

CHAPTER 8-5

TROPICS: EPIPHYTE GEOGRAPHIC DIVERSITY

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CHAPTER 8-5

TROPICS: EPIPHYTE GEOGRAPHIC DIVERSITY



Figure 1. Wet forest of Kohala Mountain, Hawaii, with abundant epiphytes. Photo by Melora Purell, through Creative Commons.

Diversity

As is generally true in the tropics, many species have been named multiple times under different names in different countries (Pócs 1984). Hence, understanding the diversity is difficult, as is understanding the bryogeography. As herbaria have become established in more tropical locations, comprehensive studies of various genera and families is untangling some of these taxonomic problems (see, for example, the revision of African **Lepidoziaceae** (Figure 2) by Pócs 1984).



Figure 2. *Bazzania hookeri* (Lepidoziaceae) from the Neotropics. Photo by Michael Lüth, with permission.

The **Pterobryaceae** (Figure 21), a family restricted to the tropics, is almost exclusively epiphytic and mostly large, including **dendroid** and **pendent** forms (Churchill & Salazar Allen 2001). Consequently, that family, along with **Neckeraceae** (Figure 3), **Sematophyllum** (Figure 10), and **Taxithelium** (Figure 4), indicates very shady, wet habitats (Pócs 1982). Typically, mosses dominate the base of the trunk, but leafy liverworts, especially the ever-present **Frullania** (Figure 48-Figure 49) and **Lejeuneaceae** (Figure 14), dominate the branches (Pócs 1982; Gradstein 1992).



Figure 3. **Neckeraceae** (*Neckera cephalonica*), a family that indicates very shady, wet habitats in the tropics. Photo by Jan-Peter Frahm, with permission.



Figure 4. **Taxithelium planum**; **Taxithelium** indicates very shady, wet habitats in the tropics. Photo by Scott Zona, with permission.

Australia

The largest number of tropical and subtropical species in the world occur as epiphytes (Ramsay *et al.* 2017). Australia is no exception, where more than 85% of the epiphytic bryophytes occur in the Wet Tropics of north Queensland (Ramsay & Cairns 2004). Of the 21 species of **Orthotrichaceae** reported by Vitt and Ramsay (1985) reported 21 species of **Orthotrichaceae** in all of Australia, but now we know there are at least 24 in tropical Queensland alone (Cairns *et al.* 2019). Many of these Queensland **Orthotrichaceae** species occur above 1200 m, including *Macromitrium dielsii*, *M. funiforme*, and *M. erythrocomum*, all endemic to the Australian Wet Tropics (Ramsay *et al.* 2017). In the **Orthotrichaceae**, 17 taxa are endemic (Ramsay *et al.* 2012). Vitt *et al.* (1995) suggested that such high-elevation taxa are often narrow endemics.

Ramsay *et al.* (1987) found seven genera of mosses that occur in all the major rainforest types in Australia (not all Australian rainforests are tropical): **Macromitrium** (Figure 5), **Racopilum** (Figure 6), **Hymenodon** (Figure 7; not in tropical Australia), **Rhizogonium** (Figure 8), **Pyrrhobryum** (Figure 9), **Sematophyllum** (Figure 10), and **Thuidium** (*Pelekium?*; Figure 11). Epiphyte succession there can occur rapidly in the right microclimate. In the crown, species change from prostrate or small upright plants to large cushion mosses such as **Leptostomum inclinans** (Figure 12; not in tropical Australia). These large mosses occur only on the upper surfaces of branches. But large cushions become unstable, falling to create new habitats. Bark furrows create niches where mosses can become established.

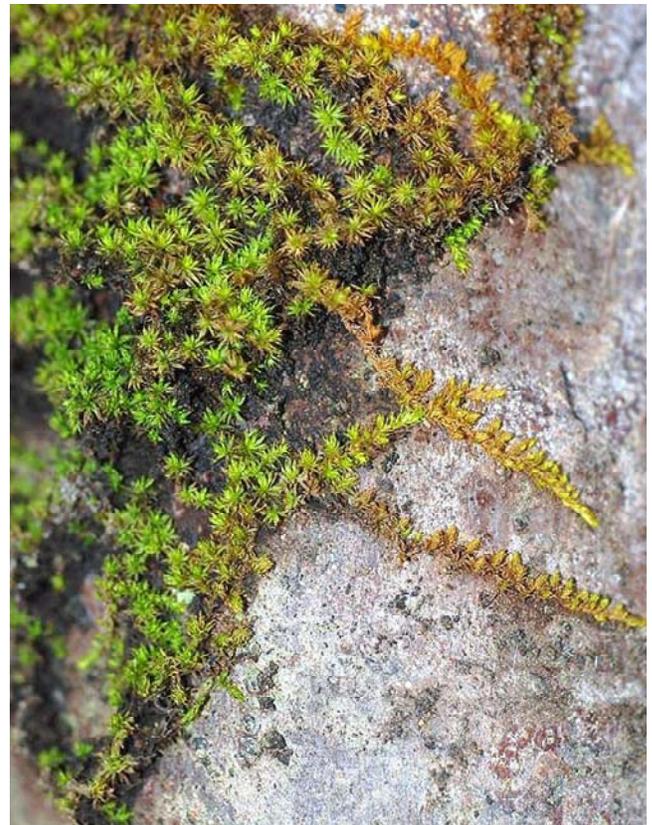


Figure 5. **Macromitrium archeri**, member of a genus of mosses that is in all major rainforests in Australia, forming mats. Photo by David Tng, with permission.



Figure 6. *Racopilum* cf. *cuspidigerum*; *Racopilum* is a genus of mosses that is in all major rainforests in Australia. Photo by Peter Woodard, through Creative Commons.



Figure 7. *Hymenodon pilifer*, member of a genus of mosses that is in all major rainforests in Australia, but this species is not in the Australian Wet Tropics. Photo by Niels Klazenga, with permission.



Figure 8. *Rhizogonium* sp., member of a genus of mosses that is in all major rainforests in Australia. Photo by Andras Keszei, with permission.



Figure 9. *Pyrrhobryum paramattense*, member of a genus of mosses that is in all major rainforests in Australia. Photo by David Tng, with permission.



Figure 10. *Sematophyllum homomallum*, representing a genus of mosses that is in all major rainforests in Australia; in the Wet Tropics. Photo by David Tng, with permission.



Figure 11. *Pelekium cf. gratum*, member of a genus of mosses that is in all major rainforests in Australia, forming **welts**. Photo by Shyamma L., through Creative Commons.



Figure 12. *Leptostomum inclinans* with capsules, a species that forms cushions in the crowns of Australian rainforests, but not in tropical rainforests of Australia. Photo by Clive Shirley, Hidden Forest, with permission.

Asia

The **Lejeuneaceae** (Figure 14, Figure 51) is the most abundant and diverse tropical family. In Asia, Gradstein (1991) found 88 species in 17 genera of **Lejeuneaceae**, subfamily **Ptychanthoideae**. This subfamily has more species but fewer genera in Asia than in the Neotropics, and the species in these two floras are very different. Asia is the center of diversity for the tribe **Ptychantheae** (Figure 13); the Neotropics, on the other hand, has its greatest number of species of **Ptychanthoideae** in the tribe **Brachiolejeuneae** (Figure 14). The two floras (Asia vs Neotropics) are distinctly different taxonomically. Gradstein considered the higher species diversity in Asia to

be related to the greater latitudinal extension of the rainforest in the Far East. In the Far East, 22% of the **Ptychanthoideae** are non-tropical species, whereas in the Neotropics the non-tropical species are less than 2%.



Figure 13. *Ptychanthus striatus*, tribe **Ptychantheae**, in Thailand. Photo by Soonthree Kornochalart, courtesy of Robert Gradstein.



