

# CHAPTER 8-10

## TROPICS: CLOUD FORESTS, SUBALPINE, AND ALPINE

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# CHAPTER 8-10

## TROPICS: CLOUD FORESTS, SUBALPINE, AND ALPINE



Figure 1. Ecuadorian mountains and cloud forest. Photo by Arthur Anker, with permission.

### Cloud Forests

Neotropical **cloud forests** (Figure 2, often known as **elfin forests** or **mossy forests**, extend from 23°N to 25°S (Churchill *et al.* 1995). These researchers suggested that the cloud forests of the Neotropics are a subset of the montane rainforest. They are isolated in Mexico on the north by xeric vegetation and on the south in Chile and Argentina by temperate rainforest. These cloud forests generally occur at 1000-3000 m asl. But the seasonal variation in precipitation is low and there are no months in which the evapotranspiration exceeds the rainfall. Rather, cloud cover is nearly continuous, with 2,000-4,000 mm precipitation per year. The temperature decreases from 18-22°C at 1,000 m to less than 10°C at 3,000 m asl. The taxa of these cloud forests are strongly influenced by their connections with both North and South America. The low generic level of endemism and high species endemism suggest recent and rapid speciation.



Figure 2. Cloud forest at Parque Nacional Montana de Santa Barbara at 2,180 m asl in Honduras. Photo by Josiah Townsend, with permission.

**Cloud forests** carry an intrigue that matches their names. Generally perched atop high mountains where they are blanketed in the fog of low-lying clouds or recipients of moisture-laden air that results in a mist zone most of the time (Vitt 1991), these forests must survive the harsh, uninterrupted winds and the continuous moisture that accompanies such a lofty abode. (See also Lawton 1980, 1982.) Consequently, trees there tend to be short compared to forests at lower elevations. For example, in Taveuni, Fiji, the forest trees on top of Mt. Koroturanga at 1,210 m asl were about 3-7 m tall, increasing to 10 m at 1,140 m elevation, and to 30 m at sea level (Ash 1987). Sadly, these dwarfed forests are rapidly disappearing from the face of the Earth before we can begin to understand a fraction of their complexity. In the northern Andes alone, 90% of these remarkable forests have disappeared, compared with 20% loss of the Amazon rainforest (Wuethrich 1993). In Peru alone, the mountainous areas house more than 25,000 plant species.

One problem that keeps these elfin forests out of the public eye is their relative lack of trees. Instead, they are dominated by herbs, shrubs, epiphytic ferns and seed plants, and mosses, with the diversity of all of these increasing with altitude (Wuethrich 1993). Nevertheless, they are the source of more than 3,000 species of plants that are used by the local people and house the ancestors of some of the most important world food crops.

Gotsch *et al.* (2017) showed that vapor pressure deficit could predict the epiphyte abundance in a tropical elevational gradient where the montane cloud forests occupy only a narrow band of microclimate and are thus vulnerable to climate change that changes the heights of the clouds and brings drought to the area. Their predictions are supported by their data showing that epiphyte abundance increases with elevation and leaf wetness and that it decreases as vapor pressure deficit (VPD) increases. VPD differences, however, are not always correlated with elevation and thus serve as better predictors of the epiphyte abundance.

In cloud forests of the Amazon, a high density of 21,900 trees per hectare belies the low tree species richness of 15 species, whereas the lower elevation tabonuco has 170 species with only 1750 trees per hectare (Gorchov & Cornejo 1993). The area behaves as an **ombrotrophic** (low-nutrient) wetland with its 5000 mm rainfall per year and another 10% moisture contributed by clouds. Poor soil oxygenation due to water logging results in most roots being above the soil. These buttress roots are usually covered by numerous bryophytes, and one might suppose that these bryophytes steal most of the nutrients returned by stemflow. Research has begun only recently on the ecological role of these cloud forest bryophytes.

Terrestrial bryophyte cover in the elfin forest is strikingly different from that of the lowland rainforest. The bryophytes are less specialized, with many of the same taxa occurring on the soil and on the trees. And the higher moisture permits bryophytes to grow higher on the bole, often reaching the canopy (Richards 1984).

Russell and Miller (1977) found that at Pico del Oeste in Puerto Rico, 55% of their collections of *Campylopus* (Figure 3) also contained the moss *Hemiragis* (Figure 4), but *Hemiragis* never occurred with *Leucoloma* (Figure 5). As in the submontane rainforest, the leafy liverworts

dominated the upper branches (Russell & Miller 1977). This high humidity no doubt accounts for the high percentage of leafy liverworts, estimated up to 90% of the bryophyte flora (Fulford *et al.* 1970). Yet at Monteverde, Costa Rica, Gradstein *et al.* (2001b) found that 36% of the 190 bryophyte species occurred exclusively in the canopy. The thick, lower branches had the highest diversity, with 99 species, presenting a sharp delineation of communities (Figure 6).



Figure 3. *Campylopus introflexus*, in a genus that occurs in the Pico del Oeste cloud forest in Puerto Rico. Photo by Paul Wilson, with permission.



Figure 4. *Hemiragis aurea*, in a genus that occurs in the Pico del Oeste cloud forest in Puerto Rico. Photo by Elisabeth Lavocat Bernard, with permission.



Figure 5. *Leucoloma* from the Neotropics, a genus that never occurs with *Hemiragis* in the cloud forest. Photo by Michael Lüth, with permission.

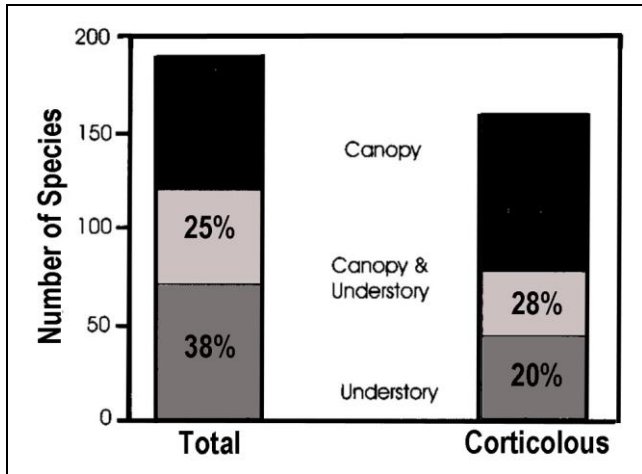


Figure 6. Total bryophyte species richness vs corticolous bryophyte species diversity in the canopy vs the understory in a cloud forest at Monteverde, Costa Rica. Species of rotten logs and epiphylls are not included in the corticolous counts. Redrawn from Gradstein *et al.* 2001b.

Merwin *et al.* (2001) reported 198 epiphytic bryophyte taxa in the Monteverde Cloud Forest Preserve. As is typical, the liverwort species (120) considerably outnumbered the moss species (77), with only 1 hornwort. Of these bryophyte species, 63 occurred in secondary forest and 84 in pastureland, whereas 178 species occurred in the primary forest.

These forests have such dense bryophyte growths on every trunk, branch, and twig that the forests appear "furry" (Gradstein & Pócs 1989). Biomass is high, with 11,000 kg ha<sup>-1</sup> dry weight in a Tanzanian elfin forest (80% of total canopy biomass), compared to the lower submontane rainforest with 1,773 kg (Pócs 1982). By comparison, an oak forest in Atlantic Europe had 355 kg (Schnock 1972) and a continental European oak forest had only 41 kg (Simon 1974).

One can find accumulations of organic matter in the crowns of trees of tropical wet forests such as the cloud forests. Bohlman *et al.* (1995) investigated the moisture and temperature patterns of these organic soils in the canopy and on the ground in Costa Rica. These two soil groupings ranged in temperature from 11.5°C to 21.0°C throughout the 42-month study period, but the soil from the two locations generally were within 1°C of each other. Both soils remained moist (>70% water content) during the wet and misty seasons. Nevertheless during dry periods the canopy soils dropped to a water content of 20-40% while the forest floor soils retained 60-70% water content.

Gotsch *et al.* (2016) considered that a shift in the heights of the cloud base or precipitation due to climate change would make a huge impact on the cloud forest epiphyte community.

For a more general understanding of cloud forests one can consult such publications as that of Stadtmüller (1987).

### Adaptations and Water Relations

In two Venezuelan cloud forests (Figure 7) in the northern Andes at 2000-2400 m, rainfall in January and February is typically 20 mm or less, but in August to October it can be 200 mm or more (León-Vargas *et al.* 2006). Nevertheless, it is quite variable in all seasons. The longest record for a dry period is only 143 hours. Humidity

typically rises to more than 90% relative humidity at night, with one night in two typically reaching 100%. Six **pendent** (Figure 16) bryophytes were all able to survive at least a few days of desiccation; their recover was, however, better from high humidities. Their ability to reach light-saturation reached 95% at 110-256  $\mu\text{mol m}^{-2} \text{s}^{-1}$ , levels only slightly higher than that of typical field levels. The **pendent** and other diffuse life forms are especially able to intercept cloudwater droplets, a feature that permits them to maximise conditions during periods of low rainfall.



Figure 7. Cloud forests, Venezuelan Andes. Photo by Gianfranco Cardogna, through Creative Commons.

The horizontal plane of a **fan** provides maximum surface area to capture light for photosynthesis as well as intercepting water from the moving air (Song *et al.* 2015). In three of the common **fan** bryophytes [moss *Homaliodendron flabellatum* (Figure 8), liverworts *Plagiochila arbuscula* (Figure 9), *P. assamica*] in an Asian subtropical montane cloud forest, the plants experienced high relative humidity coupled with low light and temperatures in the understory. Fog is a major source of water. Data suggest that photosynthetically active periods for these bryophytes are short because they lose most of their free water within an hour. These **fan** bryophytes are further adapted to their low-light understory position by having low light saturation and compensation points for photosynthesis. The researchers expressed concern that these **fan** bryophytes would experience a net carbon loss if the frequency and severity of dry periods increase.



Figure 8. *Homaliodendron flabellatum*, a **fan** form found in the Asian subtropical montane cloud forest. Photo by Jiang Zhenyu, Mou Shanjie, Xu Zawen, Chen Jianzhi, through Creative Commons.



Figure 9. *Plagiochila arbuscula*, a **fan** life form found in the Asian subtropical montane cloud forest. Photo by Peter de Lange, through public domain.

In the Asian subtropical montane cloud forest, there is high relative humidity accompanied by low light levels and temperatures in the understory (Song *et al.* 2015). Fog provides good water availability for the bryophytes. In this habitat, **fan** life forms (Figure 8-Figure 9) thrive. This life form loses its free water within one hour. Without sufficient water content, net photosynthesis can become negative. Song *et al.* (2015b) considered the **fan** life form to be especially suited to the cloud forest regime. The **fan** life form, extending outward from the vertical surfaces of trees (or rocks), is able to capture water from fog efficiently (Song *et al.* 2015). Furthermore, the cell walls have a high elasticity and osmoregulatory capacity that permit these life forms to tolerate desiccation. Additionally, these **fan** species have low light saturation and low compensation points for photosynthesis, all providing shade tolerance. While these characteristics provide ideal adaptations to the humid, low-light conditions of the cloud forest, the inability to tolerate and succeed under desiccating conditions puts these **fan** species at risk under changing climatic conditions that increase both the frequency and severity of droughts.

### Biomass

Van Dunne and Kappelle (1998) estimated biomass of epiphytic bryophytes on *Quercus copeyensis* (Figure 10) in a Costa Rican montane cloud forest. They found 22 species each of mosses and liverworts. Biomass of bryophytes was correlated with frequency, with mosses contributing 54-99% of that biomass. Of these, 14% of the species accounted for 90% of the biomass. These bryophytes are important in controlling water flow. Dominant taxa include *Pilotrichella flexilis* (Figure 11), *Rigodium* sp. (Figure 12), *Porotrichodendron superbum* (Figure 13), *Prionodon densus* (Figure 14), *Neckera chilensis* (see Figure 15), and *Plagiochila* (Figure 16).

