CHAPTER 8-14
TROPICS: DISTURBANCE AND CONSERVATION

TABLE OF CONTENTS

Natural Disturbance ................................................................. 8-14-2
El Niño and Hurricanes ................................................................. 8-14-2
Nutrient Relationships ................................................................. 8-14-3
Recovery .................................................................................. 8-14-3
Bryophyte Loss Effect on Tracheophytes ..................................... 8-14-4
Fire ........................................................................................ 8-14-5
Volcanoes .............................................................................. 8-14-5
Animal Activity ........................................................................ 8-14-6
Rare and Threatened Species ....................................................... 8-14-7
Pollution and Disturbance ............................................................. 8-14-8
Deforestation .......................................................................... 8-14-9
Fragmentation Effects ................................................................. 8-14-16
Harvesting .............................................................................. 8-14-17
Industrialization and Air Pollution ............................................. 8-14-19
Radiation .............................................................................. 8-14-21
Man-made Habitats .................................................................. 8-14-22
Climate Change ....................................................................... 8-14-24
Recovery .................................................................................. 8-14-24
Conservation Issues .................................................................. 8-14-26
Current Status ........................................................................ 8-14-30
Summary ................................................................................ 8-14-30
Acknowledgments .................................................................... 8-14-31
Literature Cited ......................................................................... 8-14-31
From a northern perspective, most of what we hear about the tropics is about massive disturbance. Hence, it would be irresponsible to discuss this region without at least a glimpse of the impact of disturbance on the bryophyte flora. Unfortunately, we have no before-and-after data for the vast areas that have been converted from tropical rainforest into short-lived agricultural land and that are now experiencing the jungle of plants tolerant of low nutrients, shallow soil, and exposure. However, some recent comparative studies may help us understand what we have lost.

**Natural Disturbance**

Nature has her own form of devastating disturbances. These include events such as hurricanes, tornadoes, and other high winds, animal activities, volcanoes, fire, and extreme drought.

**El Niño and Hurricanes**

Despite the frequency of hurricanes in some tropical areas, it appears that few studies have addressed the effects on bryophyte communities. Weber (1985) seems to be one of the earliest. He assessed the effects on both bryophytes and lichens resulting from the El Niño in the Galápagos Islands.

Hurricanes can have severe impacts on the epiphytic bryophytes in the tropics (Loope et al. 1994). Hurricanes can be very powerful forces that destroy nearly everything in their paths. In Puerto Rico, Hurricane Hugo created mass destruction in 1989. Recovery in the cool cloud forest has been slow compared to that of the lowland. Bryophytes were stripped from the trees by the high-powered winds and rain. Fortunately, the return frequency of hurricanes to any given area is low, usually occurring after years or decades (Lodge & McDowell 1991). But at the same time, the life span of a canopy tree or a forest ecosystem is longer than that interval.

Considering the number of hurricanes in the tropics, and the considerable damage I have witnessed to epiphytic bryophyte communities following Hurricane Hugo (Weaver 1999) in Puerto Rico, I am surprised at how few
studies have addressed the damaging effects of hurricanes on these communities.

**Nutrient Relationships**

Nutrient levels can affect the damage to trees and their adhering bryophytes. Herbert et al. (1999) found that large trees sustained damage at twice the frequency of smaller trees. Thus, trees that had a richer phosphorus environment were more susceptible to damage due to greater growth.

Hurricanes alter the nutrient cycling in tropical forests (Lodge et al. 1991). Hurricane Hugo (Figure 2), in September 1989, struck Puerto Rico, severely damaging wet forest sites. This, and other hurricanes since, have caused a massive increase in fine litter as leaves (Figure 3), small twigs, and other miscellaneous debris were ripped from the trees and deposited on the forest floor. Concentrations of N and P increased as much as 1.5 times for N and 3.3 for P compared to normal litter fall. This raises the question of effects on competition and the success of bryophytes under these conditions.