Figure 14. *Drepanolejeunea hamatifolia* (**Brachiolejeuneae** in the **Lejeuneaceae**), a genus represented in the Neotropics. Photo by Barry Stewart, with permission.

Gradstein and Culmsee (2010) reported 150 bryophyte species on tree bases of only eight canopy trees in montane Sulawesi (Figure 15), Indonesia. Using only tree bases, they compared bryophyte communities based on tree diameter and bark roughness at a series of elevations. Low elevation bryophytes were characterized by the mosses in **Calymperaceae** (Figure 52-Figure 53), **Fissidentaceae** (Figure 16), **Hypopterygiaceae** (Figure 17-Figure 18), **Leucobryaceae** (Figure 19), **Meteoriaceae** (Figure 20), **Neckeraceae** (Figure 3), **Pterobryaceae** (Figure 21), and

Thuidiaceae (Figure 11), and the leafy liverworts in **Lejeuneaceae** (Figure 14, Figure 51), **Lophocoleaceae** (Figure 22), **Porellaceae** (Figure 23), and **Radulaceae** (Figure 24).



Figure 15. Tangkoko National Park, North Sulawesi, Indonesia. Photo by Lip Kee Yap, through Creative Commons.



Figure 16. *Fissidens pacificus* (Fissidentaceae), in a family that characterizes low-elevation bryophytes. Photo by Jan-Peter Frahm, with permission.



Figure 17. *Hypopterygium didictyon* (Hypopterygiaceae) on tree, in a family that characterizes low-elevation bryophytes. Photo by Juan Larrain, with permission.



Figure 18. *Hypopterygium didictyon* (Hypopterygiaceae), a dendroid moss, in a family that characterizes low-elevation bryophytes. Photo by Felipe Osorio-Zúñiga, with permission.



Figure 19. *Leucobryum boninense* (Leucobryaceae), an epiphytic species in Asia, in a family that characterizes low-elevation bryophytes. Photo by Tomio Yamaguchi, through Creative Commons.



Figure 20. *Floribundaria plumaria* (Meteoraceae), in a family that characterizes low-elevation bryophytes. Photo by Michael Lüth, with permission.



Figure 23. *Porella canariensis* (Porellaceae), a low elevation tropical genus in Sulawesi. Photo by Michael Lüth, with permission.



Figure 21. *Calypothecium duplicatum* (Pterobryaceae), a low elevation genus in Sulawesi, shown here from the Neotropics. Photo by Michael Lüth, with permission.



Figure 24. *Radula flaccida* (Radulaceae) habit with gemmae, in a family that characterizes low-elevation bryophytes. Photo by Michaela Sonnleitner, with permission.



Figure 22. *Lophocolea cf. polychaeta* (Lophocoleaceae) from the Neotropics, in a low-elevation genus in Sulawesi. Photo by Michael Lüth, with permission.

By contrast, bryophytes at higher elevations in Sulawesi (Figure 25) were predominately in the leafy liverwort families **Herbertaceae** (Figure 26), **Lepidoziaceae** (Figure 2), **Mastigophoraceae** (Figure 27-Figure 28), **Scapaniaceae** (Figure 29), **Schistochilaceae** (Figure 30), and **Trichocoleaceae** (Figure 31-Figure 32) (Gradstein & Culmsee 2010). In the submontane and lower montane, **Lejeuneaceae** (Figure 14, Figure 51) has the most species; **Plagiochilaceae** (Figure 33) is also important in the lower montane forest. In the upper montane forest that high diversity is found in the **Lepidoziaceae** (Figure 2). Rough bark is preferred by some species, but none prefer smooth bark. A few species correlate with trunk diameter, but species composition and richness do not. As elevation increases, liverwort species richness generally increases and moss richness decreases. This is a common trend in the tropics. Differences between communities on tree trunks increase with distance, reaching only about 25% similarity between Sulawesi and Borneo. At continental distances, similarity is nearly zero.



Figure 25. Montane mossy cloud forest in Sulawesi, 2300 m at summit of Mt Lokilalaki. Photo courtesy of Robbert Gradstein.



Figure 28. *Mastigophora flagellifera* (Mastigophoraceae), member of a family that predominates at high elevations in Sulawesi. Photo by Jan-Peter Frahm, with permission.



Figure 26. *Herbertus aduncus* (Herbertaceae), member of a family that predominates at high elevations in Sulawesi. Photo from Botany Website, UBC, with permission.



Figure 29. *Scapania cuspiduligera* (Scapaniaceae) with gemmae, member of a family that predominates at high elevations in Sulawesi. Photo by Michael Lüth, with permission.



Figure 27. *Mastigophora diclados* (Mastigophoraceae), member of a family that predominates at high elevations in Sulawesi. Photo by Jan-Peter Frahm, with permission.



Figure 30. *Schistochila* sp. (Schistochilaceae) in China, member of a family that predominates at high elevations in Sulawesi. Photo by Li Zhang, with permission.



Figure 31. *Trichocolea* sp. from the Neotropics, member of a family that predominates at high elevations in Sulawesi. Photo by Michael Lüth, with permission.



Figure 32. *Trichocolea* sp. from the Neotropics, member of a family that predominates at high elevations in Sulawesi. Photo by Michael Lüth, with permission.



Figure 33. *Plagiochila dendroides* (Plagiochilaceae), member of a family that predominates at high elevations in Sulawesi. Photo from Taiwan mosses color illustrations, through Creative Commons.

Ariyanti *et al.* (2008) considered that forest disturbance and land use altered for agriculture was changing the landscape in Central Sulawesi, Indonesia (Figure 34), at a drastic rate. Nevertheless, total bryophyte richness did not differ among forest types. But mosses and liverworts reacted differently. Moss richness was lowest in the cacao agroforests (Figure 34); liverwort richness was equal in all forest types. But in contrast, moss cover was unaffected, whereas liverwort cover decreased significantly in the agroforest. These differences resulted because species composition changed in the cacao agroforests. The more open agroforests were populated by drought-tolerant species. The species composition also differed markedly between large and small trees in the agroforests, but not in the natural forests. The authors suggested that these effects of tree size were due to changes in stemflow of precipitation water.



Figure 34. Cacao plantation in Sulawesi. Photo courtesy of Robbert Gradstein.

Kürshner (2008) identified six floral elements in southwest Asia, creating a heterogeneous flora. This included endemics with various origins. There is a very strong tropical influence on the bryophyte flora, particularly of the palaeotropical and Afrotropical elements. Nevertheless, nearly 10% (>95 taxa) are of xerotropical origin. Many are unique relicts of a formerly more widely distributed flora and are concentrated primarily in the escarpment mountains of the Arabian Peninsula and Socotra Island.

Magdum *et al.* (2017) collected nine species of corticolous mosses in Panhalgad in the Western Ghats, India, in different seasons, providing the first record of the mosses from the Kolhapur District. These mosses were *Pogonatum microstomum*, *Campylopus flexuosus* (Figure 35), *Leucobryum bowringii* (Figure 36), *Fissidens bryoides* (Figure 37), *Fissidens macrosporoides*, *Loiseaubryum nutans*, *Anomobryum auratum* (Figure 38), *Bryum capillare* (Figure 39), and *Bryum uliginosum* (Figure 40).



Figure 35. *Campylopus flexuosus*, an epiphyte in Panhalgad of the Western Ghats. Photo by Štěpán Koval, with permission.



Figure 38. *Anomobryum auratum* in India, an epiphyte in Panhalgad of the Western Ghats. Photo by Michael Lüth, with permission.



Figure 36. *Leucobryum bowringii*, an epiphyte in Panhalgad of the Western Ghats. Photo through Creative Commons.



