceae**, **Erpodiaceae**, **Orthotrichaceae**, **Sematophyllaceae**, ***Frullania***, and **Lejeuneaceae**. The outer canopy contrasts with the inner canopy by having more light and less moisture, creating a stressful environment.

Logs and decaying wood are the primary substrate on the forest floor, raised above the thick litter layer. Dominant bryophytes are in the **Sematophyllaceae**, **Hookeriaceae**, and **Leucobryaceae**. Under stable climatic conditions, **perennial stayers** precede **wefts** and **mat**, a succession similar to that of the trunk epiphytic communities. Flood disturbance favors **dendroid** and **mat**-forming **shuttle species** that utilize a diaspore bank. In dry conditions, species are more likely to be **short-turf**-forming colonists. Shady sites are most suitable for **wefts**.

Epiphyte sampling is best done with ropes or bow and arrow, unless cranes or skywalks are available, minimizing damage to the trees and their flora. Quadrats in all tree zones can permit quantitative sampling. **Life forms** are suitable for assessing functional ecology.

Bryophyte clumps can provide moist rooting media for adventitious roots, and rooting media for ferns and orchids. They retain water, and store nutrients that can be released in pulses. Numerous invertebrate and amphibian species live among them.

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