CHAPTER 8-7
TROPICS: LOWLAND RAINFORESTS

TABLE OF CONTENTS

Lowland Rainforests ................................................................................................................................. 8-7-2
Amazonia Lowlands ............................................................................................................................... 8-7-7
Terra Firme ........................................................................................................................................... 8-7-11
  Dense Forest ................................................................................................................................. 8-7-14
  Open Forest without Palms ......................................................................................................... 8-7-14
  Open Forest with Palms .............................................................................................................. 8-7-14
  Liana Forest ............................................................................................................................... 8-7-16
  Dry Forest .................................................................................................................................. 8-7-16
  Restinga ...................................................................................................................................... 8-7-16
  Caatinga ..................................................................................................................................... 8-7-20
Savannah Vegetation ............................................................................................................................. 8-7-22
South Atlantic Islands .......................................................................................................................... 8-7-23
Summary ............................................................................................................................................... 8-7-25
Acknowledgments ............................................................................................................................... 8-7-25
Literature Cited ..................................................................................................................................... 8-7-25
CHAPTER 8-7
TROPICS: LOWLAND RAINFORESTS

Figure 1. Amazon rainforest near Manaus, Brazil aerial view. Photo by Neil Palmer, through Creative Commons.

**Lowland Rainforests**

Undeveloped areas of the humid tropics are characterized by tropical rainforest. As shown by Frahm and Gradstein (1991) there are five tropical rainforest belts and their elevational limits are higher on continents than on islands due to the "mass elevation effect." On the continent the forest line is normally ca. 4,000 m asl but has been lowered to ca. 3,200 m in many places due to human impact, reaching as high as 1,500 m asl near the Equator and up to 700 m at the upper and lower tropical borders (Pócs 1982). The area covered, originally at 12% of Earth's surface, is estimated at only about 5% of Earth's surface now (Butler 2006), and it is still rapidly diminishing.

The lowland tropical rainforests (up to 500 m asl) are characterized by their great height, up to 60 m tall (Pócs 1982), with many evergreen species, particularly in areas that have a dry season. With annual rainfall greater than 1500 mm and an average temperature of 20-27°C (Pócs 1982), with little seasonal change, the trees flourish and the canopy is dense. Thus, the forest floor is characterized by limited light, even for a bryophyte. This unfavorable light level, in particular in the lowland rainforest, is made more unfavorable to bryophytes by the heavy leaf litter (Gradstein 1992; Delgadillo & Cardenas 2002). The result is that the tropical rainforest floor has lower moss species diversity than in temperate regions (Hallingbäck 1992).

Richards (1954) was among the first to attempt a description of these lowland forests. He recognized four main bryophyte synusiae in the Moraballi Creek rainforest of British Guiana: high epiphytes, shade epiphytes, epiphyllae, dead wood, noting their distinctness in both structure and floristic composition. Nevertheless, few species are very frequent. Exceptions to this are *Calypnepes lonchophyllum* (see Figure 2) and *Octoblepharum albidum* (Figure 3); with the exception of the epiphyllous habitat, these two species occur in all the other synusiae. The epiphylls are almost entirely highly specialized species exclusive to the phyllosphere. Richards noted that growth/life forms differ among the synusiae. He further remarked on the absence of bryophyte synusiae on the ground at Moraballi Creek, the presence of an epiphyllous community, and the distinct dominance of liverworts, especially *Lejeuneaceae* (Figure 62-Figure 64). Although he noted that the forest was probably poorer in species than many temperate forests, his basis for this statement did not include knowledge of the diverse canopy bryophytes. Richards further claimed that these
comparisons would likewise apply to the lowland rainforests in Africa or the Indo-Malayan region. They would not, however, apply to the montane forests.

Figure 2. *Calymperes* sp.; *C. lonchophyllum* is a species found in all synusiae except epiphyllous at Moraballi Creek rainforest of British Guiana. Photo by Niels Klazenga, with permission.

Figure 3. *Octoblepharum albidum*, a species found in all synusiae except epiphyllous at Moraballi Creek rainforest of British Guiana. Photo by Portioid, through Creative Commons.

In lower elevations, below 1500 m, the forest typically has a complex canopy. Trees have a variety of heights, some of which may reach 50-60 m tall. Levels in these forests can be classified as emergent, canopy, understory, and forest floor. This provides a variety of conditions for bryophytes, and often the within-tree diversity is greater than that between trees.

The canopy buffers and protects the lower strata of the forest. It reduces turbulence by absorbing wind energy; in one Costa Rican study, canopy (10 m) wind speeds were 11.3 m sec\(^{-1}\) while those on the forest floor (2 m) were 4.0 m sec\(^{-1}\) (Lawton 1980). The canopy modifies the temperature by absorbing heat and radiation (Nadkarni 1994). Its leaf surfaces absorb CO\(_2\) and emit water vapor.

It modifies the light quality by absorbing red and transmitting green, and it can reduce light intensity by as much as 98% before it reaches the forest floor (Cachan 1963). But for the canopy dwellers, being near the upper surface means intense sunlight, more temperature and humidity extremes, higher water stress, and a nutrient supply dependent on that in rainfall (Nadkarni 1994).