Walker et al. (1996) mentioned bryophytes in their study comparing altitudinal responses by hurricane-damaged forests in Puerto Rico. Nutrient treatments initiated 1-6 months after the hurricane decreased the bryophytes threefold while causing graminoids to increase 10-fold in the cloud forest (Walker et al. 1996).

The cloud forest understory is dominated by bryophytes; epiphytes are common. Walker et al. (1996) tested the effects of fertilization on the vegetation following hurricane damage. Fertilization increased biomass of the graminoids (grasses, sedges) in the elfin cloud forest by a factor of 10, whereas bryophytes decreased 3-fold. The same differences were absent in the lowland forest. Cover of ferns did not respond to differences in treatment or time. At the high elevations, bryophyte biomass is most likely sustained by the constant high humidity. It is likely that the bryophytes were negatively affected by the fertilizer salts. They could also have been out-competed by the graminoids. Recovery of the bryophytes was most likely facilitated by their ability to spread. As I have observed in Puerto Rico after Hurricane Hugo (Figure 2), the bryophytes are removed from the trees in patches, leaving behind the source for new growth. This removal is due to high winds and driving rain.

**Recovery**

Some bryophytes escape damage by living in protected locations. The rare liverwort species *Lejeunea paucidentata* (Lejeuneaceae; Figure 4) occurs in the rainforests of Dominica (Figure 5) (Schäfer-Verwimp 1999). Fortunately, it escapes hurricane damage because it lives on small fern fronds in the undergrowth and benefits from similar conditions in humid secondary vegetation or in heavily damaged old growth rainforest. On the other hand, Schäfer-Verwimp considers that the disappearance of *Phycolepidozia exigua* (Figure 6) is possibly due to hurricane damage to bark. This species most commonly grows on the bark of old trees, but old trees tend to be more susceptible to hurricane damage than the more pliable young trees.
Many have tried to determine what limits the species that become established on a given tree. Yeaton and Gladstone (1982) tried to determine what determines the structure of the tracheophytic epiphyte community on the calabash tree (*Crescentia alata*; Figure 7-Figure 8). As a result of their data analysis, they hypothesized that the colonization pattern is the result of the quantity of propagules produced by each species. It is possible that this is an important factor for bryophytes as well.

Nadkarni (2000) found a 30% reduction in bryophyte cover at severely impacted sites. She demonstrated, by experimental branch stripping, that epiphyte colonization occurs upwards from the *abaxial* (in this case, lower) branch surface. She considered that the shading by the branch permitted these abaxial sites to retain more water, increasing the time that the surface provided a suitable microclimate.

**Bryophyte Loss Effect on Tracheophytes**

Batke and Kelly (2015) documented the effects of a hurricane on the epiphytic bryophytes in the Cusuco National Park, northwest Honduras (Figure 9). They considered the epiphytes to be mechanically dependent plants and examined how hurricanes affected these dependents (Figure 10). Although the effect on bryophytes was not discussed directly, the researchers found that differences in life forms and families of tracheophytes among the tree branches resulted from branch surface area and bryophyte cover. Hence, the destruction of bryophyte mats led to reduced communities of tracheophytic epiphytes. They found that branches on trees that were more severely impacted had significantly lower cover. They considered that branches that were stripped of bryophytes and their dependent (Figure 10) plants during the severe gusts are less likely to experience early recolonization.
Damage to the bryophyte communities can affect other epiphytes as well. Tremblay (2008) assessed the relationships of a rare epiphytic orchid after Hurricane Georges. At first he could find no correlation with the percent cover of mosses on standing trees. But a non-parametric density contour map revealed that the moss density does seem to affect the population size of the orchids. Using this technique, Tremblay demonstrated that the orchids are present more frequently when there is a 40-90% moss cover.

Fire

Many forests around the world are subject to fire. In the tropical cloud forests, the bryophytes may actually reduce fire damage. They not only reduce the likelihood of fire because of the moisture they hold, they also facilitate growth of additional epiphytes through their moisture-absorbing and moisture-holding capacity (Proctor 1982; Frahm & Gradstein 1991). This moisture-holding capacity reduces the flammability of the forest (Bruijnzeel & Proctor 1995).