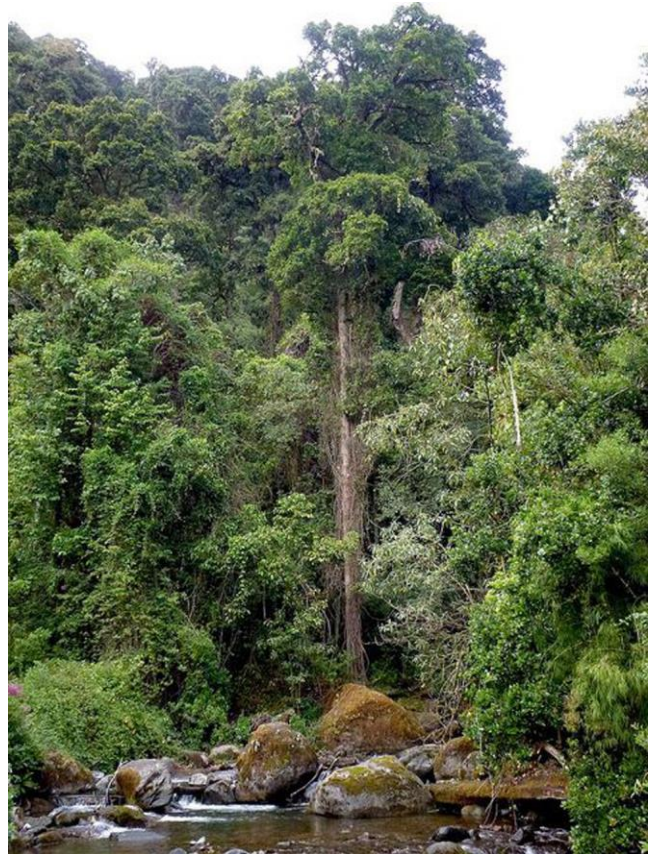


Figure 10. *Quercus copeyensis*, a good bryophyte substrate in a Costa Rican montane cloud forest. Photo through Creative Commons.

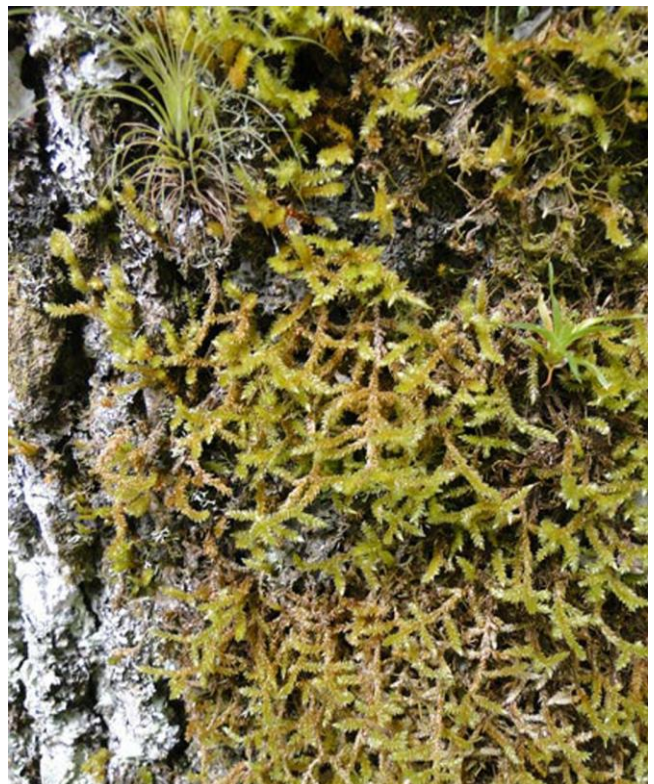


Figure 11. *Pilotrichella flexilis*, a species that occurs on *Quercus copeyensis* (Figure 10) in a Costa Rican montane cloud forest. Photo by Claudio Delgadillo Moya, with permission.



Figure 12. *Rigodium pseudo-thuidium*, a species that occurs on *Quercus copeyensis* (Figure 10) in a Costa Rican montane cloud forest. Photo by Juan Larrain, through Creative Commons.



Figure 13. *Porotrichodendron superbum*, a species that occurs on *Quercus copeyensis* (Figure 10) in a Costa Rican montane cloud forest. Photo by Jan-Peter Frahm, with permission.



Figure 14. *Prionodon densus*, a species that occurs on *Quercus copeyensis* (Figure 10) in a Costa Rican montane cloud forest. Photo by Jan-Peter Frahm, with permission.



Figure 15. *Neckera cephalonica*; *N. chilensis* occurs on *Quercus copeyensis* (Figure 10) in a Costa Rican montane cloud forest. Photo by Jan-Peter Frahm, with permission.



Figure 16. *Plagiochila adianthoides* from the Neotropics, in a genus that occurs on *Quercus copeyensis* (Figure 10) in a Costa Rican montane cloud forest. Here it is showing a **pendent** life form. Photo by Michael Lüth, with permission.

Nadkarni (1984) was among the early Neotropical researchers who investigated ecology of the epiphytes. Unfortunately for us, these typically included the bryophytes, lichens, and tracheophytes together. Nevertheless, we can generally consider that most of the dead epiphyte biomass that accumulates is comprised of bryophytes. On a single large tree (*Clusia alata*), the standing crop was 141.9 kg, with the nutrient concentrations of N 3062 g, P 97 g, K 678 g, ca 460 g, Mg 126 g, and Na 207 g. Despite contributing only 2% to the biomass of the elfin forest dry weight, they contribute approximately 45% of the nutrients. This gives them a considerable role in the nutrient cycling of the cloud forest.

In a later study, Nadkarni *et al.* (2004) distinguished the role of bryophytes. The canopy organic matter in a primary montane cloud forest of Monteverde, Costa Rica, was 63% dead organic matter. Bryophytes comprised 12% of this. However, in the secondary cloud forest, bryophytes provided 95% of the biomass, with only 3% as dead organic matter. Branch junctions in the primary forest supported only dead organic matter and roots, whereas branch tips, subcanopy, and understory substrates supported only bryophytes. Trunks had diverse organic matter components, but little associated dead organic matter. The secondary forest, on the other hand, exhibited little differentiation between trunks and branches due to the dominance of bryophytes. The absence of bryophytes in branch junctions of both forest types is in stark contrast to their common appearance in these location in temperate forests.

### Colonization and Life Strategies

A major problem for tropical bryophytes is that those with the common epiphytic life style must get dispersed and then become established on a vertical or otherwise elevated substrate. It is likely to be even more difficult for seeds of larger plants to become so established, so the bryophytes have an important role in providing a catchment for these propagules. Hence, the establishment of the bryophyte biomass is crucial to the cloud forest ecosystem. Nadkarni and coworkers (2000) attempted to determine how successful the bryophytes were in becoming

established from macroscopic fragments onto branches in a tropical cloud forest in Costa Rica (Figure 17). Not surprisingly, only 1% of the bryophyte fragments managed to land and remain on saplings for the six months of study. However, those dropped on the canopy were more successful. Those branches with intact epiphytes retained 24% of the fragments, whereas stripped branches in the same area retained only 5%. This suggests that larger-diameter branches are more successful at retaining the fragments, as are other epiphytes. After 10 years, the bryophytes showed good recovery (Figure 18) (Nadkarni 2000).

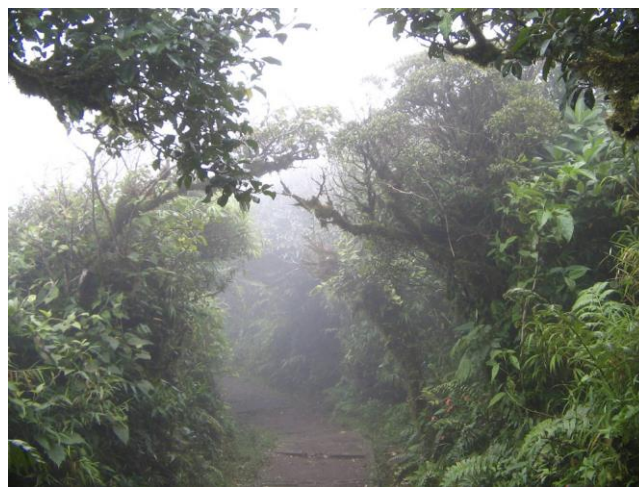


Figure 17. Cloud forest fog at Monte Verde, Costa Rica. Photo courtesy of David Fenlon.

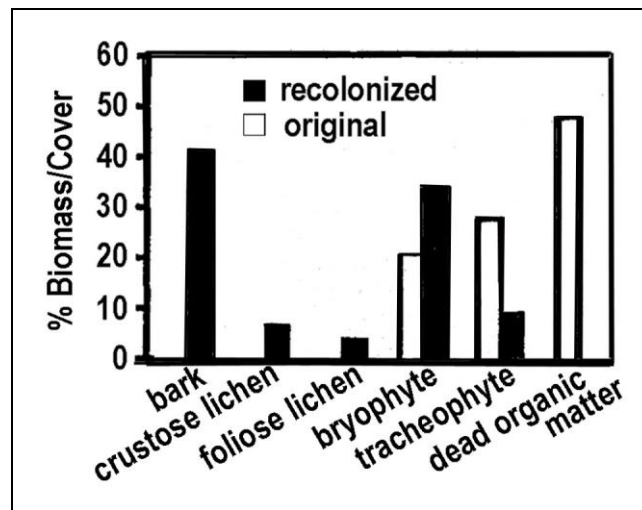


Figure 18. Comparison of component abundance in percent biomass of **original** epiphytic vegetation and percent total cover of **recolonizing** vegetation after 10 years on 75 m segments of inner canopy branches of mature trees at Monteverde, Costa Rica. Redrawn from Nadkarni 2000.

Life forms such as **feather**, **dendroid**, and **large cushions**, and **pendent** forms of **Meteoriaceae** (Figure 72-Figure 73), **Phyllogoniaceae** (Figure 40), **Frullania** (Figure 54), and **Taxilejeunea** (Figure 19) on horizontal branches of small trees and shrubs are often dominant and much more common than in lowland forests (Gradstein & Pócs 1989). Among the cloud forest species is **Fissidens polypodioides** (Figure 20), a member of a very large genus

with more than 500 species (Pursell 1994). In Central America, this is the largest *Fissidens* species, reaching 8 cm. In a Colombian cloud forest (Figure 21), van Leerdam and coworkers (1990) found **tall turfs** and **smooth mats** to predominate in the crowns, with forms differing between the inner and outer canopy. While **smooth mats** are common forms in the higher branches of temperate forests, the **tall turf** would seem to be possible only where moisture is abundant. Surprisingly, they found that growth and life forms differed dependent upon phorophyte species. Epiphyllous forms seem to be limited by frost, occurring up to only about 3,000 m (Pócs 1982).



Figure 19. *Taxilejeunea*, a genus that occurs on horizontal branches of small trees and shrubs in the Neotropics. Photo by Michael Lüth, with permission.



Figure 20. *Fissidens polypodioides*, a cloud forest species that is the largest *Fissidens* species in Central America. Photo by Janice Glime.

The **perennial shuttle species** take advantage of vegetative reproduction to become very important in the epiphytic communities on Mt. Kanabalu, North Borneo, whereas **perennial stayers** take advantage of the spores ultimately resulting from sexual reproduction or the occasional successful fragment to reach a new substrate, where they can persist for a long time (Frey & Kürschner 1991).



Figure 21. Montane cloud forest of Colombia. Photo courtesy of S. Robbert Gradstein.

### Species Diversity

The humid cloud forests are important habitats for the leafy liverworts that typically exceed the mosses in number of species. For example, Russell and Miller (1977) found 60 species of epiphytic liverworts, but only 23 of mosses, in an elfin forest in Puerto Rico.

Mandl *et al.* (2010) questioned whether certain species groups could be used as surrogates for diversity in Neotropical montane forests in Ecuador (Figure 22). To test this, they surveyed 28 plots (400 m<sup>2</sup> each) of both terrestrial and epiphytic species in the ridge and slope forests in three locations in southern Ecuador. The epiphytic habitat had significantly more liverworts than the ground habitat. Mosses, on the other hand, were predominantly ground dwellers. Liverwort diversity proved to be a good indicator of fern  $\alpha$  diversity. Moss  $\alpha$  diversity was similar to that of ferns and liverworts only in epiphytic habitats.  $\beta$  diversity of ferns, mosses, and liverworts was similar among ground species, but not among epiphytic species. Thus,  $\alpha$  diversity is not a good surrogate for  $\beta$  diversity in these cloud forests.