Although irradiation and desiccation are high in the canopy, the inner canopy affords some protection (Gradstein & Pócs 1989). Hence, dense mats or cushions are able to develop here, including the liverwort *Frullania* (Figure 4) and the moss *Macromitrium* (Figure 5). When it is very humid, *pendent* bryophytes and epiphyllous lichens and liverworts become established. In Bolivia (Figure 6), Acebey *et al.* (2003) found that rough mats appeared almost exclusively in the canopy, apparently requiring the high light intensity. This same restriction of rough mats to the high light zone of the upper canopy occurs in Guyana (Cornelissen & ter Steege 1989), and undoubtedly other areas of the tropics.

Figure 4. *Frullania* sp. in the Neotropics, where it can form dense cushions in the lowland rainforest inner canopy. Photo by Michael Lüth, with permission.

Figure 5. *Macromitrium* sp. (*Orthotrichaceae*) in the Neotropics, where it can form dense cushions in the lowland rainforest inner canopy. Photo by Michael Lüth, with permission.
Costa (1999) studied the rainforest epiphytes in six forest types in the lowland rainforest of Rio de Janeiro, southeastern Brazil (Figure 7). She found 39 moss species and 36 liverwort species. The highest species richness occurred in the mature secondary hillside rainforest (43 species) whereas the lowest diversity was in the highly degraded hillside rainforest (6 species) and hillside secondary rainforest (5 species). As in Guyana (Cornelissen & Gradstein 1990), Costa found that the Lejeuneaceae (Figure 62-Figure 64) was one of the most important families (30% of species), with the moss family Sematophyllaceae (Figure 41) being second with 7 species (10%). In this case, 45% of the species were exclusively in the canopy. Mats were the most common life form of the six found there. Shade epiphytes are more susceptible to deforestation damage than are sun epiphytes, with many species not returning after 20-45 years. However, after 80 years, the bryophyte flora has recovered to that of the primary forest.

As expected, the lowest diversity was in the Lowland Atlantic Rainforest; the highest was in the Montane Atlantic Rainforest. The moss family Sematophyllaceae (Figure 41) had 19% of the taxa in the lowland forest, Meteoriaceae (Figure 8) had 10% in the montane forests, and Dicranaceae (Figure 9) had 18% in the upper montane forests. Taxa with wide distributions in the Neotropics accounted for 40% of the total taxa and were important in all the forests. The taxa restricted to Brazil were second most important in the upper montane and montane forests.

In Australian rainforests (Figure 10), liverworts usually dominate the bryophytes in lowland vine forests (Ramsay et al. 1987). Mosses are the more common bryophytes in wet higher altitudes or valley forests. Such bryophytes as Chandonanthus (Figure 11), Dicnemon (Figure 12), and Leptostomum (Figure 13) can be so heavy when they are wet that they become important in pruning the upper and dead branches.
Figure 10. Rainforest at Daintree, Australia. Photo by Thomas Schoch, through Creative Commons.

Figure 11. *Chandonanthus squarrosus*, representative of a genus that gets so heavy from collected water in the tropics that it contributes to loss of canopy and dead branches. Photo by Tom Thekathyil, with permission.

Figure 12. *Dicnemon* sp. from NZ, representative of a genus that gets so heavy from collected water in the tropics that it contributes to loss of canopy and dead branches. Photo by Jan-Peter Frahm, with permission.

Figure 13. *Leptostomum* sp. Seno Courtenay Cape Horn, representative of a genus that gets so heavy from collected water in the tropics that it contributes to loss of canopy and dead branches. Photo by Blanka Shaw, with permission.

In Australia, members of the epiphytic and *saxicolous* (growing on or among rocks) moss genus *Macromitrium* (Figure 5) are found primarily in the rainforest (Figure 10) (Ramsay et al. 1987). These reach their greatest diversity in the lower elevation ravine rainforests. These habitats form an archipelago of refugia where the remnant patches of forest occur along the eastern and northern coast of the continent.

Streams often create a habitat suitable for a rich bryophyte flora (Dixon 1935; Shevock et al. 2017). At Tenompok in Borneo, smaller shrub and tree vegetation is adorned with thin pendulous mosses and liverworts. Tree trunks are thinly covered, but cushions are nearly absent. However, on the more exposed steeper slopes the small trees have moss and liverwort cushions. At higher elevations, these cushions are dominated by liverworts. Above ~2,000 m, up to ~3,000 m asl, the liverwort *Mastigophora* (Figure 14) and other liverworts provide most of the ground cover in the open ridge forest. In more sheltered places, different liverworts occur. Mosses, while present, are not abundant in the ridge forest. *Sphagnum* (Figure 15) cushions can be found, but not abundantly.
Figure 14. *Mastigophora diclados*; in Borneo, this genus, along with other liverworts, provides most of the ground cover in the open ridge forest. Photo by Cesar Garcia, through Creative Commons.

Figure 15. *Sphagnum junghuhnianum*; *Sphagnum* cushions are present but uncommon in the ridge forests of Borneo. Photo from Taibif, through Creative Commons.