Nepstad et al. (2008) noted that forest degradation and dieback and subsequent drought increase the susceptibility to forest fires. And fires increase drought, further increasing the susceptibility to bryophyte loss. Furthermore, deforestation and smoke can inhibit rainfall, further increasing fire risk. These researchers predicted that in the next 20 years following 2008 approximately 55% of the Amazon forests will be cleared, logged, damaged by drought, or burned.

Diaspore banks can facilitate recovery of bryophytes after a fire. In a diaspore bank, Zander and During (1999) found the moss Neophoenix matoposensis (Pottiaceae) in Zimbabwe as a new species. They recommended the "forced diaspore bank analysis" as a means to find small species with short life cycles, giving them only limited above-ground exposure. In this case the method was used to uncover species in experimental fire plots. Two additional species were uncovered as new to Zimbabwe and new to Africa. One of these was previously known only from Brazil and Australia.

Volcanoes

Air pollution is not always of human origin. Volcanic activity (Figure 11, Figure 15) can be a major contributor. Baudoin (1985) reported that epiphyllous bryophytes can be used satisfactorily as indicators of volcanic air pollution.

Volcanoes offer opportunities for observing effects of elevation with fewer environmental variables than most substrates. However, when they erupt, they create severe disturbances. These severe habitats, following cooling, create bare rock substrate that differs drastically from the surrounding area. Smith (1981) compared the bryophyte and lichen communities of these severe substrates with those of the surrounding ecosystems at the Puhima Geothermal Area in the Hawaii Volcanoes National park. He found very few of the species from surrounding areas to be present on the volcano ground in geothermal areas. The center of the geothermal area is nearly lacking in any vegetation. Only small communities of vegetation, dominated by the endemic moss Campylopus praemorsus (see Figure 12) are scattered here. The mosses seem to provide a safe haven for the lichen Cladonia oceanica (see Figure 13), where it grows epiphytically on the mosses in areas lacking the high temperatures. Outside that central zone, where temperatures are lower, the grass Andropogon (Figure 14) dominates. Here, both Campylopus praemorsus and Cladonia oceanica commonly produce reproductive structures.
In Costa Rica, Griffin (1974) suggested that sulfur gassees downwind from a volcano might account for the paucity of mosses there. Both species composition and cover of mosses are diminished on the downwind side of the Poas Volcano (Figure 15).

Ah-Peng et al. (2007) found 70 species of bryophytes on a 19-year-old lava flow. They suggested that the high diversity is promoted by the host substrate and the bryophyte adaptations to colonize this new substrate. Hence, the disturbance by the volcano brought new space there to house a wide diversity of pioneer organisms.

Animal Activity

Forest animals can likewise be very destructive to bryophytes (Nadkarni 2000). Howler monkeys (*Alouatta* spp.; Figure 16) and tayras (*Eira barbara*; Figure 17) knock clumps of moss and other epiphytes from the branches as they climb and jump about. White-faced capuchins (*Cebus capucinus*; Figure 18) remove them to look for invertebrates in the bromeliads. Most literature indicates that such disturbances are easily and quickly healed with recolonization coming primarily through encroachment from the sides of the plots, thus having the same species. But in the detailed study at Monteverde, Costa Rica, mimicking effects of animal activity, Nadkarni found something quite different when she removed 75 cm strips of epiphytes from canopy branches. Despite the presence of neighboring plants, recolonization was extremely slow, with no colonization during the first five years after stripping. When it did occur, the communities were quite different. Crustose and foliose lichens began the colonization, two groups that were totally absent originally. And rather than encroaching from the sides, colonization extended from the bottoms of the branches. By the sixth year, there were some algae and bryophytes on the undersides of branches. It was not until the eighth year that some of the bryophytes from the underside had joined on the top side. Small seedlings began to appear in the tenth year.
Rare and Threatened Species

By their very nature, severe habitats often have rare and endangered species. That is because bryophytes must have special adaptations to survive in these extreme habitats. Perhaps they sacrifice competitive ability to achieve this physiological adaptation.