Figure 22. Montane cloud forest in Ecuador. Photo by Nils Köster, courtesy of S. Robbert Gradstein.

In a lower montane cloud forest at Monteverde, Costa Rica, Gradstein *et al.* (2001b) identified 133 liverwort, 56 moss, and 1 hornwort species. The thick branches of the lower canopy were the most species rich, with 99 species,



whereas trunks 1 m and above supported only 65 species. The lianas, shrubs, saplings, and understory leaves had only 36-46 species. Rotten logs were even more limited, with only 16 species. Roughly 36% of the species were exclusively in the canopy, with half the corticolous ones occurring there. In this case, the percentage of bryophyte species restricted to the canopy differs little from that of lowland and montane rainforests.

The Monteverde cloud forest has many rotting logs and fallen branches (Gradstein *et al.* 2001b). These serve as important habitats for the thallose liverworts *Monoclea gottschei* (Figure 23) and *Riccardia* spp. (Figure 24) and the mosses *Trachyxiophium guadalupense* (Figure 25) (*Pilotrichaceae*), *Mittenothamnium reptans* (*Hypnaceae*; Figure 26-Figure 27), *Plagiomnium rhynchophorum* (*Mniaceae*; Figure 28), and *Pyrrhobryum spiniforme* (*Rhizogoniaceae*; Figure 29). Only one hornwort (*Nothoceros vincentianus*; Figure 30) was found in the study, and this could be found on rotten logs. The rotten log species were also frequently encountered on tree bases, especially rotten humus ones.



Figure 23. *Monoclea gottschei*, a common inhabitant of rotting logs and fallen branches in cloud forests of Monteverde, Costa Rica. Photo by Jan-Peter Frahm, with permission.



Figure 24. *Riccardia fucoidea* from the Neotropics; the genus *Riccardia* is a common inhabitant of rotting logs and fallen branches in cloud forests of Monteverde, Costa Rica. Photo by Michael Lüth, with permission.



Figure 25. *Trachyxiophium guadalupense*, a common inhabitant of rotting logs and fallen branches in cloud forests of Monteverde, Costa Rica. Photo by Michael Lüth, with permission.



Figure 26. *Mittenothamnium reptans*, a common inhabitant of rotting logs and fallen branches in cloud forests of Monteverde, Costa Rica. Photo by Michael Lüth, with permission.



Figure 27. *Mittenothamnium reptans* from the Neotropics. Photo by Michael Lüth, with permission.



Figure 28. *Plagiomnium rhynchophorum*, a common inhabitant of rotting logs and fallen branches in cloud forests of Monteverde, Costa Rica. Photo by Michael Lüth, with permission.



Figure 29. *Pyrrhobryum spiniforme*, a common inhabitant of rotting logs and fallen branches in cloud forests of Monteverde, Costa Rica. Photo by Jan-Peter Frahm, with permission.

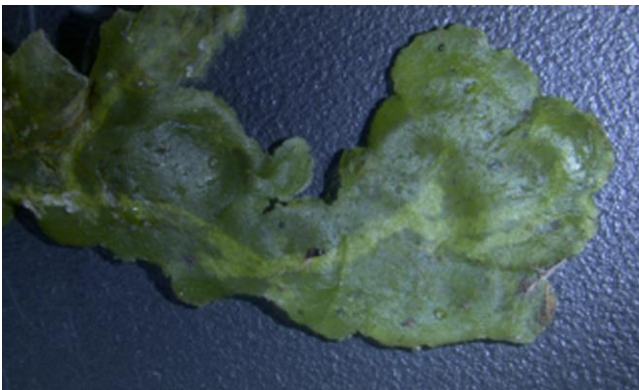


Figure 30. *Nothoceros vincentianus*, a common inhabitant of rotting logs and fallen branches in cloud forests of Monteverde, Costa Rica. This one is inhabited by a leaf-miner that has made the lighter green paths. Photo courtesy of Juan Carlos Villareal.

Gradstein *et al.* (2001b) elaborated on the species found in the various levels of this Monteverde cloud forest, where they identified 190 species. Unlike some wet forests where *Lejeunea* (Figure 31) presents the most species, in this case that role belonged to *Plagiochila* (Figure 16). In the understory, the most frequent bryophytes on trunks, shrubs, lianas *etc.* were the moss *Porotrichum korthalsianum* (see Figure 32) and the leafy liverworts *Plagiochila* spp. and *Radula antillana* (see Figure 33),

with other common taxa including *Lepidopilum muelleri* (see Figure 34-Figure 35), *Metzgeria leptoneura* (Figure 36), *Omphalanthus filiformis* (Figure 37), *Taxilejeunea pterigonia* (see Figure 38), and *Trichocolea tomentosa* (Figure 39). The well-lit sites were largely characterized by the pendent mosses *Phyllogonium fulgens* (Figure 40) in particular and various *Meteoriaceae* (Figure 54; Figure 72-Figure 73). These often occurred together with the robust liverworts *Porella swartziana* (see Figure 41), *Bryopteris filicina* (Figure 42), *Plagiochila* spp. (Figure 9, Figure 16), and *Radula gottscheana* (see Figure 33).



Figure 31. *Lejeunea flava* on a leaf; *Lejeunea* is common in wet forests, but not in the cloud forests of Monteverde. Photo by Yang Jia-dong, through Creative Commons.



Figure 32. *Porotrichum madagassum*; in a Montverde cloud forest, *Porotrichum korthalsianum* is common on trunks, shrubs, lianas *etc.* Photo by Nicola van Berkel, through Creative Commons.



Figure 33. *Radula* from the Neotropics, a genus that is frequent in the understory on trunks, shrubs, and lianas in the cloud forests of Monteverde. Photo by Michael Lüth, with permission.



Figure 36. *Metzgeria* from the Neotropics; in a Montverde cloud forest, *M. leptoneura* is common on trunks, shrubs, lianas etc. Photo by Michael Lüth, with permission.



Figure 34. *Lepidopilum* from the Neotropics; *Lepidopilum muelleri* is common on trunks, shrubs, lianas etc. in the Montverde cloud forest. Photo by Michael Lüth, with permission.



Figure 37. *Omphalanthus filiformis*, an understory species in the Montverde cloud forest. Photo by Jan-Peter Frahm, with permission.



Figure 35. *Lepidopilum* from the Neotropics. Photo by Michael Lüth, with permission.



Figure 38. *Taxilejeunea* Neotropics; *T. pterigonia* is common on trunks, shrubs, lianas etc. in the Montverde cloud forest. Photo by Michael Lüth, with permission.



Figure 39. *Trichocolea* sp.; *T. tomentosa* is common on trunks, shrubs, lianas *etc.* in the Montverde cloud forest. Photo by George Shepherd, through Creative Commons.



Figure 40. *Phyllogonium fulgens* from the Neotropics, a species common on trunks, shrubs, lianas *etc.* in the Montverde cloud forest. Photo by Michael Lüth, with permission.



Figure 41. *Porella obtusata*; *P. swartziana* is a species common on trunks, shrubs, lianas *etc.* in the Montverde cloud forest. Photo by Kristian Hassel, through Creative Commons.



Figure 42. *Bryopteris filicina*, a species common on trunks, shrubs, lianas *etc.* in the Montverde cloud forest. Photo by Eliana Calzadilla, through Creative Commons.

Trunk bases at Monteverde (Figure 44) typically had the liverworts *Cephalozia crassifolia* (Figure 43), *Lophocolea connata* (see Figure 45), *Telaranea nematodes* (Figure 46), and various species of *Lejeunea* (Figure 31). Mosses here included *Fissidens* spp. (Figure 20) and *Hypopterygium tamariscinum* (Figure 47) (Gradstein *et al.* 2001b). Less common, but nevertheless characteristic trunk base species, were the leafy liverworts *Calypogeia* spp. and the thallose liverwort *Pallavicinia lyellii* (Figure 48), and the mosses *Cyrto-hypnum schistocalyx* (Figure 49), *Leskeodon andicola* (Figure 50), *Octoblepharum erectifolium* (Figure 51), and *Syrrhopodon* spp. (Figure 52). Species of the liverwort *Bazzania* (Figure 53) could also be found, but these are much more common in the forest canopy.

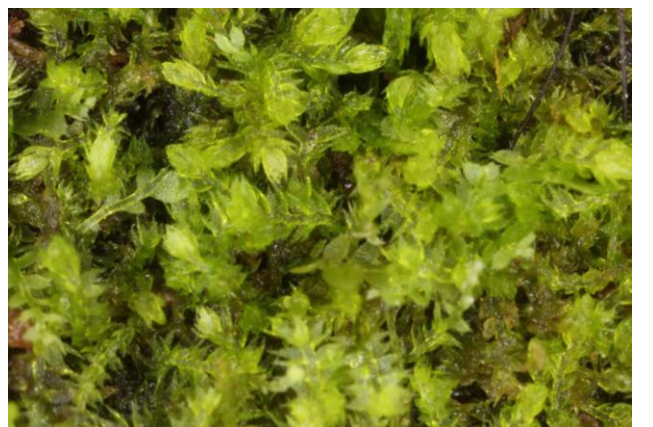


Figure 43. *Cephalozia crassifolia*, a species found on trunk bases at Monteverde, Costa Rica. Photo by Jan-Peter Frahm, with permission.

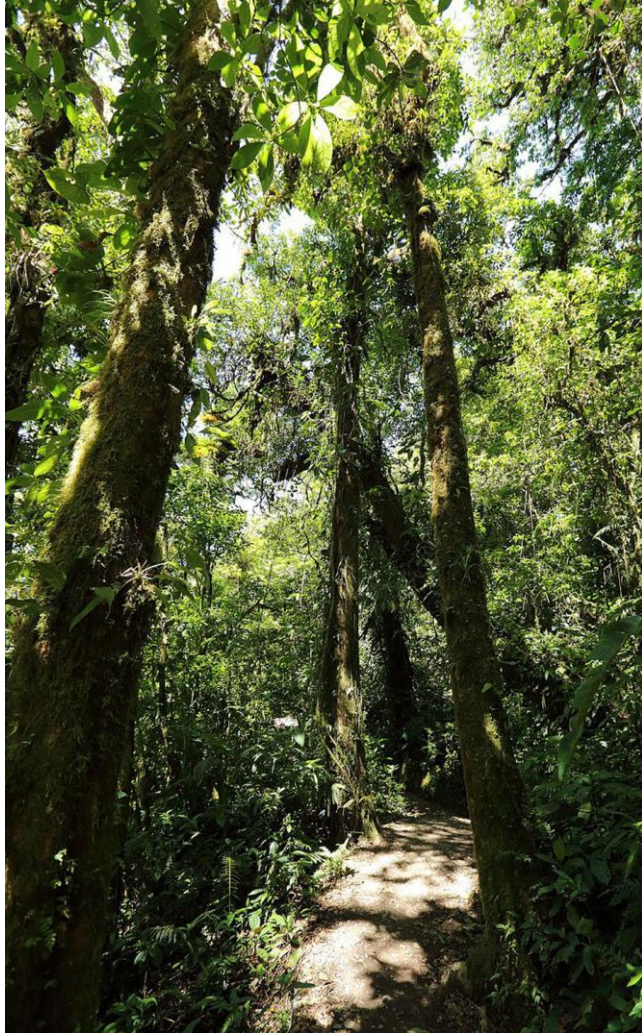


Figure 44. Cloud forest, Monteverde Reserve, Costa Rica. Photo by Cephas, through Creative Commons.



Figure 46. *Telaranea nematodes*, a species found on trunk bases at Monteverde, Costa Rica. Photo by Michael Lüth, with permission.



Figure 47. *Hypopterygium tamariscinum*, a species found on trunk bases at Monteverde, Costa Rica. Photo by Efrain de Luna, with permission.



Figure 45. *Lophocolea cf. polychaeta* from the Neotropics; *L. connata* is a species found on trunk bases at Monteverde, Costa Rica. Photo by Michael Lüth, with permission.