In the Guianas, Pardow *et al.* (2012) described a new type of tropical lowland forest, the tropical lowland cloud forest. This forest type has a high epiphytic bryophyte species richness. This diversity is facilitated by frequent early morning fog in valley locations. Lowland cloud forests and lowland rainforests differed in the functional composition of bryophytes in the canopy, especially the mid and outer canopy. The cloud forest reached a higher biomass and cover of both bryophytic and tracheophytic epiphytes. It similarly had a greater diversity of bryophyte life forms. The typical cloud forest life forms of tail, weft and pendants were almost completely absent in the lowland rainforests, making life forms an easy way to characterize differences in these two forest types.

Figure 16. Top of lowland rainforest canopy in French Guiana. Photo by Renske Ek, courtesy of Robbert Gradstein.

Obregón *et al.* (2011) studied the fog frequency in tropical lowland forests. Its occurrence is frequent in the lowland valleys of central French Guiana (Figure 17). It reaches its maximum before sunrise, with a duration of about 4.6 hours. This fog forms when rain saturates the soil, creating greater evapotranspiration. This morning fog follows an increase in temperature differences between the valleys and hill sites after the sun sets. This increase in fog provides an early morning moisture that provides suitable conditions for photosynthesis while the day is still somewhat cooler, supporting a higher epiphyte diversity in the lowland cloud forest compared to the hills. This fog even makes photosynthesis possible in the early mornings of the dry season.
In 1985, Amazonia occupied nearly 6,000,000 km$^2$ of South America (Pires & Prance 1985). Since then, deforestation for agriculture, cattle ranching, and logging has greatly reduced its size (Fearnside 2005; Heckenberger et al. 2007; Nepstad et al. 2008; Clement et al. 2015; Butler 2017). Some of the sub-basins have lost up to 33% since 1970 (RAISG 2015). In 2018, the Amazon Basin of 7,000,000 km$^2$ had only 5,500,000 km$^2$ covered by the rainforest (Wikipedia 2018). Although these numbers do not seem to agree, they nevertheless indicate that considerable loss of Amazonian lowland rainforest is disappearing.

The Amazonian lowland occurs mostly below 100 m asl and rarely rises above 200 m asl. Classification of the vegetation is based primarily on the topography. Two main types of forest vegetation occur: the terra firme (dry land) and the inundated formations [igapó (Figure 20) and várzea (Figure 21)], terms exclusive to Amazonia and all of which are primarily forest land. In addition, some areas have savannah vegetation, but this is a much smaller percentage of the land. Additional more specialized wetland vegetation types are mangrove swamps, restinga (spit and distinct type of coastal tropical and subtropical moist broadleaf forest in eastern Brazil), buritizal (periodically inundated palm thicket characterized by buriti – the palm Mauritia flexuosa), and pirizal (cariazal – extensive, emergent vegetation of small, stagnant lakes and puddles). The terra firme forest occupies the largest percentage of the area in Amazonia.
The lowland forests typically have a strong gradient of humidity and light, with humidity decreasing and light intensity increasing from the ground to the upper canopy (Figure 22-Figure 23) (Leon-Vargas 2001).

Amorim et al. (2017) compared bryophyte distribution in southeastern Brazil. They considered two distinct groupings, the inland areas and the coastal areas, with annual precipitation and temperature influencing the floristic similarity among the coastal areas. Distance from the ocean and altitude were the dominant factors influencing the bryophyte composition of the inland areas.

Lisboa (1976) characterized the Amazonian plain as having poor soil nutrients. Unlike many rainforests, the light intensity can in some areas be very high, resulting in high air (38°C) and soil (42.3°C) temperatures. This combination of high light and high temperatures restricts the bryophyte community. Nevertheless, they found 34 bryophyte species, representing the moss families Calymperaceae (Figure 2), Leucobryaceae (Figure 40), Leucodontaceae (Figure 24), Plagiotheciaceae (Figure 25), Sematophyllaceae (Figure 41), and liverwort families Frullaniaceae (Figure 4, Figure 26), Lepidoziaceae (Figure 53), Lejeuneaceae (Figure 62-Figure 64), Odontoschiaceae (currently included in Cephaloziaceae; Figure 27), Plagiochilaceae (Figure 28), Radulaceae (Figure 73), and Zoopsidaceae (currently included in Lepidoziaceae; Figure 29). The liverwort Frullania nodulosa (Figure 26) stood out as the most frequent species, a species with wide ecological amplitude. Bark of the tree Aldina heterophylla (Rubiaceae) proved to be a preferred substrate, providing old age, thick bark, and otherwise good conditions for bryophyte community development.

Figure 21. Várzea forest, Marajó, Brazil. Photo by Dayse Ferreira, through Creative Commons.

Figure 22. Humidity in ascending heights in the Amazon lowland forest. Modified from Leon-Vargas 2001.

Figure 23. Light intensity at ascending heights in a Neotropical lowland forest. Modified from Leon-Vargas 2001.

Figure 24. Antitrichia curtipendula a member of the Leucodontaceae. Photo from Proyecto Musgo through Creative Commons.

Figure 25. Plagiothecium undulatum, a member of the Plagiotheciaceae. Photo by Christian Peters, with permission.
Figure 26. *Frullania nodulosa* underside, the most frequent species in the Amazonian plain. Photo by Matt von Konrat, with permission.