Gradstein (1992a) noted that loss of tropical species may vary considerably in deforested areas, depending on the size of the area affected and degree of habitat change. This damage is greatest for shade epiphytes, with an estimated 10% of rainforest species under threat by 1992. Gradstein listed 19 endangered species and 27 rare ones that are disappearing from the rainforests. Costa Rica and Panama have been particularly vulnerable, along with the Greater Antilles, the Chocó, southeastern Brazil, and parts of Amazonia.

Koponen (1992) considered the bryophytes in the tropical (and temperate) regions to have much more danger of becoming rare or extinct than those of the boreal and Arctic regions. The richest tropical floras are in the rainforests and montane forests, and deforestation creates disjunct patterns. Deforestation is particularly problematic in China, where nearly all the forests have been cut for agriculture. Very few bryophyte species from virgin tropical forests are able to survive in manmade habitats.

On the other hand, some disturbed habitats, created by agroforestry, can provide the conditions needed for some of the rare species. For example, Gradstein (1999) rediscovered the endangered leafy liverwort *Spruheaanthus theobromae* (*Lejeuneaceae*; Figure 19) on cacao trees (*Theobroma cacao* (Figure 20) in western Ecuador.)
lack of information, the real loss of tropical rare and endangered species is difficult to assess. Many areas were destroyed before any bryophyte assessment occurred. And many species considered rare or endemic have proven to be synonyms of species in a neighboring country or mountain.

**Pollution and Disturbance**

Managing for bryophytes often does not coincide with the best management plan for the forest. Andersson and Gradstein (2005) studied the biodiversity of bryophyte and lichen epiphytes in cacao plantations (Figure 21) in western Ecuador. They found 51 bryophyte and 61 lichen species. The managed cacao plantation epiphyte assemblages resembled those of natural tropical rainforests, but with lower species richness. Species also were typically found lower on the trunks. The species on cacao were typically widespread Neotropical or pantropical species. But *Spruceanthus theobromae* (Figure 19) is endemic to cacao plantations in western Ecuador. Management involving manual removal of epiphytes in the plantations significantly impacted the epiphyte species diversity. High management intensity particularly affected diversity of liverworts and lichens, but not mosses. As one might expect, plantations with low management had the highest percent cover of bryophytes. Plantations with low and moderate management serve as reserves for some ecological specialists, making them important in the conservation of epiphytes.

Working in tropical rainforests of the Pacific, Pócs and Tóthmérszé (1997) found that the average species richness in the most diverse epiphyll communities was 8-9 per leaf. Degraded habitats exhibited as few as 3-4 species. At the habitat level, the number of species could reach 24-25 species. The number of species per habitat does not typically decrease as a result of habitat degradation because **beta diversity** (differences in species composition among sites; regional diversity) tends to increase while the number of species per leaf decreases. The study emphasizes the importance of the scale of the study in order to assess the impacts of disturbance.

Some of our understanding of microhabitat differences can be derived from studies on the effects of disturbance. For example, Werner and Gradstein (2009) compared various degrees of disturbance in closed-canopy mixed acacia forest (old secondary), pure acacia forest (old secondary), forest edge, young semi-closed secondary woodland, and isolated trees in grassland. They found that density of bryophytic epiphytes on 100 trees of *Acacia macracantha* (Figure 22) in northern Ecuador at 2,300 m asl is significantly lower in edge habitat and on isolated trees than in closed forest. Forest edge is more
impoverished than semi-closed woodland and has similar floristic affinity to isolated trees and to closed forest types. The microhabitats among these habitat types vary, contributing to the diversity. As they point out, "Assemblages were significantly nested; habitat types with major disturbance held only subsets of the closed forest assemblages, indicating a gradual reduction in niche availability." They found no diversity effect from distance to the forest for epiphytes on isolated trees. Species density is closely correlated with crown closure. They concluded that microclimate, not dispersal constraints, determine most of the epiphyte assemblage. The researchers also concluded that the bryophytic epiphytes are sensitive indicators of changes in microclimate and human disturbance in the montane dry forests. A major treatise on the canopy community is that of Lowman et al. (2013).