Figure 48. *Pallavicinia lyellii* with sporophytes, a tree base species in the Monteverde, Costa Rica, cloud forest. Photo by Jan-Peter Frahm, with permission.



Figure 49. *Cyrt-hypnum schistocalyx*, a tree base species in the Monteverde, Costa Rica, cloud forest. Photo by Michael Lüth, with permission.



Figure 52. *Syrrhopodon gaudichaudii* from the Neotropics; there are several *Syrrhopodon* tree base species in the Monteverde, Costa Rica, cloud forest. Photo by Michael Lüth, with permission.



Figure 50. *Leskeodon andicola*, a tree base species in the Monteverde cloud forest, Costa Rica. Photo from Natural History Museum, London, through Creative Commons.



Figure 51. *Octoblepharum albidum*; *O. erectifolium* is a tree base species in the Monteverde, Costa Rica, cloud forest. Photo by Javier Alejandro, through Creative Commons.



Figure 53. *Bazzania* from the Neotropics; a tree base genus in the Monteverde, Costa Rica, cloud forest. Photo by 3 Michael Lüth, with permission.

The canopy in the Monteverde cloud forest (Figure 44) demonstrated different communities (Gradstein *et al.* 2001 b). The nearly horizontal branches of the lower canopy displayed these mats of bryophytes. These included the leafy liverworts *Bazzania* (Figure 53), *Frullania convoluta* (Figure 54), *Herbertus* (Figure 55-Figure 56), *Lepidozia* (Figure 57), and *Plagiochila* (Figure 16), and the moss *Macromitrium* (Figure 58). Thick canopy branches added more *Frullania* plus the leafy liverworts *Adelanthus* (Figure 59), *Ceratolejeunea* (Figure 60), *Kurzia capillaris* (Figure 61), *Leptoscyphus porphyrius* (see Figure 62), *Syzygiella pectiniformis* (see Figure 63), and *Acrobolbus laxus* (Figure 64).



Figure 54. *Frullania convoluta*, a canopy species in the Monteverde, Costa Rica, cloud forest. Photo by Jan-Peter Frahm, with permission.



Figure 55. *Herbertus aduncus* forming deep cushions on branches, a typical sight to be found in the Monteverde, Costa Rica, cloud forest. Botany Website, UBC, with permission.



Figure 56. *Herbertus runcinatus* from Chile. Photo by Blanka Agüero, with permission.



Figure 57. *Lepidozia cupressina* from the Neotropics; *Lepidozia* is a common genus on the horizontal branches in the cloud forest at Monteverde, Costa Rica. Photo by Michael Lüth, with permission.



Figure 58. *Macromitrium microstomum* on rock; *Macromitrium* is frequent on lower branches in the Monteverde, Costa Rica, cloud forest. Photo by Tom Thekathyl, Blue Tier, with permission.



Figure 59. *Adelanthus decipiens*; the genus *Adelanthus* occurs on thick canopy branches in the cloud forest of Monteverde, Costa Rica. Photo by Michael Lüth, with permission.



Figure 60. *Ceratolejeunea cubensis*; thick canopy branches support mats of members of *Ceratolejeunea* in the cloud forest of Monteverde, Costa Rica and in the lowland cloud forest in French Guiana. Photo by Scott Zona, through Creative Commons.



Figure 61. *Kurzia capillararis* from the Neotropics, a species that occupies thick branches in the canopy of the Monteverde, Costa Rica, cloud forest. Photo by Michael Lüth, with permission.



Figure 62. *Leptoscyphus azoricus*; thick canopy branches support mats of members of *Leptoscyphus* in the cloud forest of Monteverde, Costa Rica. Photo by Jan-Peter Frahm, with permission.



Figure 63. *Syzygiella autumnalis*; thick canopy branches support mats of members of *Syzygiella* in the cloud forest of Monteverde, Costa Rica. Photo by H. Tinguy, French National Museum of Natural History, with online permission.



Figure 64. *Acrobolbus laxus*, a species that occupies thick branches in the canopy of the Monteverde, Costa Rica, cloud forest. Photo by Jan-Peter Frahm, with permission.



Mosses of the canopy included *Acroporium pungens* (Figure 65), *Bryum capillare* (Figure 66), *Campylopus arctocarpus* (Figure 67), *Leucobryum giganteum* (Figure 68), *Leucoloma cruegerianum* (Figure 69), *Pilotrichella flexilis* (Figure 11), *Squamidium nigricans* (see Figure 70), and *Syrrhopodon lycopodioides* (Figure 71) (Gradstein *et al.* 2001). Some moss species were generalists: *Toloxis imponderosa* (Figure 72-Figure 73), the pendent *Phyllogonium* (Figure 40), and *Cheilolejeunea filiformis* (see Figure 74), occurring in both the canopy and the understory. The fine twigs in the outer canopy supported communities of the moss *Daltonia gracilis* (see Figure 75) and many small species of the leafy liverwort family *Lejeuneaceae* (Figure 31, Figure 74). And of course the *Lejeuneaceae* predominated on leaves, especially in the understory. These *Lejeuneaceae* included *Cololejeunea* (Figure 76), *Cyclolejeunea convexistipa* (Figure 77), *C. peruviana* (Figure 78), *Drepanolejeunea* (Figure 79), and *Odontolejeunea lunulata* (Figure 80). Overall, 52% of the species are exclusive to the canopy and 20% to the forest understory.



Figure 65. *Acroporium pungens* in the cloud forest of the Luquillo Mountains, Puerto Rico. Photo by Janice Glime.



Figure 66. *Bryum capillare* with capsules, a species that occupies the canopy of the Monteverde, Costa Rica, cloud forest. Photo from Northern Defences, through Creative Commons.



Figure 67. *Campylopus arctocarpus*, a species that occupies the canopy of the Monteverde, Costa Rica, cloud forest. Photo by Jan-Peter Frahm, with permission.



Figure 68. *Leucobryum giganteum*, a species that occupies the canopy of the Monteverde, Costa Rica, cloud forest. Photo by Jan-Peter Frahm, with permission.



Figure 69. *Leucoloma cf. cruegeriana*, a species that occupies the canopy of the Monteverde, Costa Rica, cloud forest. Photo by Michael Lüth, with permission.



Figure 70. *Squamidium* from Toro Negro, Puerto Rico; *S. nigricans* occupies the canopy of the Monteverde, Costa Rica, cloud forest. Photo by Janice Glime.



Figure 73. *Toloxis imponderosa* from the Neotropics, where it is a generalist in the canopy. Photo by Michael Lüth, with permission.



Figure 71. *Syrrhopodon lycopodioides* from the Neotropics, a species that occupies the canopy of the Monteverde, Costa Rica, cloud forest. Photo by Michael Lüth, with permission.



Figure 74. *Cheilolejeunea* from the Neotropics; *Cheilolejeunea filiformis* is a **pendent** generalist species in the canopy and understory of the Monteverde, Costa Rica, cloud forest. Photo by Michael Lüth, with permission.



Figure 72. *Toloxis imponderosa* from the Neotropics, a species that occupies the canopy of the Monteverde, Costa Rica, cloud forest. Photo by Michael Lüth, with permission.



Figure 75. *Daltonia cf. longifolia* with capsules; *D. gracilis* occurs on the fine twigs of the outer canopy in the Monteverde, Costa Rica, cloud forest. Photo by Michael Lüth, with permission.



Figure 76. *Cololejeunea cardiocarpa*; the genus *Cololejeunea* occurs on leaves in the Monteverde, Costa Rica, cloud forest. Photo by Paul Davison, with permission.



Figure 77. *Cyclolejeunea convexistipula*; this species occurs on leaves of the understory in the Monteverde, Costa Rica, cloud forest. Photo by Jan-Peter Frahm, with permission.

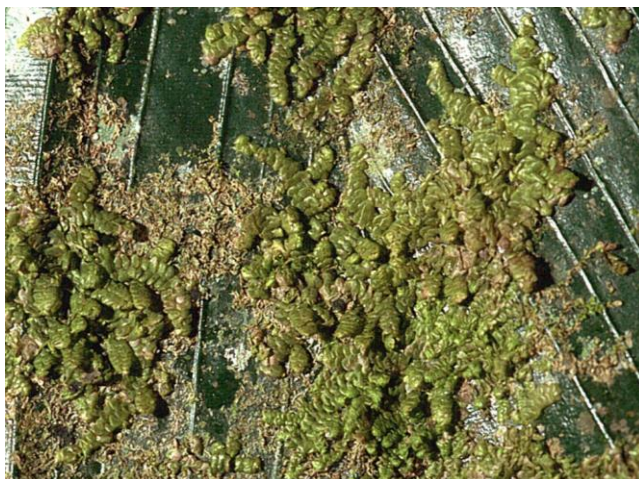


Figure 78. *Cyclolejeunea peruviana*; this species occurs on leaves in the understory of the Monteverde, Costa Rica, cloud forest. Photo by Michael Lüth, with permission.



Figure 79. *Drepanolejeunea mosenii*; the genus *Drepanolejeunea* occurs on leaves, especially in the understory of the Monteverde, Costa Rica, cloud forest. Photo by Jan-Peter Frahm, with permission.



Figure 80. *Odontolejeunea lunifolia*; this species occurs on leaves of the understory in the Monteverde, Costa Rica, cloud forest. Photo by Jan-Peter Frahm, with permission.

The epiphytic biomass and the associated canopy humus and canopy water storage capacity vary greatly among old-growth tropical montane cloud forests (Köhler *et al.* 2007). Köhler and coworkers compared the epiphytes in an old-growth cloud forest and a 30-year-old secondary forest on wind-exposed slopes in the Cordillera de Tilarán (Figure 81) in northern Costa Rica where bryophytes were the dominant epiphytes. Epiphyte biomass and canopy humus of the old-growth forest (16,215 kg ha<sup>-1</sup>) greatly exceeded that of the secondary forest (1,035 kg ha<sup>-1</sup>). These old-growth forests held water contents of 36%-418% of their dry weights. Stand water storage of the non-tracheophyte epiphytes in the secondary forest was only 0.36 mm, compared to 4.95 mm in the old-growth forest. The bryophytes experienced more dynamic wetting and drying cycles when compared to canopy humus.



Figure 81. Monteverde, Costa Rica, cloud forest, Cordillera de Tilarán. Photo by Peter Andersen, through Creative Commons.

Bubb *et al.* (2004) suggested that bryophytes could serve as indicator species to map the distribution of cloud forests. Because the cloud forest bryophyte species are so sensitive to levels of atmospheric humidity, many have very restricted habitat requirements.

In the Pacific region, many tropical montane cloud forests occur as isolated patches on peaks of volcanoes or rugged upland ridges (Merlin & Juvik 1995). These typically have high rainfall, but also receive "horizontal precipitation" from wind-driven cloud water.

Nadkarni and Solano (2002) expressed concern that climate change models predict reduced cloud water in the tropical montane forests. This could greatly reduce the number of cloud forests in the world. They tested the effects of reduced cloud water on epiphytes by transplanting them, along with their arboreal soil, from the upper cloud forest trees to trees at slightly lower elevation where less cloud water was available. There were no transplantation effects among the controls that remained in the cloud forest. However, those transplanted to the lower elevations had significantly higher leaf mortality, lower leaf production, and reduced longevity. Although these were predominately tracheophytes, it raises the question of survivability of bryophytic epiphytes as well.

Sillett *et al.* (1995) demonstrated a reduction in species when comparing bryophytes in inner tree crowns of *Ficus tuerckheimii* (Figure 82) isolated in a pasture (76 species) with those from an intact cloud forest (109 species) in Costa Rica. Of these, 52 species occurred only on the intact forest trees, whereas only 18 were exclusive to the pasture trees. The intact forest similarly had significantly higher bryophyte species richness, cover, and frequency of **pendants, tall turfs, tails, and fans**. The isolated pasture tree epiphytes experienced higher rates of evaporation and more sunlight compared to those on forest trees. This corresponded with a desiccation gradient from the intact forest to the isolated trees.



Figure 82. *Ficus tuerckheimii*, a species that has more inner crown epiphytes in the forest than when the tree is in the open. Photo by Dick Culbert, with online permission.

Additional studies include those on the microclimate and ecology (Baynton 1968) and ecology of leafy liverworts (Fulford *et al.* 1971a, b) of Puerto Rican cloud forests.