Figure 27. *Odontoschisma longiflorum* (*Cephaloziaaceae*) from the Neotropics. Photo by Michael Lüth, with permission.

Figure 28. *Plagiochila adianthoides* (*Plagiochilaceae*) from the Neotropics. Photo by Michael Lüth, with permission.

Figure 29. *Zoopsis liukuensis* (*Lepidoziaceae*, formerly *Zoopsidaceae*). Members of the *Zoopsidaceae* are common in the Amazonian lowland rainforests. Photo by Rui-Liang Zhu, with permission.

Benavides *et al.* (2006) claimed the first bryophyte surveys from the Colombian Amazon. They divided the bryophytes into mosses and liverworts and into four life-form classes to describe floodplains, swamps, terra firme forests, and white-sand areas. They identified 50, 45, 45, and 32 species respectively. The higher number of species in the floodplains and swamps suggested the importance of moisture in delimiting communities. **Fan** life forms in the floodplains (Figure 30) further attested to the higher humidity there. Liverworts were more likely to form **mats** in both floodplain and terra firme habitats. And liverworts had greater species richness in the white-sand plots, suggesting a greater importance of light intensity than humidity for these species. Tree bark was the most important substrate for both bryophytes and liverworts in both floodplain and terra firme (Figure 31) (Benavides *et al.* 2004). The floodplain (várzea – Figure 21) differed markedly in species from the other three habitats.

![Figure 30. Bryophyte life forms in Tierra Firme vs Floodplain. Modified from Benavides *et al.* 2004.](image-url)
Leal et al. (2010) considered the possibility of using bryophytes (and other taxa groups) as surrogate taxa to indicate species richness in the Brazilian Atlantic forest and caatinga. But they did not include the bryophytes in their sampling of the caatinga. They found that the species richness of the various taxa groups (bryophytes, pteridophytes, trees, ants, euglossine bees, birds, and mammals; total of 768 species) were significantly correlated with each other. Only two taxa (trees and ants) were required to have excellent surrogacy for species richness of all groups. Bryophytes did not seem to be good surrogates for the richness of the other taxa groupings.

Valente et al. (2009) described the mosses in a segment of the Atlantic forest in Bahia State, Brazil. They found 61 moss species, distributed in 23 families. The most species-rich family was Sematophyllaceae (7 spp.; Figure 41), followed by Orthotrichaceae (6 spp.; Figure 5), Pilocryptaceae (5 spp.; Figure 32), Calymperaceae (5 spp.; e.g. Figure 2), Leucobryaceae (5 spp.; e.g. Figure 40), and Meteoraceae (4 spp.; Figure 8). Corticolous species predominated, with 70% of the species, followed by epixylic (on wood with no bark) having 23% of the species. The area was species-rich, with 24% of the bryophytes in the Bahia State represented there.

Epixylic bryophytes (living on logs with no bark) in the Atlantic forest of Brazil supported 35 species of bryophytes, not counting the Lejeuneaceae (Figure 62-Figure 64) (Germano & Pôrto 1996, 1997). These comprise 11 families of mosses: Calymperaceae (Figure 2), Pilocryptaceae (Figure 32), Fissidentaceae (Figure 71, Figure 90-Figure 92), Hookeriaceae (Figure 33), Hypnaceae (Figure 34), Leucobryaceae (Figure 40), Leucocariceae (Figure 35), Orthotrichaceae (Figure 5), Plagiоtheciaceae (Figure 28), Sematophyllaceae (Figure 41), and Thuidiaceae (Figure 36), and 5 families of liverworts: Aneuraceae (Figure 55), Frullaniaceae (Figure 4), Geocariceae (Figure 37), Plagiоbileae (Figure 28), and Radulaceae (Figure 73). These included 8 species new for northeastern Brazil.
Chapter 8-7: Tropics: Lowland Rainforests 8-7-11

Figure 35. *Leucomium strumosum* (*Leucomiaceae*), a family that occurs on logs in the Atlantic forest in Brazil. Photo by Claudio Delgadillo Moya, with permission.

Figure 36. *Cyrto-hypnum involvens* (*Thuidiaceae*) on a log in the Neotropics. Photo by Michael Lüth, with permission.

Figure 37. *Geocalyx graveolens* (*Geocalycaceae*), a widespread species in a family that occurs on logs in the Atlantic forest of Brazil. Photo by Michael Lüth, with permission.

Pires and Prance (1985) considered the dense tropical forests of the Amazon to be fireproof. These dense forests create many niches, permitting the occurrence of many species. Costa (2003) reported 514 species in the Amazonian rainforest. Nevertheless, only 106 species are known from the state of Acre, Brazil, suggesting that the area has been understudied. After only two field trips, Costa was able to increase the known flora by 50%. These trips yielded 50 species that were new for the state and 10 more that were "interesting." In an earlier study, Vital and Visnadi (1994) reported only 76 species, and at that time 66 were new records for the state of Acre. This report included one hornwort, *Notothylas vitalii* (see Figure 38).

Figure 38. *Notothylas orbicularis; Notothylas vitalii* is the only species of *Notothylas* known to Costa in 1985 for the Amazonian lowland rainforest. Michael Lüth, with permission.