Figure 39. *Bryum capillare*, an epiphyte in Panhalgad of the Western Ghats. Photo by Michael Lüth, with permission.

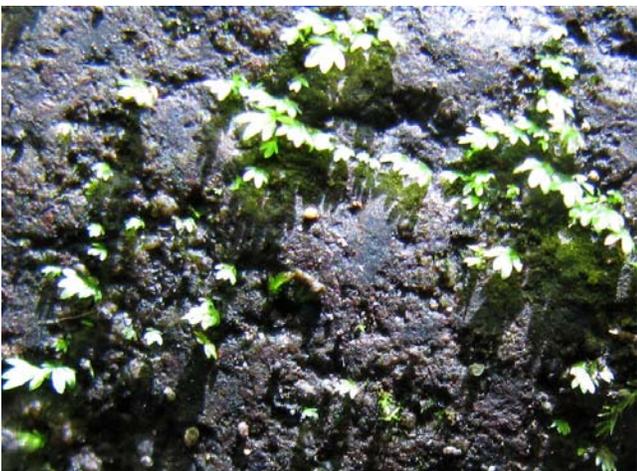


Figure 37. *Fissidens bryoides*, an epiphyte in Panhalgad of the Western Ghats. Photo by Janice Glime.

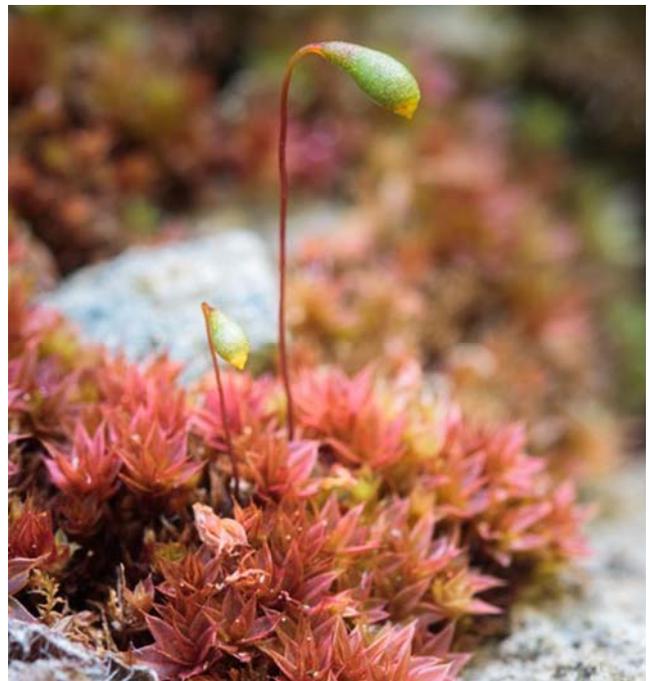


Figure 40. *Bryum uliginosum*, an epiphyte in Panhalgad of the Western Ghats. Photo by Štěpán Koval, with permission.

Kürschner (2003) conducted a phytosociological analysis in southwestern Arabia in the Asir Mountains. The characteristic species are drought-tolerant Afromontane mosses, with *Orthotrichum diaphanum* (Figure 41) and *Syntrichia laevipila* (Figure 42) being most prominent. Life forms and life strategies correlate with the environment. The *Orthotricho-Fabronietum socotranae* (see Figure 43) is a drought-tolerant association that is both xerophytic and tolerant of high light. This formation is dominated by **cushion**, **short-turf**, and **mat-forming perennial stayers** that have regular sporophyte production. The *Leptodonto* (Figure 44)-*Leucodontetum schweinfurthii* (see Figure 45) association is typical of sub-humid areas with **sciophytic** (shade-loving) vegetation. Its bryophytes are liverworts in addition to the mosses that are predominantly tails or fan-forming pleurocarpous perennial shuttle species. The mosses typically have large spores, adapting them for short-range dispersal that is either passive (with moderately low reproduction) or generative reproduction. This sciophytic group has a much higher diversity of life forms and life strategies than the xerophytic group.



Figure 41. *Orthotrichum diaphanum*, a species of dry locations in the Asir Mountains of southwestern Arabia. Photo by Michael Lüth, with permission.



Figure 42. *Syntrichia laevipila* with capsules, a prominent species in the Asir Mountains in southwestern Arabia. Photo by Michael Lüth, with permission.



Figure 43. *Fabronia* sp.; *Fabronia socotrana* is a prominent epiphytic species in the Asir Mountains in southwestern Arabia. Photo by Michael Lüth, with permission.



Figure 44. *Leptodon smithii*; the *Leptodon* community is typical of the sub-humid area in the Asir Mountains in southwestern Arabia. Photo courtesy of Jeff Duckett and Silvia Pressel.



Figure 45. *Leucodon treleasii*; the *Leptodonto-Leucodontetum schweinfurthii* community is typical of the sub-humid area of the Asir Mountains in southwestern Arabia. Photo by Jan-Peter Frahm, with permission.

Additional references that may be useful regarding tropical epiphyte diversity in the Asian region include Frahm (1990 – Malaysia), Tixier (1966 – Indonesia), Osada & Amakawa (1956 – Tsushima Islands, Japan).

African Region

Exploration of tropical African bryophytes is relatively new. Augier (1974) listed **corticolous** (growing on bark) bryophytes in the submontane forest of western Cameroon (Figure 46). Akande *et al.* (1982) examined **corticolous** bryophytes in Ibadan, Nigeria. On the 8 phorophytes on two sites they examined, they identified 20 bryophyte species. *Entodontopsis nitens* (Figure 47) is common and present on both sites. They considered *Frullania dilatata* (Figure 48-Figure 49) and *Entodontopsis tenuinervis* to be accidental species. They found the pH of the bryophytes to be similar to that of their bark substrate. In 28 comparisons, 11 bryophyte species combinations have a similarity of 50% or more. *Entodontopsis nitens* and *Pelekium gratum* (Figure 50) have a high degree of association, as do *E. nitens* and *Mastigolejeunea florea* (see Figure 51), *Entodontopsis nitens* and *Erythrodontium barteri*, *Entodontopsis nitens* and *Calymperes palisotii* (Figure 52-Figure 53), and *Erythrodontium barteri* and *M. florea*. Light is important in determining the height of the bryophytes on the trees. There seems to be no indication of preference for tree species, but the number of trees sampled was limited.



Figure 46. Menchum Falls, NW Province, Cameroon. Photo by Nick Annejohn and family, through public domain.



Figure 47. *Entodontopsis nitens*, a common epiphytic species in Ibadan, Nigeria. Photo from Wilding *et al.* 2016, with permission.



Figure 48. *Frullania dilatata* on smooth bark, a species considered to be accidental in this habitat in Ibadan, Nigeria. Photo by Bernd Haynold, through Creative Commons.

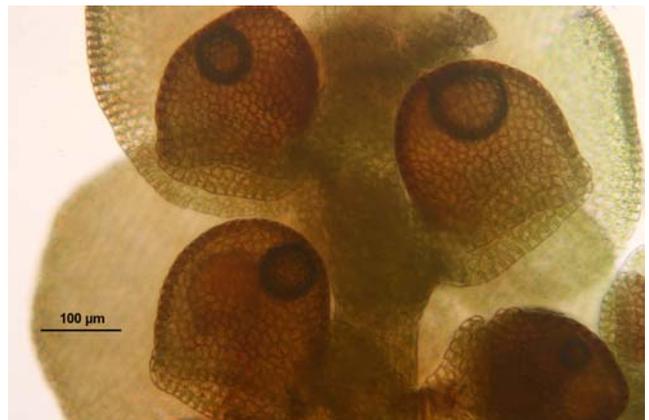


Figure 49. *Frullania dilatata* lobules. Photo by Hermann Schachner, through Creative Commons.