Figure 22. *Acacia macracantha*, a species where density of bryophytic epiphytes in northern Ecuador at 2300 m asl is significantly lower in edge habitat and on isolated trees than in closed forest. Photo by Vladeq, through Creative Commons.

**Deforestation**

Deforestation has become a major factor impacting diversity and biomass in the tropics (Figure 23). "Between 1990 and 1997, 5.8 ± 1.4 million hectares of humid tropical forest were lost each year, with a further 2.3 ± 0.7 million hectares of forest visibly degraded." (Achard et al. 2002) although the rate has slowed in recent years, deforestation continues, increasing the total impact.

Scatena et al. (2010) noted that the cloudy, wet, difficult terrain of the tropical montane cloud forests had afforded the bryophytes some protection from deforestation. However, in the late 1970's and early 1980's, even these forests were being torn down or fragmented. By the 1990's they became one of the most threatened ecosystems in the world, with a loss rate exceeding that of the lowland tropical forests (1.1% y⁻¹ vs. 0.8% y⁻¹).

Costa (1999) compared epiphytic bryophyte diversity in primary and secondary lowland rainforests of southeastern Brazil. The highest species richness occurs in mature secondary hillside rainforest (43 species). The lowest is in a highly degraded hillside rainforest (6 species and a hillside secondary rainforest (5 species). As seen elsewhere, the important families are *Lejeuneaceae* (Figure 4; 23 species, 30%) and *Sematophyllaceae* (Figure 24; 7 species, 10%). And as in other studies, the canopy has the highest number of exclusive species (45% of canopy species). The shade epiphytes are the most affected by deforestation and many do not return 20-45 years after the destruction. However, after 80 years the species composition is similar to that of the primary forest.

Figure 23. 70 years of Borneo deforestation. Photo courtesy of Robbert Gradstein.

Figure 24. *Sematophyllum* (*Sematophyllaceae*); *Sematophyllaceae* is among the important families from the lowland rainforests of southwestern Brazil. Photo by Michael Lüth, with permission.
In a different location in southeastern Brazil, Costa (1998) found the highest species richness in the mature secondary hillside rainforest (43 species). The lowest is again the highly degraded hillside rainforest (6 species).

Hyvönen et al. (1987), however, found that many mosses can find suitable niches even in disturbed areas, unless destruction of the habitat is complete. Nevertheless, some are eliminated by current practices of land use. In their study on the Huon Peninsula of Papua New Guinea, they used 18,000 specimens to determine effects of disturbance on the bryophytes. Of 43 species, 14 were restricted to undisturbed habitats, 16 occurred about equally in both, and 23 were preferentially in disturbed areas. Primeval habitats were dominated by terrestrial & epiphytic mosses; weedy species occurred in disturbed habitats. The sensitive epiphytic species that decreased with disturbance include *Meteorium buchananii* (Figure 25), *Trachypus bicolor* (Figure 26), *T. humilis* (Figure 27), *Pseudotrachypus wallichii*, *Cryptopapillaria fuscascens*, and *Pelekium contortulum* (Figure 28). In addition, *Campylopus clemensiae* (see Figure 39) and *Leptocladiella flagellaris* grow on living trees as well as rotten wood. Soil species that are sensitive include *Dawsonia grandis*, *D. papuana* (see Figure 29), *Rhodobryum giganteum* (Figure 30), with less substrate-discriminating *Macrothamnium hylocomioides* (see Figure 31), *Thuidium cymbifolium* (Figure 32), and *T. glaucinum* (Figure 33). Persistent species include *Bryum apiculatum* (Figure 34) and *Plagiomnium integrum* (see Figure 35), although they decrease in altered habitats. On the other hand, the outer crown epiphyte *Leptostomum intermedium* (see Figure 36) seems to increase with human influence, but that could be an artifact due to the difficulty of sampling it. The species that clearly increase with disturbance include *Brachymenium nepalense* (Figure 37), *Bryum billarderi* (Figure 38), *Campylopus exasperatus*, *C. umbellatus* (Figure 39), *Elmeriobryum philippinense*, and *Orthomnion elimbatum* (Figure 40). Species that were clearly present only following disturbance include *Bryum argenteum* (Figure 41) and *Gemmabryum subapiculatum* (syn. = *Bryum microerythrocarpum*; Figure 42).
Figure 28. *Pelekium contortulum*, a sensitive moss species that decreases with disturbance. Photo through Creative Commons.