New species most likely await us in these forests. Moura et al. (2012) noted the abundance of *Lejeunea* (Figure 39) species in the low várzea (Figure 21) forest in lower Amazon, Pará, Brazil, and reported the new species *Lejeunea combuensis*.

Figure 39. *Lejeunea* from the Neotropics, an abundant species in the low várzea of the Amazon. Photo by Michael Lüth, with permission.

**Terra Firme**

Oliveira and ter Steege (2013) used standardized sampling methods for epiphytic bryophytes in nine localities in the Amazon basin terra firme forests. They sampled five height zones from forest floor to canopy on
eight canopy trees at each locality, generating 3,014 records and 222 species plus 39 morphospecies. As is typical in the tropics, the most common family was **Lejeuneaceae** (Figure 62-Figure 64) (55% frequency), along with the mosses **Calymperaceae** (Figure 2) (8%), **Leucobryaceae** (Figure 40) (4%), and **Sematophyllaceae** (Figure 41) (4%). No geographical gradient was evident in species richness or composition. Nevertheless, richness differences were evident, with the greatest richness in Saul of French Guiana and Tiputini of Ecuador, compared to other localities. Of the 155 species occurring in more than one locality, 57 were specialists. A total of 29 species were found only in the canopy.

Alvarenga and Lisboa (2009) reported 120 species of bryophytes from the Amazon lowlands. Among these, the **Lejeuneaceae** (Figure 62-Figure 64) species are by far the most abundant with 58 species, followed by **Calymperaceae** (Figure 2) (13 spp.), **Sematophyllaceae** (Figure 41) (9 spp.), and **Plagiochilaceae** (Figure 42). Of these 120 species, 97 are epiphytic; 65 are **epixylic** (growing on wood that has lost its bark). Only 27 species are epiphyllous and only 15 occur on the ground. The most diverse ecosystem is the terra firme forest. The liverworts are strong dominants on leaves, with dominance gradually shifting among the habitats. Liverworts are only slightly dominant on live and dead trunks, and mosses are dominant on the other substrates.

**Figure 40.** *Leucobryum martianum*. Members of its family, **Leucobryaceae**, are common on trees in the Amazon basin. Photo by Jan-Peter Frahm, with permission.

**Figure 41.** *Sematophyllum* sp. (Sematophyllaceae), a well-represented family from the Amazon lowlands. Photo by Michael Lüth, with permission.

**Figure 42.** *Plagiochila* sp. from the Neotropics; **Plagiochilaceae** is a common family in the Amazon lowlands. Photo by Michael Lüth, with permission.

Sierra *et al.* (2018) provided a more comprehensive study on the Amazon lowlands, listing 150 species from 712 collections. These were comprised of 109 liverworts and 41 mosses. Of these 104 species lived as epiphytes and 38 as **epiphylls** (species living on leaves). Another 31 species occurred on decaying logs, 16 on rocks, and 24 on soil. But of these species, 68 occurred in only one or two samples. As is obvious from the numbers in each habitat, many were not exclusive to one habitat.

As in many other communities, the most species-rich liverwort families in the studied Amazon lowlands were **Lejeuneaceae** (81 species) and **Lepidoziaceae** (11 species) (Sierra *et al.* 2018). The three most species-rich genera were **Cheilolejeunea** (15 spp.; Figure 43), **Cololejeunea** (12 spp.; Figure 60-Figure 61), and **Ceratolejeunea** (6 spp.; Figure 63), all in the **Lejeuneaceae**. The most common liverwort species were **Cheilolejeunea anegyyna** (see Figure 43), **Pycnolejeunea contigua** (see Figure 44), **Cheilolejeunea neblinensis**, **Cololejeunea surinamensis** (see Figure 60-Figure 61), **Archilejeunea fuscescens** (see Figure 45), **Acrolejeunea torulosa** (see Figure 46), and **Vitallanthus aphanellus**, all in the **Lejeuneaceae**.
Figure 43. *Cheilolejeunea* sp., a species-rich genus in the Amazon lowlands. Photo by Michael Lüth, with permission.

Figure 44. *Pycnolejeunea pilifera; Pycnolejeunea contigua* is one of the common species in Amazonian lowlands. Photo from the Paris, Muséum National d'Histoire Naturelle, MB, through Creative Commons.

Figure 45. *Archilejeunea olivacea; Archilejeunea fuscescens* is one of the common species in Amazonian lowlands. Photo by John Braggins, through Creative Commons.

Figure 46. *Acrolejeunea* sp.; *Acrolejeunea torulosa* is one of the common species in Amazonian lowlands. Photo by Peter de Lange, through Creative Commons.

The most species-rich moss families in the studied Amazon lowlands were *Calymperaceae* (16 species), and *Sematophyllaceae* (9 species), again being common families throughout the Neotropics (Sierra *et al.* 2018). The most species-rich genus of mosses was *Syrhopodon* (12 spp.) in the *Calymperaceae*. The most common moss species were *Leucobryum martianum* (*Leucobryaceae*; Figure 40) and *Syrhopodon xanthophyllus* (see Figure 47).
Benavides et al. (2006) suggested that the periodic flooding added nutrients to the tree trunks, possibly contributing to the high diversity of bryophytes there compared to the swamps, terra firme forests, and white-sand habitats.