Figure 50. *Pelekium cf. gratum*, a species that shares a 50% similarity index with *Entodontopsis nitens*. Photo by Shyamma L., through Creative Commons.



Figure 51. *Mastigolejeunea repleta*; *M. florea* shares a 50% similarity index with *Entodontopsis nitens*. Photo by Y. M. Wei, courtesy of Robbert Gradstein.



Figure 52. *Calymperes palisotii* on bark. Photo by Scott Zona, through Creative Commons.



Figure 53. *Calymperes palisotii*, a species that shares a 50% similarity index with *Entodontopsis nitens*. Photo by Scott Zona, through Creative Commons.

Odu (1985) found a greater species richness of epiphytic bryophytes in lowland and freshwater forests than in the mangrove forests of the Niger Delta in Nigeria (Figure 54). He suggested that atmospheric humidity and air impurities may be influencing the bryophytes found. *Calymperes* (Figure 52-Figure 53, Figure 55) and *Octoblepharum* (Figure 56) occur all over the Niger Delta, whereas others are restricted to the lowland freshwater forests. Those in the mangrove forests require adaptations that permit their tolerance of salt water. Further discussion of the mangrove forest is in the subchapter Hydric and Xeric Habitats.



Figure 54. Mangrove roots in the Niger Delta, Nigeria. Photo through Creative Commons.



Figure 55. *Calymperes tenerum*, a common species in the mangrove forests of Thailand. Photo from the Auckland Museum, through Creative Commons.



Figure 56. *Octoblepharum albidum*, a common species in the mangrove forests of Thailand. Photo by M. C. Nair, K. P. Rajesh, and P. V. Madhusoodanan, through Creative Commons.

Akinsoji (1991) reported 26 tracheophytic epiphytes from a tropical rainforest in southwestern Nigeria. As noted elsewhere regarding bryophytes, bark texture makes a difference. Akinsoji found that rough bark is able to collect soil, nutrients, and moisture for epiphytic growth, all features that could benefit bryophytes as well. Trees with smooth bark lacked debris and dust accumulation or moisture retention and had only one or two epiphytes.

More recently, Ezukanma *et al.* (2019a, in review) examined corticolous bryophytes in agroforests of southwestern Nigeria. Only 14 bryophytes were identified. Seven leafy liverwort species were present, but in only two families – **Lejeuneaceae** (Figure 14, Figure 51) and **Radulaceae** (Figure 24). Similarly, seven moss species were found, but they were distributed in five families – **Calymperaceae** (Figure 52-Figure 53), **Entodontaceae** (Figure 57), **Fissidentaceae** (Figure 16), **Hypnaceae** (Figure 58), and **Leucomiaceae** (Figure 59) with one species each, and **Plagiotheciaceae** (Figure 60) with two species. Cashew forests (Figure 61) had eight species, kola (Figure 62) had seven, and cocoa (Figure 63) had six. Only the liverworts *Thysananthus nigrus* (see Figure 64) and *Mastigolejeunea auriculata* (Figure 65) were found in all three forest types. *Entodontopsis nitens* (Figure 47) was the most frequent species, occurring in the kola forest and having a frequency of 27.6%. Next in frequency were *Mastigolejeunea auriculata* (23.65%) and *Entodontopsis nitens* (18.92%) in the cocoa agroforest.



Figure 57. *Entodon* sp. (**Entodontaceae**); this family is frequent on trees in the agroforests of Nigeria. Photo by Cindy Hough, through Creative Commons.



Figure 58. *Chryso-hypnum diminutivum* (**Hypnaceae**) from the Neotropics; this family is frequent on trees in the agroforests of Nigeria. Photo by Michael Lüth, with permission.



Figure 59. *Leucomium strumosum* (**Leucomiaceae**), a family that occurs on trees in agroforests in Nigeria. Photo by Claudio Delgadillo Moya, with permission.



Figure 60. *Plagiothecium undulatum* (**Plagiotheciaceae**), a family that occurs on trees in agroforests in Nigeria. Photo from Proyecto Musgo, through Creative Commons.



Figure 61. Cashew trees in Brazil. Photo by Ben Tavener, through Creative Commons.



Figure 64. *Thysananthus repletus* (= *Mastigolejeunea repleta*) from China; *Thysananthus nigrus* is present in all three forest types in southwestern Nigeria. Photo by Y. M. Wei, courtesy of Robbert Gradstein.



Figure 62. Kola (*Cola nitida*) plantation in Malaysia. Photo by Michael Hermann, through Creative Commons.



Figure 65. *Mastigolejeunea auriculata*, a liverwort found in all three of these types of agroforests in Nigeria. Photo by Paul Davison, with permission.



Figure 63. *Cacao* plantation in Cameroon. Photo by Barada-Nikto, through Creative Commons.

Ezukanma *et al.* (2019b, in press) also assessed the epiphytic bryophytes in the urban agroforests of Ibadan, Nigeria. They studied the corticolous bryophytes up to 2m on the phorophytes of 30 trees in *Citrus* (Figure 66) and *Mangifera* (Figure 67) plantations. Here they identified 19 species, 13 leafy liverworts and 6 mosses. Five species

were in both forest types. The mango forests had higher bryophyte diversity and more even distribution of species. The researchers suggested that this might relate to the frequent pruning of the crowns in the mango agroforest. The moss *Calymperes palisotii* (Figure 52-Figure 53) was the most abundant species, especially in the *Citrus* plantations. Corticolous species were generally absent at the base of the phorophyte, occurring with a mean height of 1.39 m (range of 1.17-1.60) on *Mangifera* and 1.11 m (range of 0.48-1.8) on *Citrus*. The moss *Rhacopilopsis trinitensis* (Figure 68) had the highest mean height, extending up to 1.8 m. *Ceratolejeunea beninensis* (see Figure 80-Figure 81) was second in abundance, likewise in the *Citrus* forest. As in the cashew, kola, and cacao forests, *Mastigolejeunea auriculata* (Figure 65; in the *Mangifera* forests) and *Entodontopsis nitens* (in the *Citrus* forests; Figure 47) were species with high frequencies. There were 13 liverwort species, 12 in *Lejeuneaceae* (Figure 14, Figure 51) and 1 in *Jubulaceae* (Figure 69). The six moss species were in four families, with 3 in *Stereophyllaceae* (Figure 47) and 1 each in *Calymperaceae* (Figure 52-Figure 55, Figure 82), *Hypnaceae* (Figure 58), and *Leucomiaceae* (Figure 59). Twelve species occurred in both forest types.



Figure 68. *Rhacopilopsis trinitensis*, the species that reaches the greatest heights on *Mangifera* and *Citrus* phorophytes. Photo by Juan David Parra, through Creative Commons.



Figure 66. *Citrus* (orange) plantation. Photo by Hans Braxmeier, through Creative Commons.



Figure 69. *Jubula hutchinsiae* (*Jubulaceae*), a family that occurs on *Citrus* trees in Nigeria. Photo by Jonathan Sleath, with permission.



Figure 67. *Mangifera* (mango) picking, Réunion Island. Photo by B. Navez, through Creative Commons.

Biedinger and Fischer (1996) compared the diversity of epiphytic tracheophytes, bryophytes, and lichens in the montane rainforests and dry forests of Rwanda and Zaïre. They identified 167 species of tracheophytes, 45 of mosses, 82 of liverworts, 78 corticolous lichens, and 57 epiphyllous lichens. While the numbers may be replaced with more recent studies, the proportions are likely to be more accurate.

In South Africa, Dilg and Frahm (1997) explored the epiphytic flora in southern Drakensberg. They found only 38 species, 12 of which were liverworts and 26 were mosses. The *Podocarpus* (Figure 70) forest provides a habitat with high humidity and fire protection; it has the highest number of bryophyte species.