As in so many other studies, Gradstein *et al.* (1977) found "numerous" species of **Lejeuneaceae** (Figure 31, Figure 74), as well as **Plagiochilaceae** (Figure 16). Characteristic species were *Lepicolea pruinosa* (see Figure 83), *Riccardia fucoidea* (Figure 24), and *Scapania portoricensis* (see Figure 84), as well as multiple species of *Bazzania* (Figure 53), *Frullania* (especially **pendulous** species of the section *Meteoriopsis*; Figure 54), *Herbertus* (Figure 55-Figure 56), *Lepidozia* (e.g. *L. wallisiana*; see Figure 57), *Lophocolea* (Figure 45), *Metzgeria* (Figure 36), and *Radula* (Figure 33).



Figure 83. *Lepicolea ochroleuca*; *L. pruinosa* is a characteristic cloud forest species in the tropics. Photo by Jan-Peter Frahm, with permission.



Figure 84. *Scapania ornithopodioides*; *Scapania portoricensis* is a characteristic cloud forest species in the tropics. Photo by Michael Lüth, with permission.

### Mount Kenya

Mount Kenya (Figure 85-Figure 86) is the highest mountain in Kenya (5,199 m), exceeded in Africa only by Mount Kilimanjaro (Figure 87). The wettest climate on the mountain is the lower southeastern slopes where the predominating weather system comes from the Indian Ocean (Wikipedia 2018b). This area is dominated by very dense montane forest. The mountain experiences two distinct wet seasons and two distinct dry seasons. Hedberg (1969) described the mountain as having winter every night and summer every day – a challenging climate for most organisms. See also Chamberlin and Okoola (2003) for a discussion of the rainy and dry seasons in eastern Africa.



Figure 85. Mt. Kenya at sunrise. Photo by Alpsdake, through public domain.



Figure 86. Near timberline forest with mosses, Mt. Kenya. Photo by Mehmet Karatay, through Creative Commons.



Figure 87. Mt. Kilimanjaro at Amboseli National Park, Tanzania. Photo by Ninara, through Creative Commons.

The mountain straddles the equator, so in the northern summer the sun shines on the north side of the mountain and in the southern summer it shines on the south side (Wikipedia 2018b). There is only a one-minute difference between the shortest and longest day of the year, a phenomenon that eliminates the possibility of photoperiod as a trigger for life cycle events or preparation for seasonal changes.

The summit of the mountain is alpine, with most of the precipitation occurring as snow (Figure 85). However, frost serves as the primary water source. Between 2,400 m and 3,000 m asl (the lower part of the mountain), moist air rising from Lake Victoria forms clouds over the western forest zone (Clemens *et al.* 1991). Winds carry these clouds to the summit, where they protect the glaciers from melting by screening out direct sun (Hastenrath 1984).

Karlén *et al.* (1999) provide an historic climate perspective based on fluctuations in the glacier on Mount Kenya (Figure 85). Coe (1967) discusses the ecology of the alpine zone of Mt. Kenya. A somewhat recent expedition to Mt. Kenya revealed 10 new taxa, with two being new to all of Africa (Chuah-Petiot & Pócs 2003). These researchers found many protozoa living in the lobules of the leafy liverwort *Colura kilimanjarica* (see Figure 88).



Figure 88. *Colura leratii* from Fiji; *C. kilimanjarica* houses protozoa on Mt. Kilimanjaro in Africa. Photo courtesy of Tamás Pócs.

## Lowland Cloud Forest

Following the lead of Gradstein (2006) in French Guiana, Gehrig-Downie *et al.* (2011) defined this new type of cloud forest in northern South America, the lowland cloud forest (Figure 89). This type of forest occurs in river valleys in hilly areas where high air humidity and morning fog occur (Gradstein *et al.* 2010; Gehrig-Downie *et al.* 2011). The area is a rich epiphyte habitat in central French Guiana (Gehrig-Downie *et al.* 2011). This is most likely a result of the much longer periods of high relative humidity after sunrise. These researchers found significantly more epiphytic biomass in the lowland cloud forest ( $59 \text{ g m}^{-2}$ ) than in the lowland rainforest that lacked fog ( $35 \text{ g m}^{-2}$ ). Furthermore, epiphyte cover in the lowland cloud forest exceeded that of the lowland rainforest in all forest height zones (Figure 90).



Figure 89. Lowland fog in French Guiana. Photo by Delome, through Wikimedia Commons.

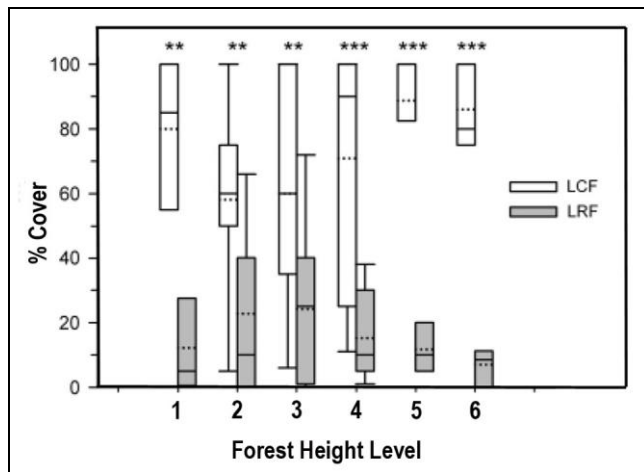


Figure 90. Abundance of all epiphytes as percentage of bark coverage in lowland cloud forest (LCF - white) and lowland rainforest (LRF - grey) in different height zones (1-6) on the tree; N=24 trees per forest type. Boxes indicate upper and lower quartile of data, unbroken line gives the median, dotted line the mean, and whiskers 95th percentile. Levels of significance with unpaired Student t-tests are shown by asterisks, \*  $P < 0.05$ , \*\*  $P < 0.01$ , \*\*\*  $P < 0.001$ . Modified from Gehrig-Downie *et al.* 2011.

Gradstein (2006) referred to the lowland cloud forest (400 m) of French Guiana (Figure 89) as a "liverwort hotspot." The species richness here is three times that of the Amazonian lowland forest. He found the species

richness of epiphytic liverworts to be similar to that at 2,000 m asl in the Andes. Daytime fog prevents desiccation, permitting a positive net photosynthesis despite the high temperatures. About 30% of the liverwort species are restricted to the canopy and several are obligate epiphylls. Asexual reproduction in the understory is significantly more common than in the canopy. The greater dispersal ability of canopy species, particularly by spores, may explain the greater distributional ranges of species that occur there.

Following up on their earlier studies, Gehrig-Downie *et al.* (2013) described the species differences between lowland cloud forests (Figure 89) and lowland rainforests (Figure 91) in French Guiana. The species composition differs in all height zones, with three times as many indicator species in the lowland cloud forest. The liverwort richness differs more strongly between these two forest types than among the sampled elevations, with lowland cloud forests sometimes being richer in species than even the montane rainforests. Species restricted to the lowland cloud forest and occurring on more than one tree include *Bazzania hookeri* (Figure 92), *Ceratolejeunea coarina* (Figure 93), *Cyclolejeunea chitonina* (see Figure 77-Figure 78), *Metzgeria leptoneura* (see Figure 36), *Pictolejeunea picta*, *Plagiochila cf. gymnocalycina* (see Figure 16, Figure 94), *P. raddiana* (Figure 94), *P. rutilans* (see Figure 16, Figure 94), and *Radula flaccida* (Figure 95). *Ceratolejeunea cubensis* (Figure 60) is the commonest species, occurring in more than 50% of the plots. In the lowland rainforest and collected on more than one tree, the exclusive species are *Anoplolejeunea conferta*, *Diplasiolejeunea cf. cavifolia*, and *D. rudolphiana* (Figure 96). *Cheilolejeunea adnata* (see Figure 74) was present in 80% of lowland rainforest samples, but only in 40% of the lowland cloud forest samples. Liverwort species richness increased with height zone in both forest types. However, in the lowland cloud forest it was the middle and outer crowns where most species occurred, whereas it was highest only in the middle crowns in the lowland rainforest.



Figure 91. French Guiana tropical lowland forest. Photo by Cayambe, through Creative Commons.



Figure 92. *Bazzania hookeri* from the Neotropics, where in French Guiana it is restricted to the lowland rainforests. Photo by Michael Lüth, with permission.



Figure 93. *Ceratolejeunea coarina* perianth, a species that in French Guiana is restricted to the lowland cloud forest. Photo by Michaela Sonnleitner, with permission.



Figure 94. *Plagiochila raddiana* from the Neotropics, where in French Guiana it is restricted to the lowland rainforests. Photo by Michael Lüth, with permission.



Figure 95. *Radula flaccida* habit with gemmae, a species restricted to the lowland cloud forest in French Guiana. Photo by Michaela Sonnleitner, with permission.



Figure 96. *Diplasiolejeunea rudolphiana* from the Neotropics, a species exclusive to the lowland rainforest in French Guiana. Photo by Michael Lüth, with permission.

Cloud forest life forms are benefitted if they are able to take advantage of the moisture in the clouds. Even in lowland rainforests, such as those found in French Guiana, the clouds increase the diversity of epiphytic bryophytes. Compared to other lowland rainforests, the lowland cloud forest exhibits higher biomass and cover of bryophytes, especially in the mid and outer canopy. These bryophytes likewise exhibit a greater diversity of life forms. Typical cloud forest life forms such as **tail**, **weft**, and **pendants** are nearly absent in the canopies of the lowland rainforest, but these are frequent in the lowland cloud forests.

### Role

Bryophytes have another important role in these cloud forests. Bruijnzeel and Proctor (1995) emphasized the importance of the tropical montane cloud forest in the water cycle, even in headwater areas. This role is especially important during dry periods, supplying water to downstream areas. Nevertheless, they are often neglected in vegetation studies.

While interception of rainfall in the submontane rainforest is high, that in the elfin forest is about 2.5 times higher and accounts for intercepting over 50% of the annual rainfall (Pócs 1980). The most effective of these receptive bryophytes were the leafy liverworts *Bazzania*

(Figure 92), *Plagiochila* (Figure 94), *Frullania* (Figure 54), *Lepidozia* (Figure 57), and *Trichocolea* (Figure 39). These bryophytes maintain a humid environment beneath by nearly continuous dripping (Lyford 1969 – Puerto Rico; Pócs 1980 – Tanzania) and this seems to create the necessary conditions for terrestrial bryophyte growth. In

montane rainforests of the Colombian Andes, at 3370 m, the epiphyte mass, primarily of bryophytes, was 12 tonnes of dry weight per hectare and held considerable rainfall (Figure 97), which was likewise released very gradually through drainage as well as slow evaporation (Veneklaas *et al.* 1990).

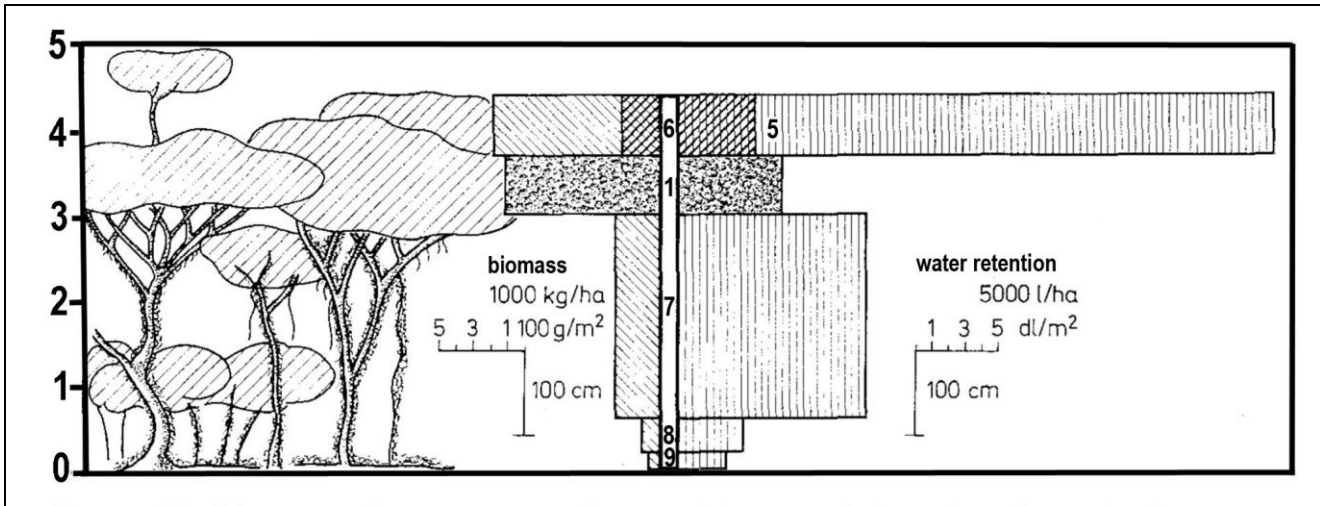


Figure 97. The biomass and interception of water by epiphytes, including bryophytes, and tree leaves in the cloud forest, showing their positions in the forest layers in Tanzania. Modified from Pócs 1980.