Most of the studies in the Amazon lowlands seem to be floristic with little ecological information on bryophytes. The following habitats can be identified, but few seem to have been described bryophytically, giving us little or no information on dominant species.

**Dense Forest**

This forest has the greatest biomass of the terra firme forests (Pires & Prance 1985). The understory is distinct, occurring where environmental conditions are optimal. Water is not limiting, having neither too much nor too little.

**Open Forest without Palms**

This forest has considerably less biomass and trees typically have a basal area of only slightly more than 20 m² per hectare (Pires & Prance 1985). The trees are lower, permitting a greater penetration of light. This allows shrubs and lianas to develop well. Large trees are only occasional. This vegetation type may be limited by a lower water table, impermeability of the soil, poor drainage, poor root penetration, somewhat long dry seasons, or lower relative humidity. Epiphytes are fewer due to the drier habitat. This forest type is not affected by fire and is predominantly not deciduous.

**Open Forest with Palms**

This forest has a similar physiognomy to that of the open forest without palms, but it has palm trees, especially *Attalea maripa* (Figure 48), *Attalea speciosa* (Figure 49), *Euterpe precatoria* (Figure 50), *Jessenia bataua* (Figure 51), and *Oenocarpus distichus* (Figure 52) (Pires & Prance 1985).

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Figure 48. *Attalea maripa*, a palm of the open forest in the Amazonian lowland. Photo by Arria Belli, through Creative Commons.

Figure 49. *Attalea speciosa*, one of the palms found in the open forest of the Amazonian lowlands. Photo by Marcelo Cavallari, through Creative Commons.

Figure 50. *Euterpe precatoria*, one of the palms found in the open forest of the Amazonian lowlands. Photo by Dick Culbert, through Creative Commons.
The biomass ratio of mosses to liverworts increased with height on the tree, but total bryophyte biomass showed no significant differences with height. The number of species increased with height sampled. They concluded that short-distance dispersal was less important than long-distance dispersal in determining the species composition. The most abundant families in this palm tree trunk habitat were Lejeuneaceae (Figure 62-Figure 64) (13 spp.) and Lepidozia (Figure 53) (9 spp.), both leafy liverwort families. The moss family Leucobryaceae (Figure 40) was represented by 6 species. The lower and middle tiers of the trunk had mosses in addition to the leafy liverwort families Calypogeiaceae (Figure 54) and Lepidozia. Only the family Lejeuneaceae was typically higher in the higher tiers. In addition, the only other families represented on this palm species were the mosses Calymperaceae (Figure 2) and Sematophyllaceae (Figure 41) and the thallose liverworts Aneuraceae (Figure 55) and Pallaviciniaceae (Figure 56).
**Liana Forest**

Lianas occur in the open forest where one might typically find Brazil nut trees (*Bertholletia excelsa*; Figure 57) and *Attalea speciosa* (Figure 49) (Pires & Prance 1985). These forests are usually discontinuous, intermeshed with dense forests lacking lianas. These forests usually are somewhat elevated and have rich deposits of such minerals as iron, aluminium, manganese, nickel, gold, and others. Some bryophytes are able to live on these woody lianas.

**Dry Forest**

The **dry forests** (Figure 58) are transitional forests and are seasonal and drier than rainforests (Pires & Prance 1985). The trees are at least partially deciduous except along the rivers and streams where flooding occurs. These forests do not occupy large areas.

**Restinga**

The **restinga** is the vegetation of coastal sand dunes. This vegetation type has few species in Amazonia.
Figure 59. Restinga forest at Itaguare beach in Bertioga State Park, Brazil. Photo by Miguel Rangel Jr., through Creative Commons.

The restinga has received at least some attention regarding its bryophytes. Working in the Setiba State Park, Espírito Santo, Brazil, Visnadi and Vital (1995) found 25 liverwort and 9 moss species, reporting the fewest species in the low and sparse restinga, with the most in the high and sandy restinga. Some of the bryophytes are specific, with the liverworts *Cololejeunea* (syn. = *Aphanolejeunea*) *subdiaphana* (see Figure 60), *Chonecolea doellingeri*, and *Cololejeunea cardiocarpa* (Figure 61) occurring only in the low and sparse restinga. *Leucolejeunea conchifolia* (Figure 62) occurs only in the medium restinga. *Ceratolejeunea laete-fusca* (see Figure 63) was only found in the high restinga; *Taxilejeunea pterigonia* (see Figure 64) only appeared in the high and sandy restinga. The mosses *Bryum capillare* (Figure 65) and *Campylopus pilifer* (Figure 9) only occur in low and sparse restinga; *Groutiella apiculata* (Figure 66) and *Schlotheimia rugifolia* (Figure 67) occur only in the high restinga. In other areas, the restinga bryophyte vegetation can be very different, with few species in common with this one. This is especially true when comparing the northwestern Amazonian restinga bryophyte vegetation with that in the southern Amazonian lowlands.

Figure 60. *Cololejeunea microscopica; C. subdiaphana* is found only in the low and sparse restinga in Setiba State Park, Espírito Santo, Brazil. Photo by Stan Phillips, through public domain.

Figure 61. *Cololejeunea cardiocarpa*, a species found only in the low and sparse restinga in Setiba State Park, Espírito Santo, Brazil. Photo by Paul Davison, with permission.