Figure 70. *Podocarpus cunninghamii* trunk with epiphytic bryophytes. Photo by Rudolph89, through Creative Commons.

In addition to these studies, Frahm (1994) reported on ecology of epiphytic bryophytes on Mt. Kahuzi in Zaire. Additional references that may be useful regarding epiphytic diversity in the African tropics include Kürschner (1984 – Saudi Arabia; 1990a – moss societies on Mt. Kinabalu, North Borneo; 1995 – Eastern Congo), Pócs & Szabo (1993 – Mt Elgon, Kenya), Gill & Onyibe (1986 – phytosociology of epiphytes on oil palm in Benin City, Nigeria), Ezukanma (2012 – agroecological corticolous species in southwestern Nigeria). A number of references by Ah-Peng and coworkers will be addressed in other appropriate subchapters of this chapter.

Neotropics

The Neotropics are rich in bryophyte species. In a six-hectare upper montane *Quercus* forest (Figure 71) in Costa Rica, Holz *et al.* (2002) found 206 species, comprised of 100 moss species, 105 liverwort species, and 1 hornwort. They found three main groups of microhabitats in the forest: forest floor, including the tree base; the **phyllosphere** (space surrounding the leaf); other epiphytic habitats. Life forms differ with the humidity and light levels, as discussed in earlier subchapters. Van Reenen (1987) noted that the epiphytic cover of bryophytes in the

Andes of Colombia increases with altitude. Wolf (2003) found that the greatest liverwort diversity occurs in the transition zone where two distinct floras are in contact.

Sillett *et al.* (1995) examined the bryophyte communities of six *Ficus tuerckheimii* (Figure 72) trees in a Costa Rican lower montane wet forest. They found 109 species on the three intact forest trees and only 76 on the three isolated trees. Of these, 52 species occurred only on the intact forest trees; 18 were only on the isolated trees. Species richness, cover, and frequency of **pendants, tall turfs, tails, and fans** were significantly higher on the trees in the intact forest. Isolated trees had higher rates of evaporation from the inner crowns, more macrolichen cover, and higher levels of sunlight compared to the intact forest trees. Ordination analysis revealed a desiccation gradient ranging from the sheltered intact forest trees to the exposed isolated trees.

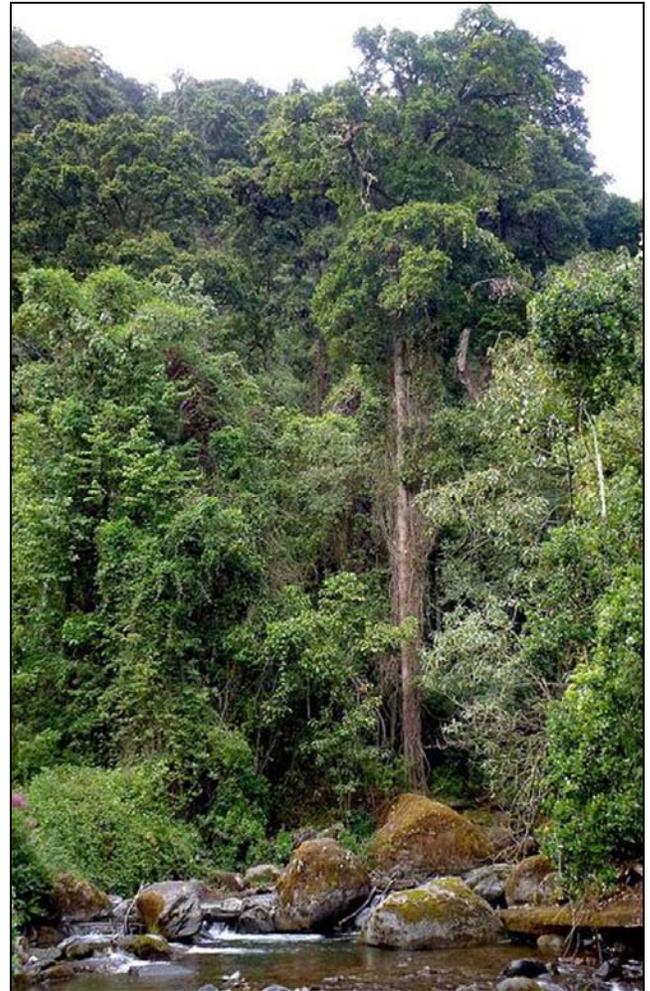


Figure 71. *Quercus copeyensis*; in Costa Rica; the *Quercus* forest is home to more than 200 bryophyte species. Photo through Creative Commons.

Delia *et al.* (2015) reported 34 epiphytic moss species from El Zancudo, Honduras. They concluded that the montane rainforest that borders Honduras and El Salvador is bryologically diverse, but is largely unexplored.



Figure 72. *Ficus tuerckheimii*, Costa Rica. Photo by Dick Culbert, with online permission.

Richards (1954) considered the Moraballi Creek in Co-operative Republic of Guyana to have four main bryophyte **synusiae** (structural units of major ecological community characterized by relative uniformity of life form or height): high epiphytes, shade epiphytes, epiphylls, dead wood communities. Although these communities are very distinct in both structure and composition, several species, such as *Calymperes lonchophyllum* (see Figure 52-Figure 55) and *Octoblepharum albidum* (Figure 56), occur in all but the epiphyllous synusiae. The epiphyllous species are highly specialized, as will be discussed in a later subchapter. Korpelainen and Salazar Allen (1999) demonstrated genetic variation in three species of *Octoblepharum*, perhaps explaining their ability to occur in multiple community types. Richards (1954) found that Moraballi Creek synusiae differ in their growth (and life) forms of the species, creating differences in community structure. This results in differences between the very dry habitat of the high epiphyte synusiae and the more moderated shade epiphyte synusiae. The latter is characterized by freely projecting or dangling shoots and large thin-walled cells. The Moraballi Creek rainforest bryophyte synusiae differ markedly from those of temperate forests by the absence of ground-dwelling bryophyte synusiae, the presence of epiphyllous bryophytes, and the preponderance of liverworts, especially **Lejeuneaceae** (Figure 14, Figure 51).

In a semi-deciduous tropical forest of southern Guyana (Figure 73), Sipman (1997) found 100 species of lichens, with 8 out of 14 trees lacking lichens on leaves completely, whereas 3 had 34-46 taxa! Instead, the foliicolous lichens are most likely to grow close to the ground. In contrast to the 34-46 species of lichens on a single tree, they were able to find only 18 bryophyte taxa on canopy leaves.



Figure 73. Guyana waterfall and forest near Paramakatoi. Photo by Kevin Gabbert, through public domain.

Large trees support more species than small ones, with a typical logistic curve of increasing numbers of species related to both plot size and tree **DBH** (diameter at breast height) (Figure 74) (Gradstein *et al.* 1996).

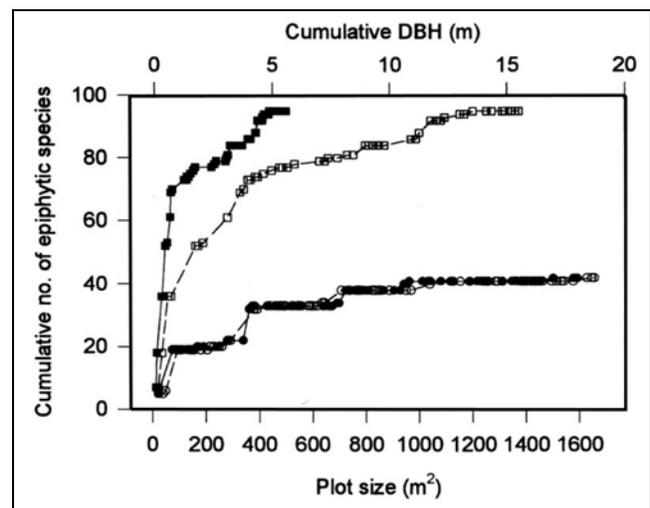


Figure 74. Relationship between number of epiphyte species and plot size and tree DBH in Mexico. Species-area curves are **solid** symbols, cumulative number of species vs cumulative diameter of all trees sampled are **open** symbols. **Squares** represent humid montane cloud forest; **circles** represent humid lowland forest. Modified from Gradstein *et al.* 1996.