Martin *et al.* (2011) remind us that the moisture in a cloud forest reduces fire risk. This same cloud immersion fosters the growth of epiphytic bryophytes (Proctor 1982; Frahm & Gradstein 1991). These bryophytes, in turn, serve as sponges that strip moisture from the air and retain it, further lowering the flammability (Bruijnzeel & Proctor 1995).

Ah-Peng *et al.* (2017) reported excellent cloud water interception ability by the bryophytes in the cloud forest on Reunion Island, using *Bazzania decrescens* (Figure 98) and *Mastigophora dicladus* (Figure 99) as study organisms. *Mastigophora dicladus* had the greater ability to intercept water, but *Bazzania decrescens* had a far greater water storage capacity. Despite having less than half the abundance of *M. dicladus*, *B. decrescens* stored more than twice the water per hectare. The two species combined stored approximately 34,500 L ha<sup>-1</sup>, the equivalent of 3.46 mm rainfall.



Figure 98. *Bazzania decrescens*, one of the bryophytes that intercepts cloud water in cloud forests on Reunion Island. Photo by Jan-Peter Frahm, with permission.



Figure 99. *Mastigophora dicladus*, one of the bryophytes that intercepts cloud water in cloud forests on Reunion Island. Photo by Claudine Ah-Peng, with permission.

In the cloud forests of Papua New Guinea, Norris (1990) found that disturbance could cause serious reduction in the moisture within an epiphytic bryophyte colony. The epiphytes in these tropical cloud forests and rain forests have a much larger biomass than those of temperate forests. He suggested that larger **colonies** might maintain moisture longer than small **colonies**. Furthermore, contiguous clones will allow lateral conduction of water, whereas separated **tufts** result in little if any transfer across the host surface.

That water trapping is not always beneficial to the trees. In places where there are trees, the bryophytes can contribute to their demise. Encircling and hanging from branches, the bryophytes often capture 25% of the precipitation and absorb up to four times their own weight



(Schofield 1985). With this added weight, they can break the branches upon which they rest.

Epiphytes have another interesting role as well in the development of some forest trees. Bryophytes, along with other components (filmy ferns, dead organic matter) of the humus on the branches, provide the moisture and nutrients needed to stimulate adventitious roots, that is, roots that develop from locations other than the base of the stem, in this case from the trunk or branches (Nadkarni 1994b). Using the shrub-tree *Jessia cooperi* (Figure 100), an inhabitant of landslides, she determined that wet epiphytes or nutrient solutions with foam sponges would stimulate the production and growth of adventitious roots, whereas dry epiphytes, distilled water with foam sponges, and dry sponges would not.



Figure 100. *Jessia cooperi*, a species that responds to wet sponges to form adventitious roots, suggesting a possible role for epiphytic bryophytes. Photo by Dick Culbert, through Creative Commons.

As with epiphytes in general, the epiphytes in the cloud forest can provide substrate, water reserves, and nutrient release that are available to tracheophytes. Orchids frequently become established in these mats (Frei 1973).

As with any thick bryophyte mat, the tropical bryophyte assemblages are home for numerous invertebrates. In the cloud forest of Costa Rica, these are likely to include amphipods, isopods, mites, Collembola, larvae, adult beetles, and ants (Nadkarni & Longino 1990). Interestingly, Nadkarni and Longino found that the composition of the fauna was basically the same in the canopy as that on the forest floor, but the ground had a mean density that was 2.6 times as great as that in the canopy, with the exception of ants, which were similar in both.

## Subalpine

The sub-alpine (Figure 101) can act like an island, presenting a temperature regime that is more like the Arctic than the tropics. This makes mountaintop extinctions and a

loss of biodiversity a danger under the influence of global climate change (Ah-Peng *et al.* 2014). On Réunion Island, Ah-Peng and coworkers found a relatively high species richness for bryophytes in the subalpine habitats, with diversity peaking at 2750 m asl for the ground-dwellers. They found that the functional richness with elevation differed between ground-dwellers and epiphytes, suggesting differences in the processes that structure these two community types. The ground-dwellers have a higher functional redundancy; the researchers interpreted this to indicate that the ground-dwellers may be more robust than the epiphytes when disturbances occur in this subalpine system.



Figure 101. Tropical subalpine dwarf forest in Peru at 3,200 m asl with Jan-Peter Frahm among the epiphytes. Photo courtesy of S. Robbert Gradstein.

## Alpine

Luteyn *et al.* (1999, p. 1; see also Smith & Young 1987) list the different local names applied to the band of vegetation between the upper limit of continuous, closed-canopy forest (**timberline**; Figure 102) and the upper limit of plant life (**snowline**; Figure 103). In tropical regions of Mexico, Central and South America, Africa, Malesia including New Guinea, and Hawaii, this zone typically has tussock grasses, large rosette plants, evergreen shrubs, and cushion plants. These areas have different local names, including *zacatonales* (Mexico, Guatemala; Figure 104), *páramo* (Central and northern South America; Figure 105), *jalca* (northern Peru; Figure 115), *puna* (drier areas of the

altiplane of central Andes; Figure 106), *Afro-alpine* or *moorland* (East Africa; Figure 107), and *tropical-alpine* (Malesia; Figure 108-Figure 109).



Figure 102. **Treeline** (timberline) in Tararua, North Island of New Zealand. Photo by William Demchick, through Creative Commons.



Figure 103. Snowline on Chimborazo volcano, Ecuadorian Andes. Photo by Bernard Gagnon, through Creative Commons.



Figure 104. Zacototal, Nevado de Toluca, Mexico. Photo by Mainau, through public domain.



Figure 105. Páramo in Colombia. Photo by Friedrich Kircher, through Creative Commons.



Figure 106. Central Andean wet puna. Photo by Idobi, through Creative Commons.



Figure 107. Afro-alpine, at Lascar, northern Chile. Photo by Jorge Lásca, through Creative Commons.



Figure 108. Mount Kinabalu, Malaysia, showing tropical alpine region in the distance. Photo by Nep Grower, through Creative Commons.



Figure 109. Mount Kinabalu summit plateau (Afro-alpine). Photo by Ariel Steiner, through Creative Commons.

Bader *et al.* (2007) examined the role of bryophytes in tree regeneration above treeline in Ecuador (Figure 110). It is difficult for tree seedlings to become established there, and the researchers hypothesized that bryophytes could facilitate that establishment. First, they found that the number of naturally occurring tree sprouts (seedlings, saplings, and ramets) was highest just outside the forest, and decreased with distance to the forest edge. They transplanted seedlings into the alpine vegetation. The forest floor is totally covered with mosses, including species of *Sphagnum* (Figure 111), especially at the forest edge, and has a peaty organic layer of 30-100 cm on top of the dark mineral soil. The transplanted seedlings had negligible growth after 2.5 years, and some decreased in size due to damage of upper parts. Others seemed to be shorter due to the growth of fast-growing forest floor mosses that served as the measurement base. The seedlings that were planted in the mosses were sometimes overgrown by the mosses. The researchers concluded that seedlings can grow among mosses in the forest where that is the only available substrate, but that they are not favored by mosses.



Figure 110. *Blechnum loxense* tree fern at treeline in the Ecuadorian Andes at 3,500 m asl, showing tropical researcher Jan-Peter Frahm. Photo courtesy of S. Robbert Gradstein.



Figure 111. *Sphagnum magellanicum*; the genus *Sphagnum* occurs on the forest floor near treeline in Ecuador. Photo by Michael Lüth, with permission.

In the Neotropics, Gradstein *et al.* (2001a) recognized páramo, Puna, and Zacatonal as the alpine habitats. Smith and Young (1987) noted how few studies existed on tropical alpine bryophytes and emphasized their importance in tropical mountain communities.

## Páramo

The **páramo** (sparsely vegetated alpine zone on tops of high mountains of Andes and other high-elevation South American mountains; Figure 112-Figure 114) is generally considered to occur in Venezuela, Colombia, and northern Ecuador, with a pocket in Costa Rica (Luteyn 1999; Daniel Stanton, pers. comm. 4 December 2011). In northern Peru, wetter grasslands are known as **jalcas** (Figure 115). As pointed out by Daniel Stanton (pers. comm. 4 December 2011), the differences in naming may be more political or cultural than a reflection of real differences.



Figure 112. Páramo Sumapaz, Colombia. Photo by Yuri Romero Picon, through public domain.



Figure 113. Páramo in Colombia. Photo by Friedrich Kircher, through Creative Commons.



Figure 114. Páramo of Rabanal, Colombia. Photo by Patricio Mena Vásconez, through public domain.



Figure 115. **Jalca** district, Chachapoyas, Peruvian Amazon Region. Photo by Pitxiquni, through Creative Commons.

There is a striking shift in the substrate of bryophytes as one goes up in elevation in many parts of the tropics. Lower elevations, ranging up through the condensation zone and only slightly into the **páramo**, one can find most of the bryophyte cover as epiphytes on trees and shrubs. However, beginning at in the lower montane and increasing dramatically in the páramo, the major bryophytic cover is found on soil and rock for both mosses and liverworts (van Reenen & Gradstein 1983).

Central America enjoys the interesting flora that is a product of influence from both North and South America. In the Cordillera de Talamanca of Costa Rica, Holz (2003) and Holz and Gradstein (2005) identified 191 liverworts, 209 mosses, and 1 hornwort. Of these, 128 liverworts, 122 mosses, and 1 hornwort occur in the oak (*Quercus*) forests. The bryophytes are represented by proportionally more tropical species than are the tracheophytes. In the páramo, by contrast, the bryophyte flora is more similar to that of temperate regions. There are fewer endemics than are found in the oak forests.

Table 1. Ten largest families and genera of páramo mosses and liverworts. From Holz &amp; Gradstein 2005.