Figure 62. *Leucolejeunea conchifolia*, a species from the medium restinga. Photo by Paul Davison, with permission.

Figure 63. *Ceratolejeunea cubensis; C. laete-fusca* occurs only in the high restinga. Photo by Scott Zona, with permission.
In the Parque Nacional da Restinga de Jurubatiba, RJ, Brazil, Imbassahy et al. (2009) reported 61 taxa. As is typical in the tropics, the Lejeuneaceae (Figure 62–Figure 64) had the most species (25), greatly exceeding other high-species families of Jubulaceae (Figure 68–Figure 69) (7), Calymperaceae (Figure 2) (4), and Sphagnaceae (Figure 70) (4). Most of the taxa are corticolous (on bark) and most are of Neotropical distribution (35%). The most common life form is the mat.
In the restingas of Northeastern Brazil, the soils have a low capacity to retain water, a low nutrient content, and a high salt concentration, coupled with occasions of high temperatures (Silva et al. 2016). In the seven areas studied, 55 species were identified. These exhibit intermediate desiccation tolerance and occupy corticolous and ground habitats. This number of species is low compared to other Brazilian restingas. The dominant families are Lejeuneaceae (Figure 62-Figure 64) (24 spp.), Fissidentaceae (Figure 71) (8 spp.), and Calymperaceae (Figure 2) (6 spp.). The families Metzgeriaceae (Figure 72), Plagiochilaceae (Figure 42), and Radulaceae (Figure 73) are absent, whereas they are common in the southeastern restingas. Life forms facilitate their success, with high (tuft and cushion) or intermediate (mat and carpet) tolerance to desiccation; the former colonize soil or live trunks, and the latter colonize live trunks and/or, more rarely, decaying trunks. Sun-tolerant species are mostly those with intermediate desiccation that colonize live trunks and decayed logs. There are fewer shade-tolerant species and these are represented by Fissidens spp. (Figure 71), which form tufts and have a terrestrial habitat, and by the pendent and corticolous Squamidium nigricans (Figure 74).
Caatinga

This vegetation type of caatinga (shrubland; Figure 75) is also known as campina, campinarana, chavascal, and charravascal (Pires & Prance 1985). The vegetation grouping grows over leached white sand. This habitat is suitable for forest vegetation, but is limited by the nutrient-poor soil and seasonality of flooding and extreme drought due to the soil (sand) porosity. Diversity is low in a given area, but great variability exists between areas, making the caatingas overall rich in diversity. The caatinga vegetation is xeromorphic (having forms adapted to dry habitats). This is exhibited in thick leaves and thick bark. Nevertheless, lichens and mosses are abundant on the branches and soil surface.

When comparing the elevational zones of the caatinga (Figure 75) biome in Brazil, Valente et al. (2013) found the highest numbers of exclusive bryophyte taxa in the forests and campos rupestres (dry, rocky grasslands; Figure 76), accounting for 51% and 40% of the taxa, respectively. The caatinga and cerrado (savanna) had only 5% and 4% respectively. The lower and upper montane zones had the highest species richness and numbers of exclusive taxa. The number of disjunct species was significant between Brazil and the Andes.

The low elevation Amazon caatinga forest (Figure 77) is an evergreen sclerophyllous forest (Klinge & Herrera 1983). It forms small "islands" in the tall Amazon caatinga. These "islands" are surrounded by a 20-m wide band of vegetation with trees over 10 m tall (tall bana). This band resembles the vegetation of the tall Amazon caatinga. The low Amazon caatinga is known as bana. Klinge and Herrera describe it as an evergreen sclerophyllous woodland with bleached quartz sands in the lowlands of southwestern Venezuela. It occurs as small islands within the tall Amazon caatinga. The outer vegetation belt is about 20 m wide with trees over 10 m tall and this is known as the tall bana. Its floristic composition is similar to that of the tall Amazon caatinga. The low bana has a maximum tree height that is typically less than 5 m. The central part is occupied by open bana where trees are even shorter and very widely spaced.

Bastos et al. (2000) found 65 taxa in the campos rupestres at Estado da Bahia, Brazil. Of these, 41 were mosses and 24 genera were liverworts. Six of the moss species were Sphagnum (Figure 70). Consistent with the argument for the need of more studies, 23 of these species are new records for this state.
The first study of bryophytes in Bahia, Brazil, was as recent as 1998 (Bastos et al. 1998). In this initial study in the state of Bahia, only 18 species were discovered, 15 mosses and 3 liverworts. These are mainly generalists and xerophilous (preferring dry habitat conditions). However, some hygrophilous (preferring moist habitats) species occur here. The generalists are represented by Hyophiladelphus agrarius (Figure 78-Figure 79), Hyophila involuta (Figure 80-Figure 81), Calymperes palisotii subsp. richardii (Figure 82), Bryum argenteum (Figure 83), Entodontopsis leucostega (see Figure 84), Octoblepharum albidum (Figure 3), Frullania ericoide (Figure 85), Helicophyllum torquatum (Figure 86) and Riccia vitalii (Figure 87) and others are restricted to this type of vegetation. Unlike most of the epiphytic flora, most of these species are erect, acrocarpous species with short turf life forms. The leafy liverworts present are incubous (leaves overlap from base of stem to tip like shingles of a roof from peak to edge).
Silva and Pôrto (2016) used mosses to determine if stem growth can be used to indicate changes in local climate change in the caatinga. But the gametophyte length is highly variable in the test moss, *Campylopus pilifer*. They concluded that stem length in this species is a poor indicator of local conditions in harsh environments. On the other hand, soil islands seemed to account for longer stems than typical values for this species.