Gradstein *et al.* (1990) investigated the epiphytic bryophytes in the dry evergreen forest and mixed forest of the Guianas (Figure 73) using mountaineering techniques. They discovered that the lowland rainforest is not as poor in species as had been thought, once the bryophytes of the canopy are included in the exploration. More than 50% of the local species may occur in the canopy. The mixed forest has the most species. A single tree can support up to 67 species, with 50 species being an average number. The 28 trees sampled supported 154 species of bryophytes. Only a few trees are needed to find most of the species of the local area. Most of the species in this area are rather common, with 80% being widespread in the Neotropics.

In the Colombian Amazon (Figure 75), Campos *et al.* (2015) established 384 plots on 64 trees in four localities.

These exhibited 160 species of epiphytic bryophytes, with a preponderance of liverworts (116 species; 44 species of mosses). These included collections from the base to the outer canopy, including 16 trees at each locality. The highest representation of families (Figure 76) included the leafy liverworts **Lejeuneaceae** (Figure 14, Figure 51) (55%) and **Lepidoziaceae** (Figure 2) (8%), and the mosses **Calymperaceae** (Figure 52-Figure 55) (10%), **Octoblepharaceae** (Figure 56) (6%), and **Sematophyllaceae** (Figure 10) (5%). The most common genera were members of **Lejeuneaceae** – *Cheilolejeunea* (Figure 77) (11%), *Pycnolejeunea* (Figure 78) (8%), *Archilejeunea* (Figure 79) (8%), and *Ceratolejeunea* (Figure 80-Figure 81) (8%) – and the moss *Syrrhopodon* (**Calymperaceae**; Figure 82) (7%).



Figure 75. Lowland rainforest in Colombian Amazon. Photo by Laura Campos, courtesy of Robbert Gradstein.



Figure 77. *Cheilolejeunea fragrantissima*, in one of the most common genera of **Lejeuneaceae** in the Colombian Amazon. Photo by Scott Zona, with permission.



Figure 78. *Pycnolejeunea pilifera*, member of a common leafy liverwort genus in the mangrove forests of Thailand. Photo by MNHN – Paris, Muséum National d'Histoire Naturelle, MB, through Creative Commons.

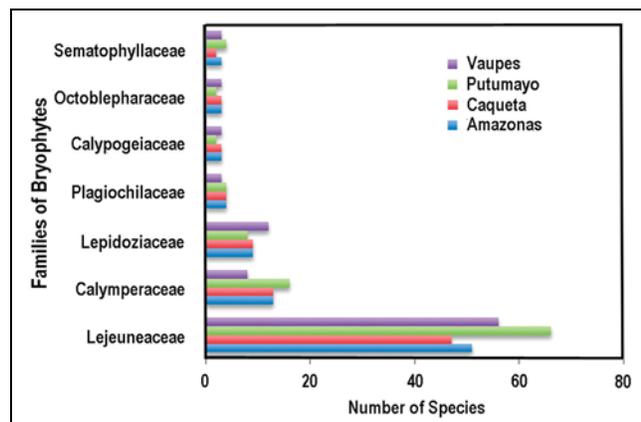


Figure 76. Species richness per family in 4 locations of Colombian Amazon. Modified from Campos *et al.* 2015.

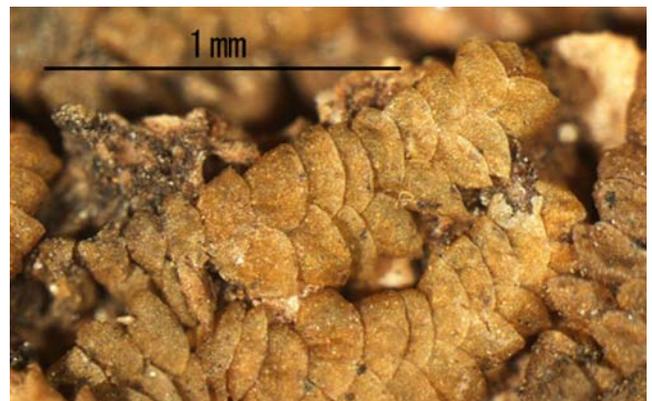


Figure 79. *Archilejeunea japonica*, in one of the most common genera of **Lejeuneaceae** in the Colombian Amazon. Photo from Digital Museum, Hiroshima University, with permission.



Figure 80. *Ceratolejeunea cubensis*, in one of the most common genera of *Lejeuneaceae* in the Colombian Amazon. Photo by Scott Zona, with permission.

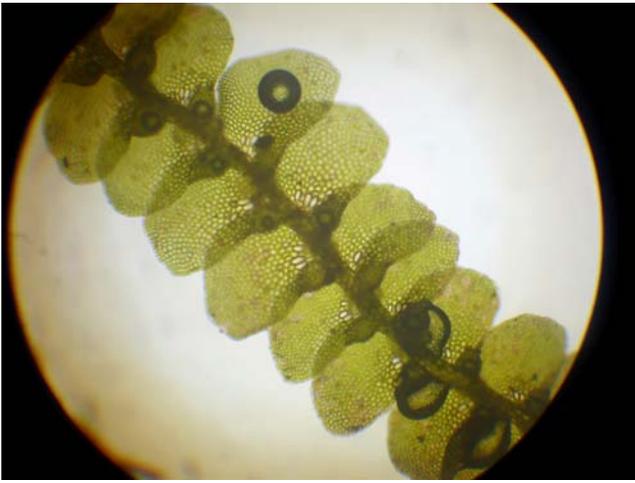


Figure 81. *Ceratolejeunea cubensis*, showing lobules at leaf insertions. Photo by Scott Zona, with permission.

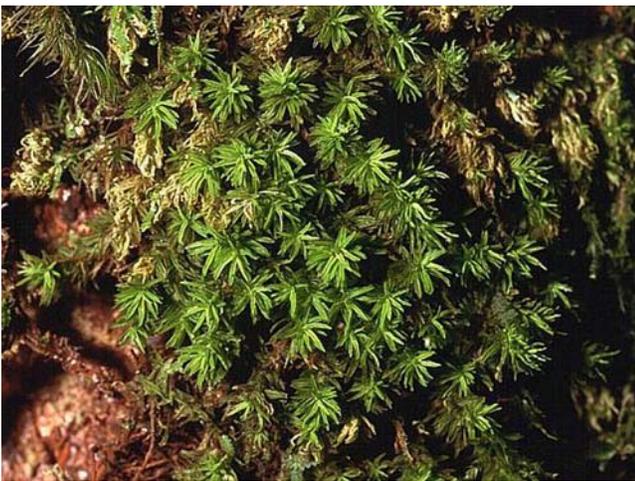


Figure 82. *Syrrhopodon gaudichaudii*, in one of the most common genera in the Colombian Amazon. Photo from Michael Lüth, with permission

Wolf *et al.* (2003) found that the richness per surface area decreases significantly with branch diameter (Figure

83) in the upper montane rainforest of the Cordillera in Colombia. Diversity is highest when the standing crop is at intermediate levels and is negatively correlated with the area of the largest species. On the other hand, **evenness** (similarity of frequencies of different units making up population or sample) is less on older branches. The inner canopy species have the smallest niche widths. When only branch segments are sampled, the vegetation is highly variable, whereas that on whole trees is more uniform. The species follow a species area curve that approaches a flat line after sampling only four trees. The liverworts have the greatest richness in the contact transition zone between two distinct floras. Wolf and coworkers suggested that the arrival time of aggressive competitors such as those that form large patches may be "crucial." Many accidental species maintain a high richness and suggest that dispersal of propagules is important in creating richness.