Family (no. genera/spp.)	Genus (family) (no. spp.)
<b>Mosses</b> (prepared by Steve Churchill and Dana Griffin III)	
<b>Dicranaceae</b> (17/67) – Figure 3	<b>Sphagnum</b> ( <b>Sphagnaceae</b> ) (37) – Figure 111
<b>Bryaceae</b> (10/65) – Figure 121, Figure 123	<b>Zygodon</b> ( <b>Orthotrichaceae</b> ) (21) – Figure 116
<b>Pottiaceae</b> (19/63) – Figure 159	<b>Bryum</b> ( <b>Bryaceae</b> ) (18) – Figure 121
<b>Bartramiaceae</b> (7/40) – Figure 120	<b>Leptodontium</b> ( <b>Pottiaceae</b> ) (16) – Figure 140
<b>Orthotrichaceae</b> (3/36) – Figure 116, Figure 117	<b>Orthotrichum</b> ( <b>Orthotrichaceae</b> ) (14) – Figure 117
<b>Sphagnaceae</b> (1/27) – Figure 111	<b>Breutelia</b> ( <b>Bartramiaceae</b> ) (13) – Figure 120
<b>Amblystegiaceae</b> (9/19) – Figure 118-Figure 119	<b>Daltonia</b> ( <b>Daltoniaceae</b> ) (13) – Figure 122
<b>Brachytheciaceae</b> (7/18) – Figure 141	<b>Macromitrium</b> ( <b>Macromitriaceae/Orthotrichaceae</b> ) – Figure 58
<b>Polytrichaceae</b> (6/16) – Figure 158	<b>Schizymerium</b> ( <b>Bryaceae</b> ) (11) – Figure 123
<b>Grimmiaceae</b> (4/17) – Figure 132-Figure 133	
<b>Liverworts</b> (prepared by Robbert Gradstein)	
<b>Lejeuneaceae</b> (16/38) – (Figure 31, Figure 74)	<b>Riccardia</b> ( <b>Aneuraceae</b> ) (20) – (Figure 24)
<b>Jungermanniaceae</b> (11/31) – Figure 149	<b>Metzgeria</b> ( <b>Metzgeriaceae</b> ) (20) – Figure 124
<b>Lepidoziaceae</b> (6/20) – Figure 57	<b>Plagiochila</b> ( <b>Plagiochilaceae</b> ) (18) – Figure 16, Figure 94
<b>Aneuraceae</b> (2/21) – (Figure 24)	<b>Frullania</b> ( <b>Jubulaceae/Frullaniaceae</b> ) (13) – Figure 54
<b>Metzgeriaceae</b> (1/20) – Figure 124	<b>Bazzania</b> ( <b>Lepidoziaceae</b> ) (13) – Figure 98
<b>Plagiochilaceae</b> (2/19) – Figure 16, Figure 94	<b>Anastrophyllum</b> ( <b>Jungermanniaceae/Anastrophyllaceae</b> ) (8) – Figure 149
<b>Geocalyceae</b> (7/18) – Figure 62	<b>Lepidozia</b> ( <b>Lepidoziaceae</b> ) (8) – Figure 57
<b>Gymnomitriaceae</b> (5/14) – Figure 129-Figure 130	<b>Leptoscyphus</b> ( <b>Geocalyceae</b> ) (7) – Figure 62
<b>Jubulaceae/Frullaniaceae</b> (1/13) – Figure 54	<b>Isotachis</b> ( <b>Balantiopsidaceae</b> ) (6) – Figure 125
<b>Balantiopsaceae</b> (2/7) – Figure 125	<b>Cephaloziella</b> ( <b>Cephaloziellaceae</b> ) (6) – Figure 126
	<b>Marsupella</b> ( <b>Gymnomitriaceae</b> ) (6) – Figure 129-Figure 130
	<b>Radula</b> ( <b>Radulaceae</b> ) (6) – Figure 33



Figure 116. *Zygodon conoideus*, with capsules, representing one of the 10 largest families in the páramo. Photo by Proyecto Musgo through Creative Commons.

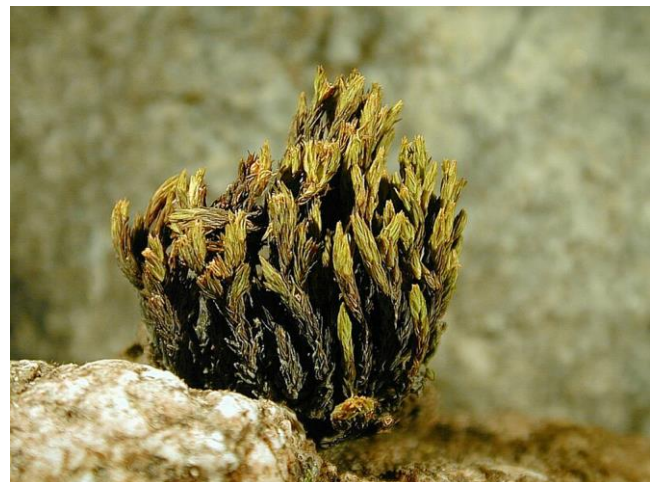


Figure 117. *Orthotrichum rupestre* from the Neotropics, representing one of the 10 largest families in the páramo. Photo by Michael Lüth, with permission.



Figure 118. *Vittia pachyloma* habitat in Chile, representing one of the 10 largest families in the páramo. Photo by Juan Larrain, with permission.

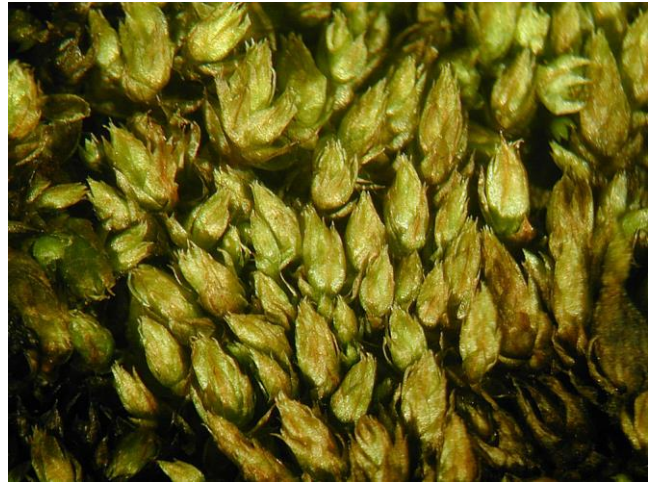


Figure 121. *Bryum apiculatum* from the Neotropics, representing one of the 10 largest families in the páramo. Photo by Michael Lüth, with permission.



Figure 119. *Vittia pachyloma*, representing one of the 10 largest families in the páramo. Photo from NYBG, through public domain.



Figure 122. *Daltonia cf longifolia* from the Neotropics, representing one of the 10 largest families in the páramo. Photo by Michael Lüth, with permission.



Figure 120. *Breutelia wainioi* from the Neotropics, representing one of the 10 largest families in the páramo. Photo by Michael Lüth, with permission.



Figure 123. *Schizymenium pontevedrense* with capsules, in a genus that is common in the páramo in the Neotropics. Photo by Michael Lüth, with permission.



Figure 124. *Metzgeria* in the Neotropics, representing one of the 10 largest families (**Metzgeriaceae**) in the páramo. Photo by Michael Lüth, with permission.



Figure 125. *Isotachis aubertii* in the Neotropics, representing one of the 10 largest families (**Balantiopsidaceae**) in the páramo. Photo by Michael Lüth, with permission.



Figure 126. *Cephaloziella exiliflora*, in a genus that is common in the páramo of the Neotropics. Photo by Tom Thekathyl, with permission.

One reason for the low number of bryophyte taxa at lower elevations might be due to nighttime respiratory losses. High nighttime temperatures in the lowlands elevate the loss of CO<sub>2</sub> and prevent the bryophytes from attaining a net positive carbon balance (Proctor 1982; Richards 1984; Frahm 1987, 1990, 1994; Zotz *et al.* 1997; Zotz 1999). This is consistent with observations that the distribution correlates with increased moisture and lower temperatures at higher elevations (Pôrto 1992), permitting more time per day for photosynthetic gain.

Other studies on the páramo include liverwort diversity in the Neotropics (Gradstein 1998) and bryophytes and lichens of the páramo (Griffin 1979). Cleef (1978) described the Neotropical páramo vegetation and its relationship to that of the subAntarctic. Mägdefrau (1983) described bryophyte vegetation in the páramo of Venezuela and Colombia.

### Moss Balls

**Moss balls**, also known as **vagrant plants**, erratic, solifluction floaters, and errant cryptogams (Pérez 1997b), are unattached plants that are blown about by the wind or moved by water or frost-heaving. Because of their movement, they frequently change their upward direction and consequently begin growth in a different direction (Shacklette 1966). This, and the tumbling that can break off extruding parts, forms them into balls. These are somewhat common on bare soils where climate conditions are subarctic, creating lenticular to spherical moss balls that are completely unattached and free to blow about on the snow and ice (Beck *et al.* 1986). These moss balls are particularly abundant in the alpine zone of high mountains of tropical Africa, especially on Mt. Kenya. In that location, the balls are formed by *Grimmia ovalis* (Figure 127-Figure 128). These are formed by continual motion of fragments of cushions that have been broken by frost or by single plants or small aggregations that occur on bare soil. These vulnerable bryophytes can be moved by wind and solifluction that occurs due to nocturnal needle-ice formation and subsequent thawing in the daytime. The outer layer of the balls that are formed is the living part; next is a layer of dead plant sections, whereas the core is a peaty material of disintegrated leaflets, rhizoids, stems, and minute soil particles.



Figure 127. *Grimmia ovalis*, a species that is able to form moss balls. Photo by Michael Lüth, with permission.



Figure 128. *Grimmia ovalis* forming balls that can break away to form moss balls. Photo by Barry Stewart, with permission.

Others, in particular *Marsupella* (Figure 129-Figure 130), occur on small soil buds and nubbins that are common on the ground surface in the high páramo (Pérez 1994). The moss balls are known in many biomes where wind or water create them. In the superpáramo zone, frost-heaving creates such moss balls, as also seen in the fruticose lichen *Thamnolia vermicularis* (Figure 131) and the acrocarpous moss *Grimmia longirostris* (Figure 132) (Pérez 1991, 1994). Members of *Grimmiaceae* seem to be suited to making vagrant populations. Shacklette (1966) reported unattached polsters (known as glacier moss) of *Schistidium apocarpum* (Figure 133) on sandy soil on Amchitka Island, Alaska, where they become detached by wind erosion.

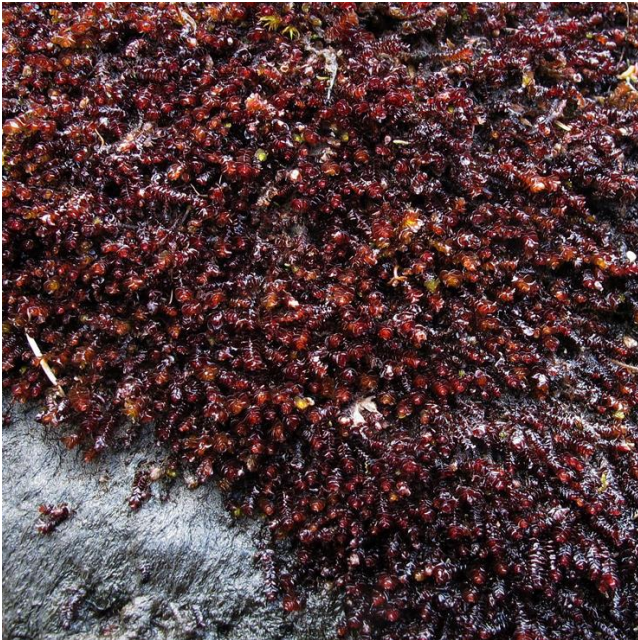


Figure 129. *Marsupella emarginata* var. *pearsonii*; *Marsupella* occurs on small soil buds and nubbins that are common on the ground surface in the high páramo. Photo by Michael Lüth, with permission.



Figure 130. *Marsupella emarginata*, a species that can form bryophyte balls. Photo by Michael Lüth, with permission.



Figure 131. *Thamnolia vermicularis*, a species that forms balls in the superpáramo. Photo by Schaudé, through Creative Commons.



Figure 132. *Grimmia longirostris* moss balls created by solifluction. Photo by Henk Greven, with permission.





Figure 133. Glacier mice – moss balls, probably *Schistidium apocarpum*. Photo from Wondergressive, through Creative Commons.

### Afro-alpine

In most people's minds, the combination of African and alpine (Figure 134) seems like an oxymoron. Nevertheless, **Afro-alpine** (high mountains of Ethiopia and tropical East Africa, which represent biological 'sky islands' with high level of endemism) zones exist and present unique communities (Hedberg 1964). The *Dendrosenecio* (Figure 135) woodlands present *Breutelia diffracta* (Figure 136), *B. stuhlmannii* (Figure 137), *Brachythecium ramicola*, *Campylopus nivalis* (Figure 138), *Sanionia uncinata* (Figure 139), and *Leptodontium viticulosoides* (Figure 140). The bottom layer is characterized by the mosses *Brachythecium ruderale* (Figure 141), *B. spectabile*, and *Hypnum bizotii*, and the liverworts *Chiloscyphus cuspidatus* (Figure 142), *Lophocolea martiana* (see Figure 45), *Metzgeria hamata* (Figure 143), *M. hedbergii*, *Mylia hedbergii* (see Figure 144), and *Plagiocilia haumanii* (see Figure 16, Figure 94).