**Savannah Vegetation**

Non-forested vegetation in Amazonian Brazil is also known as **campo** (Pires & Prance 1985). These savannahs may have trees or be treeless and are dominated by grasses. The savannahs on terra firme occupy 3-4% of Brazilian Amazonia. The littoral savannahs occur on coastal areas and have frequent lakes. The most common grass is *Paratheria prostrata* (Figure 88). **Roraima savannahs** (Figure 89) are usually open with few trees. **Campos rupestres** (Figure 76) are open formations on rocks and are often confused with open savannahs. These formations suffer drought and are unable to retain water. Lichens are common on the rocks.
Some savannas are inundated. These are created where sediments are deposited by muddy rivers. Grasses colonize these areas as the rivers recede.

Figure 88. *Paratheria prostrata*, the most common grass in the littoral savannahs. Photo by Ehoarn Bidault, through Creative Commons.

Figure 89. Roraima savannah in Gran Sabana, Venezuela. Photo by Paolo Costa Baldi, through Creative Commons.

South Atlantic Islands

The most recent studies describe the small Brazilian islands in the South Atlantic, Fernando de Noronha and Trinidade (Câmara & Carvalho-Silva 2018; Costa et al. 2018). Noronha is primarily a caatinga vegetation, but presents some interesting differences in species composition (Costa et al. 2018). Like the island of Trindade, there is a lack of endemism on Fernando de Noronha, compared to St. Helena (29 of 110 species), Tristan da Cunha (18 of 160 species), and Ascension (16 of 87 species). Nevertheless, *Riccia ridleyi*, which occurred at just one location, is critically endangered, but during the rainy season, extensive populations can appear (Pereira & Câmara 2015). *Fissidens* (Figure 90-Figure 92) is the most species-rich genus with 12 species. On the other hand, the only member of the *Lejeuneaceae* present is *Lejeunea laetevirens* (Figure 93)! On Trinidade, there are 11 species of *Lejeuneaceae*, with a total of 33 bryophyte species. Fernando de Noronha also has more species of mosses (23) compared to liverworts (3) (Costa et al. 2018), whereas Trinidade has more liverworts (20) compared to mosses (12). Fernando de Noronha island has *Notothyladaceae* (Figure 94), *Ricciaceae* (Figure 87), *Bryaceae* (Figure 95), *Dicranaceae* (*Dicranella varia*; Figure 96), *Fissidentaceae* (Figure 90-Figure 92), *Pottiaceae* (Figure 79), *Splachnobryaceae* (*Splachnobryum obtusum*; Figure 97), with very low numbers of corticolous species [*Calymeres palisotti* (Figure 82), *Frullania ericoides* (Figure 85), and *Lejeunea laetevirens*]. Many (39%) of the species on this island have worldwide distribution, including *Bryum coronatum* (Figure 95), *Entodontopsis leucostega* (see Figure 84; the only pleurocarpous moss on the island), and *Hyophiladelphus agrarius* (Figure 79). But be careful what you do to preserve species. It is only on a disturbed site with engineering activity that one can find new populations of *Notothylas* (Figure 94), *Fissidens* spp. (e.g. Figure 90-Figure 92), and *Philonotis cernua* (see Figure 98), with the most extensive populations of *Notothylas* occurring there.

Figure 90. *Fissidens bryooides*, a widespread species and one of the 12 species in this genus on Fernando de Noronha. Photo by Dick Haaksma, with permission.

Figure 91. *Fissidens crispus*, a pantropical species and one of the 12 species in this genus on Fernando de Noronha. Photo by Michael Lüth, with permission.
Figure 92. *Fissidens curvatus*, a Neotropical species and one of the 12 species in this genus on Fernando de Noronha. Photo by Des Callaghan, with permission.

Figure 93. *Lejeunea laetivirens*, the only member of *Lejeuneaceae* present on Fernando de Noronha in the South Atlantic. Photo by Scott Zona, through Creative Commons.

Figure 94. *Notothylas orbicularis*, a species that does well on disturbed habitats on Fernando de Noronha. Photo by Štěpán Koval, with permission.

Figure 95. *Bryum coronatum*, a widespread species that occurs on Fernando de Noronha. Photo by Paul Siri Wilson, with permission.

Figure 96. *Dicranella varia* with capsules, a widespread species that occurs on Fernando de Noronha. Photo by Hermann Schachner, through Creative Commons.

Figure 97. *Splachnobryum obtusum*, a widespread species in the *Splachnobryaceae* and present on Fernando de Noronha. Photo from BBS website, with permission from Barry Stewart.
references and constructive feedback and helping me to understand the various habitats. S. Robbert Gradstein was invaluable in providing me with papers, images, and constructive criticism.

**Literature Cited**