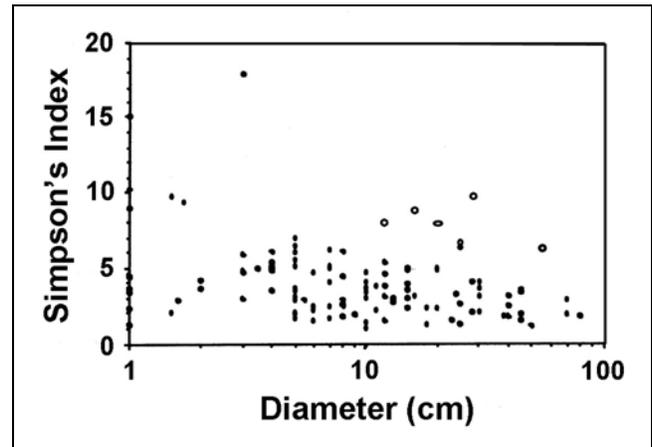


Figure 83. Branch or trunk diameter in the canopy of the upper montane rainforest and Simpson's index of diversity. **Open circles** indicate a group of seven samples that do not adhere to increasing dominance with diameter. Modified from Wolf *et al.* 2003.

In flooded (Figure 84) and "tierra firme" (Figure 85) forests of the Colombian Amazon, Benavides *et al.* (2004) found 109 bryophyte species on 14 0.2-ha plots. Mosses and liverworts had opposite responses to moisture, with many more liverworts than moss species in the tierra firme, but total richness (mosses + liverworts) differed little between the flooded and non-flooded habitats (Figure 86). The use of the habitat differed between the two forest types, with differences in humidity being the major factor in determining bryophyte communities. Nevertheless, soil was a little-used substrate for both groups in both habitats (Figure 86). Epiphyll species assemblages (*e.g.* Figure 87) were not strongly affected by floodplain vs tierra firme. Life forms differed between the two habitat types, with more **fan** and **mat** bryophyte species in the floodplains, and more epiphytic liverworts (hence, almost no **wefts**) in the tierra firme forest (Figure 88).



Figure 84. Várzea forest with açai palms, the flooded forest of the Amazon. Photo by Frank Krämer through Creative Commons.



Figure 85. Amazon rainforest, Brazil. Photo by Phil P. Harris, through Creative Commons.

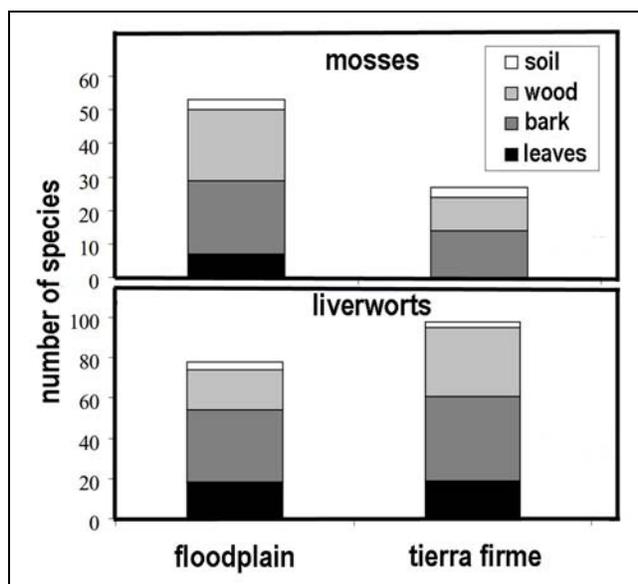


Figure 86. Distribution of bryophyte substrates in terra firme and floodplain in the Aracuara region of Colombia. Modified from Benavides *et al.* 2004.



Figure 87. Epiphylls on leaf. Photo by Jessica M. Budke, with permission.

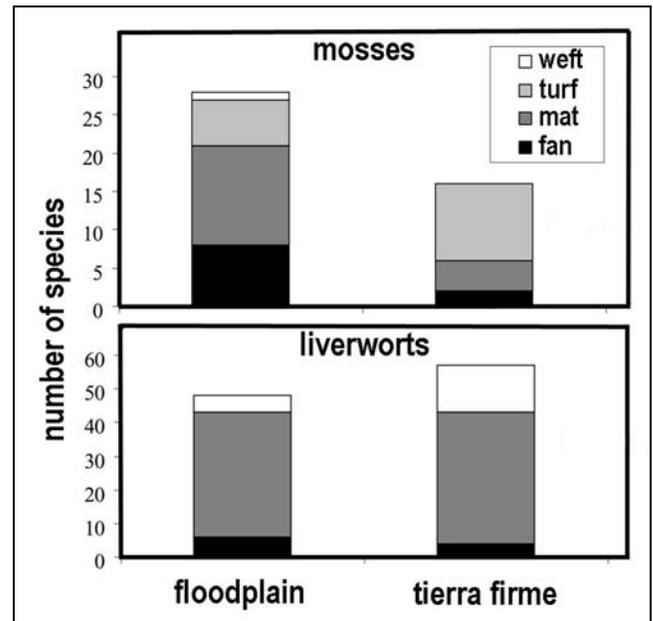


Figure 88. Distribution of bryophyte life forms in terra firme and floodplain in the Aracuara region of Colombia. Modified from Benavides *et al.* 2004.

Oliveira and ter Steege (2013) determined that epiphytic bryophytes in the terra firme forests of the Amazon Basin exhibited a typical species abundance distribution (Figure 89).

Kelly *et al.* (2004) described the epiphytic communities of a montane rainforest in the Venezuelan Andes (Figure 90). They surveyed 20 trees, all in a site of only 1.5 ha at 2600 m asl. The non-tracheophyte epiphytes were recorded in 95 sample plots and yielded 22 moss and 66 liverwort species, as well as 46 species of macrolichens. Few of the bryophytes in these communities are **endemic** (native distribution restricted to a certain country or area), although they are mostly restricted to the Neotropics. The dominant bryophyte on the lower trunks is *Syrrhopodon gaudichaudii* (Figure 91), along with the fern *Elaphoglossum hoffmannii* (Figure 92). The intermediate levels are dominated by the leafy liverwort *Omphalanthus filiformis* (Lejeuneaceae; Figure 93) and the orchid *Maxillaria miniata* (see Figure 94). The upper crowns are dominated by the lichens *Usnea* (Figure 95) and *Parmotrema* (Figure 96). Diversity of non-tracheophytes is

greatest in the upper crowns; tracheophyte diversity is greatest at the intermediate levels. As noted in a number of other studies cited herein, similarity is low among plots of the same community, but between-tree and between-stand similarities are relatively high.