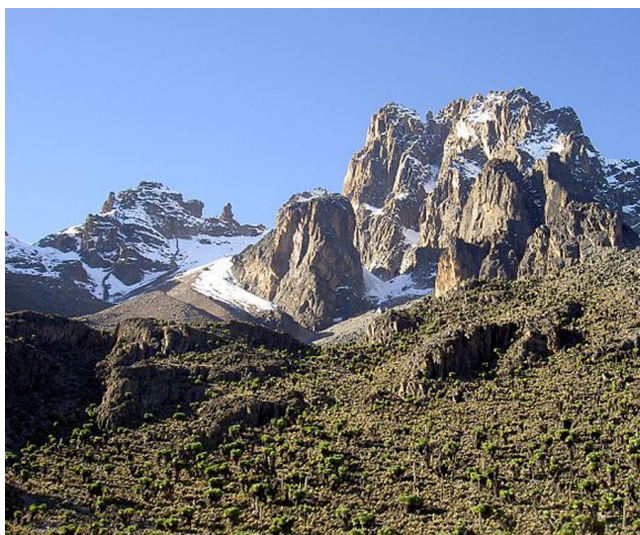


Figure 134. Mt. Kenya. Photo by Elizabeth Kiragu Wanjugu and Tobias Schonwetter, through Creative Commons.



Figure 135. *Dendrosenecio*, a tree found in the Afromontane zone. Photo through Creative Commons.



Figure 136. *Breutelia diffracta*, a species in the *Dendrosenecio* woodlands of the Afromontane region. Photo by Jan-Peter Frahm, with permission.



Figure 137. *Breutelia stuhlmannii*, a species in the *Dendrosenecio* woodlands of the Afromontane region. Photo by Jan-Peter Frahm, with permission.



Figure 138. *Campylopus nivalis*, a species in the *Dendrosenecio* woodlands of the Afromontane region. Photo by Jan-Peter Frahm, with permission.



Figure 141. *Brachythecium ruderale*, a species of the bottom layer in the *Dendrosenecio* woodlands in the Afro-alpine zones. Photo by Claudio Delgadillo Moya, with permission.



Figure 139. *Sanionia uncinata*, a species in the *Dendrosenecio* woodlands of the Afromontane region. Photo by Michael Lüth, with permission.



Figure 142. *Chiloscyphus cuspidatus*, a species of the bottom layer in the *Dendrosenecio* woodlands in the Afro-alpine zones. Photo from the TePapa collection, through Creative Commons.



Figure 140. *Leptodontium viticulosoides*, a species of *Dendrosenecio* woodlands in the Afro-alpine zones. Photo by Li Zhang, with permission.



Figure 143. *Metzgeria hamata*, a species of the bottom layer in the *Dendrosenecio* woodlands in the Afro-alpine zones. Photo by Clive Shirley, Hidden Forest, with permission.



Figure 144. *Mylia anomala*; *M. hedbergii* is a species of the bottom layer in the *Dendrosenecio* woodlands in the Afro-alpine zones. Photo by David T. Holyoak, with permission.

Older stems of the *Dendrosenecio* (Figure 135) commonly support thick cushions of moss, with lichens being relatively rare (Hedberg 1964). These include numerous bryophyte species, but the moss *Antitrichia curtispindula* (Figure 145-Figure 146) is the most abundant.

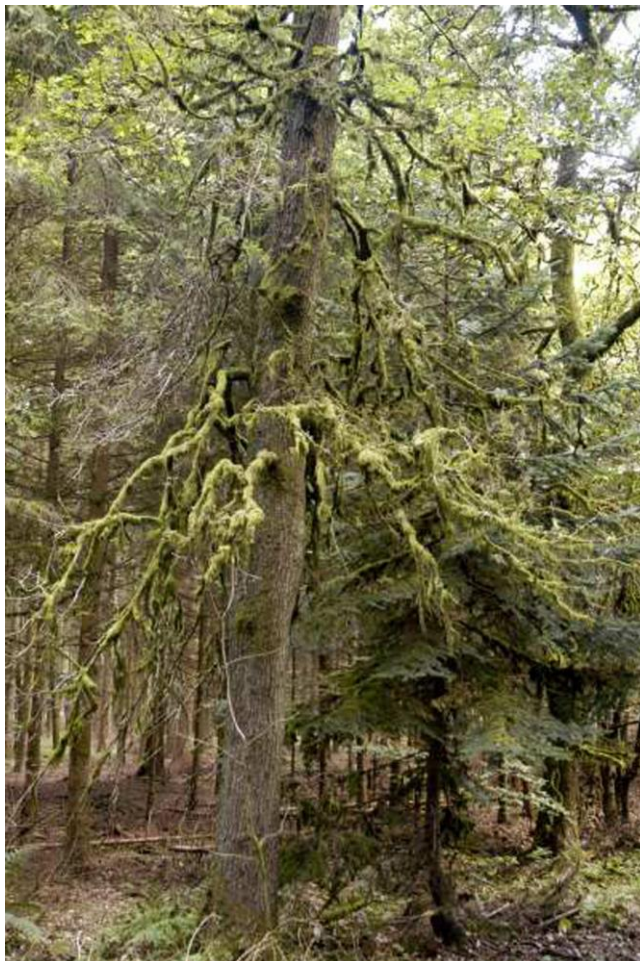


Figure 145. *Antitrichia curtispindula* habitat. This species is the most abundant on *Dendrosenecio* in the Afromontane. Photo by James K. Lindsey, with permission.

Accompanying species include the moss *Hypnum cupressiforme* (Figure 147-Figure 148) and the leafy liverworts *Anastrophyllum auritum* (see Figure 149), *Lophocolea molleri* (see Figure 150), *Plagiochila colorans* (Figure 16, Figure 94), and *Radula boryana* (see Figure 151) (Hedberg 1964). These moss mats support several tracheophytes, including *Polypodium moniliforme* var. *rigescens* (see Figure 152), *Poa schimperiana* (see Figure 153), *Cardamine obliqua* (see Figure 154), *Arabis pterosperma* (Figure 155), and juvenile *Senecio* sp. The ground layer has a nearly continuous carpet of mosses that also cover boulders and decaying stems of *Senecio/Dendrosenecio* and *Lobelia* (Figure 156). The important bryophytes in these carpets include the mosses *Brachythecium spectabile* (see Figure 141), *Breutelia diffracta* (Figure 136), *Hylocomium splendens* (common in boreal forests; Figure 157), *Pogonatum urnigerum* (Figure 158), *Syntrichia cavallii* (see Figure 159), and the liverwort *Metzgeria hamata* (Figure 143). Stones typically had a thin cover of *Homalothecium sericeum* (Figure 160). Many additional species were identified on the *Dendrosenecio*. The dominant *Sphagnum* species in the sedge (*Carex*) peatland was *S. strictum* subsp. *pappeanum* (Figure 161), with additional species on and among the grass tussocks.



Figure 146. *Antitrichia curtispindula*, the most abundant species on *Dendrosenecio* in the Afromontane. Photo by James K. Lindsey, with permission.



Figure 147. *Hypnum cupressiforme*, a worldwide species that occurs on *Dendrosenecio* in the Afromontane. Photo by Michael Lüth, with permission.



Figure 148. *Hypnum cupressiforme*, a species that occurs on *Dendrosenecio* in the Afromontane. Photo by Michael Lüth, with permission.



Figure 149. *Anastrophyllum donnianum*; *Anastrophyllum auritum* occurs on *Dendrosenecio* in the Afromontane. Photo by Michael Lüth, with permission.



Figure 150. *Lophocolea semiteres*; *Lophocolea molleri* occurs on *Dendrosenecio* in the Afromontane. Photo by David T. Holyoak, with permission.



Figure 151. *Radula bolanderi*; *R. boryana* occurs on *Dendrosenecio* in the Afromontane. Photo by Ken-ichi Ueda through Creative Commons.



Figure 152. *Polypodium glycyrrhiza* growing among mosses; *P. moniliforme* var. *rigescens* grows among mosses on *Dendrosenecio*. Photo by J. Brew, through Creative Commons.



Figure 153. *Poa annua*; *P. schimperiana* is supported by moss mats on older stems of *Dendrosenecio*. Photo by Rasbak, through Creative Commons.



Figure 154. *Cardamine* sp.; *Cardamine obliqua* grows in moss mats on *Dendrosenecio* in the Afromontane. Photo through Creative Commons.



Figure 155. *Arabis pterosperma*, a species that grows in moss mats on *Dendrosenecio* in the Afromontane. Photo by B. R. Kailash, through Creative Commons.



Figure 156. Giant lobelia (*Lobelia deckenii*) on Mt. Kenya; juvenile lobelias can establish in moss mats. Photo by Mehmet Karatay, through Creative Commons.



Figure 157. *Hylocomium splendens*, a common boreal forest species that occurs in the Afro-montane zone. Photo by Michael Lüth, with permission.



Figure 160. *Homalothecium sericeum*, a species that forms a thin layer on rocks in the Afro-alpine zones. Photo Kristian Peters, through Creative Commons.



Figure 158. *Pogonatum urnigerum*, a species that forms carpets on the forest floor in the Afro-alpine zones. Photo by Michael Lüth, with permission.



Figure 161. *Sphagnum strictum*; *S. strictum* subsp. *pappeanum* is the dominant *Sphagnum* species in the Afro-montane *Carex* peatlands. Photo by Blanka Aguero, with permission.



Figure 159. *Syntrichia ruralis*; *S. cavallii* forms carpets on the forest floor in the Afro-alpine zones. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University with permission from Russ & Karen Blisard.

## Summary

The cloud forests have dwarfed trees that are typically covered with bryophytes. Seasonal variation in rainfall in cloud forests can be low or high. **Pendent** bryophytes and **fans** effectively trap water droplets and expose maximum surface area to the light; bryophytes can intercept over 50% of the annual rainfall in cloud forests. Water conservation within the bryophytes is facilitated by elastic cell walls. **Fan** species have low light saturation and low compensation points. Because of the high moisture requirements, the bryophyte species are often restricted to these cloud forests.

Liverworts typically outnumber mosses, but mosses can contribute 54-99% of the biomass. Whereas this biomass is relatively low compared to woody biomass, the bryophytes can contribute 45% of the nutrients through nitrogen fixation and entrapment of nutrients from the air, fog, and precipitation.

Dispersal may occur by fragments, and these are more successful when landing among epiphytes. **Tall turfs** and **smooth mats** predominate in crowns. **Meteoriaceae**, **Phyllogoniaceae**, **Frullania**, and **Taxilejeunea** are the most common taxa on horizontal branches of small trees and shrubs. These are among the typically **perennial shuttles** and **perennial stayers** that dominate the life strategies. Mosses predominate on the ground, liverworts as epiphytes. Instead of the typical **Lejeunea**, **Plagiochila** predominates among the epiphytes at Monteverde, Costa Rica. Nevertheless, the **Lejeuneaceae** is common. Thallose liverworts are common on logs.

**Lowland cloud forests** are a recent discovery and have a similar high humidity to mountain cloud forests and a species richness often exceeding them. Life forms such as **tail**, **weft**, and **pendants** are nearly absent in the canopies of the lowland rainforest, but these are frequent in the lowland cloud forests. Bryophytes play a major role in the water cycle, with **Bazzania**, **Plagiochila**, **Frullania**, **Lepidozia**, and **Trichocolea** maintaining a humid environment beneath by nearly continuous dripping.

The canopy bryophytes serve to trap dust and contained nutrients, hold moisture, and in some cases provide rooting media. Their cushions hold massive amounts of water, thus maintaining a humid environment long after rainfall ceases. This minimizes fire danger. Unfortunately, their weight sometimes causes the branches to break. The bryophytes also provide habitat for a number of invertebrates.

The subalpine and alpine areas can act as islands because most of their species cannot grow at lower elevations. As one goes up into the alpine region, bryophytes are increasingly found on the soil and rocks. Glaciers and windy alpine tundra provide conditions that create moss balls that blow about on the substrate. Other moss balls are created by and carried by **solifluction** – movement by water. Members of **Grimmiaceae** are particularly common among these moss balls.

## Acknowledgments

My appreciation goes to Noris Salazar Allen for her efforts to make this chapter reliable and up-to-date. Her helpful discussions kept me going on this part of the world I know so little about.

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