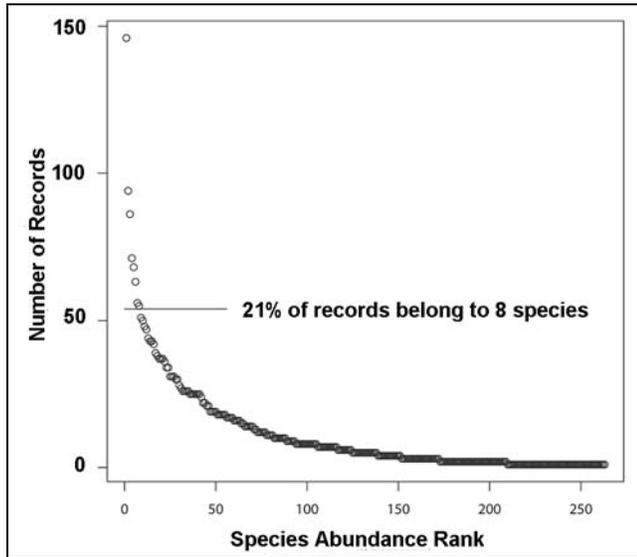


Figure 89. Species abundance distribution based on the complete dataset. Axis x is species ranked by number of records. Modified from Mota de Oliveira and ter Steege 2013.



Figure 90. Montane rainforest in Venezuelan Andes. Photo by Jorge Paparoni, through Creative Commons.

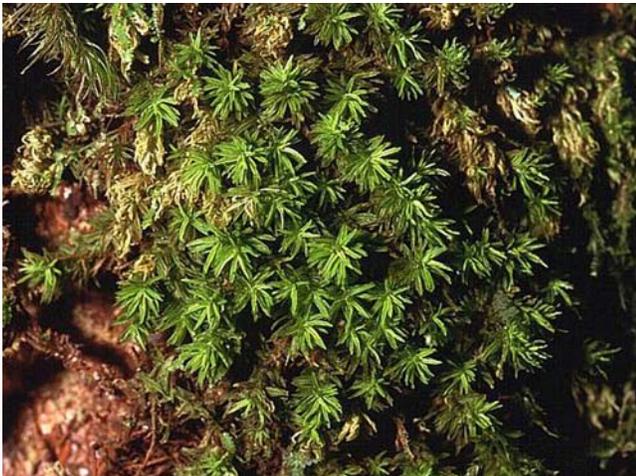


Figure 91. *Syrrhopodon gaudichaudii*, the dominant bryophyte on the lower trunks in a montane rainforest in the Venezuelan Andes. Photo by Michael Lüth, with permission.



Figure 92. *Elaphoglossum hoffmannii*, a fern that typically accompanies *Syrrhopodon gaudichaudii* on lower trunks in montane rainforests in the Venezuelan Andes. Photo by Robbin Moran, with permission.



Figure 93. *Omphalanthus filiformis*, a dominant leafy liverwort at intermediate levels of tree trunks in a montane rainforest in the Venezuelan Andes. Photo by Michael Lüth, with permission.



Figure 94. *Maxillaria molitor*; *Maxillaria miniata* is the dominant flowering plant species, along with the leafy liverwort *Omphalanthus filiformis*, at intermediate levels in the montane rainforest of the Venezuelan Andes. Photo from Megadiverso, through Creative Commons.



Figure 95. *Usnea* from Cumbre Vieja, Canary Islands. Members of this genus dominate the crowns of the montane rainforest in the Venezuelan Andes. Photo by Fährtenleser, through Creative Commons.



Figure 96. *Parmotrema perlatum*. Members of this lichen genus dominate the crowns of the montane rainforest in the Venezuelan Andes. Photo by Alan J. Silverside, with permission.

By comparison, Costa (1999) studied the epiphytic bryophyte diversity of both primary and secondary lowland rainforests in southeastern Brazil, a subtropical region. Unlike many earlier studies, hers included the forest canopy. She found 75 bryophyte species, 39 mosses and 36 liverworts. The highest species richness is exhibited by the mature secondary hillside rainforest, with 43 species. The highly degraded hillside rainforest has the lowest diversity, with only 6 species, and the hillside secondary rainforest with only 5 species. As in so many other studies, the leafy liverwort family **Lejeuneaceae** (Figure 14, Figure 51) is the "most important" with 23 species (30 %) and the moss family **Sematophyllaceae** (Figure 10) with 7 species (10%). Demonstrating the importance of the canopy species in understanding species diversity, Costa found that 45% of the bryophyte species occurred exclusively in the canopy. The most common life form is the **mat**, describing 45% of the species. Forest destruction is more detrimental to shade species than to sun species. Even after 20-45 years, many bryophytes had not returned, but after 80 years the communities were similar to those of primary forest.

In 2017, Gradstein and Benitez added 15 liverwort species to the known flora of Ecuador. They furthermore described two species new to science.

One might not think of looking in a savannah for epiphytes because of the high exposure to sunlight and low moisture. Nevertheless, bryophytic epiphytes do grow there in an Amazonian savanna in Brazil (Figure 97). Gottsberger and Morawetz (1993) found that lichens dominate on the young trees, typically becoming less abundant as the tree ages. Bryophytes are most abundant on older trees and seem to suppress the lichen growth.



Figure 97. Amazonian savanna (Cerrado) in Brazil. Photo by Paulo Q Maio, through Creative Commons.

Additional references that may be useful regarding tropical diversity in the Neotropical epiphytes include Chung (1996 – Panama), Wolf (1993 – Colombia); Jovet-Ast (1949 – groupings of epiphytic mosses in the French West Indies); Frahm (1987a, b – composition of moss vegetation in Peruvian rainforests); Frahm (1987a, c – composition of moss vegetation in Peruvian rainforests).

Summary

Full understanding of the bryogeography of epiphytes is still hampered by our need for comprehensive systematic studies that identify synonyms and demonstrated genetic relatedness.

In Australian tropical rainforests, epiphyte succession is usually rapid, with seven genera occurring in all the major rainforest types (including non-tropical ones): **Macromitrium**, **Racopilum**, **Hymenodon**, **Pyrrhobryum**, **Rhizogonium**, **Sematophyllum**, and **Thuidium (Pelekium?)**.

In general, the mosses in **Pterobryaceae** and **Neckeraceae** occur as epiphytes throughout the tropics, along with **Sematophyllum** and **Taxithelium**. The liverworts **Frullania** and **Lejeuneaceae** dominate the branches. The tribe **Ptychantheae** is predominant among Asian **Lejeuneaceae**, whereas the tribe **Brachiolejeuneae** predominates in the Neotropics. In Indonesia, the characteristic low-elevation tree-base moss families are **Calymperaceae**, **Fissidentaceae**, **Hypopterygiaceae**, **Leucobryaceae**, **Meteoriaceae**, **Neckeraceae**, **Pterobryaceae**, and **Thuidiaceae**, and the leafy liverwort families **Lejeuneaceae**, **Lophocoleaceae**, **Porellaceae**, and **Radulaceae**. By

contrast the higher elevations have mostly leafy liverworts in **Herbertaceae**, **Lepidoziaceae**, **Mastigophoraceae**, **Scapaniaceae**, **Schistochilaceae**, and **Trichocoleaceae**. In Africa, **Calymperes** and **Octoblepharum** species occur all over the Niger Delta, whereas in agroforests Ezukanma *et al.* (2019 in review) found only **Lejeuneaceae** and **Radulaceae** among the liverworts, but found five families of mosses. African studies are limited and promise many more species on future expeditions. Bryophyte diversity in the Neotropics is particularly rich and increases with altitude. Intact forests typically have **pendants, tall turfs, tails, and fans**. **Calymperes lonchophyllum** and **Octoblepharum albidum** are common in all communities except as epiphylls. Larger trees support more species than do small ones by providing more niches. For the Neotropics in general, the **Lejeuneaceae** are again the most species-rich family; the most highly represented moss families are **Calymperaceae**, **Octoblepharaceae**, and **Sematophyllaceae**. Fewer endemics occur here compared to those of the flowering plants, and as more systematic studies occur, the number is diminishing.

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. Andi Cairns helped me to resolve some of the apparent conflicts in the Australian literature and bring information up to date.

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