Figure 29. *Dawsonia superba; Dawsonia grandis* and *D. papuana* are soil species that are sensitive to disturbance. Photo by Phil Bendle, with permission from John Grehan.

Figure 30. *Rhodobryum giganteum*, a sensitive moss species that decreases with disturbance. Photo by Leonardo L. Co, with online permission.

Figure 31. *Macrothamnium submacrocarpum* from Doi Inthanon, Thailand; *Macrothamnium hylocomioides* is a sensitive soil species that decreases when faced with disturbance. Photo courtesy of Hiroyuki Akiyama.

Figure 32. *Thuidium cymbifolium* with capsules, a sensitive species of soil and other substrates that decreases when faced with disturbance. Photo by Li Zhang, with permission.

Figure 33. *Thuidium glaucinum*, a sensitive species of soil and other substrates that decreases when faced with disturbance. Photo through Creative Commons.
Figure 34. *Bryum apiculatum* with capsules, a persistent tropical soil species that is less negatively affected by disturbance. Photo by David T. Holyoak, with permission.

Figure 35. *Plagiomnium affine; Plagiomnium integrum* is a persistent tropical soil species that is less negatively affected by disturbance. Photo by Michael Lüth, with permission.

Figure 36. *Leptostomum inclinans* with capsules; *Leptostomum intermedium* is an outer crown species that actually increases with human disturbance. Photo by Clive Shirley, Hidden Forest, with permission.

Figure 37. *Brachymenium nepalense*, a species that becomes more abundant with disturbance. Photo by Li Zhang, with permission.

Figure 38. *Bryum billarderii*, a species that becomes more abundant with disturbance. Photo by Bramadi Arya, through Creative Commons.

Figure 39. *Campylopus umbellatus* with capsules, a species that becomes more abundant with disturbance. Photo by Li Zhang, with permission.
Evidence shows that logging does not have to be totally destructive. The main effect of such disturbance in tropical forests is increased desiccation due to greater wind movement and insolation, causing a reduction in biomass of epiphytic bryophytes (Norris 1990). This, in turn, decreases the water and mineral retention of the remaining bryophytes and interferes with their ability to trap and release water and mineral nutrients. In Papua New Guinea, Norris found that logging and agricultural practices may alter bryophyte species frequency, but with careful attention to logging management, there is no evidence of a significant loss of species.

When Romero (1999) compared bryophytes in logged and non-logged plots in a tropical montane forest in Costa Rica, he found that pendent epiphytes were more abundant on branches less than 1 cm in diameter. The highest biomass was that of branches supporting shade-tolerant species, i.e., non-logged plots.

A comparison of fallow land (4-15 years) vs submontane rainforest in Bolivia reveals considerably less diversity of both bryophyte families and species in the fallows (Acebey et al. 2003). Surprisingly, there is little difference in liverwort diversity between them except in the very young (4-year-old) fallows. Life forms differ, with significantly more smooth mats (72%) in the fallows. Nevertheless, in just 10-15 years, approximately half of the bryophyte taxa of the rainforest are re-established among the trees of the fallows. Most of these arrivals are ecological generalists and sun-loving epiphytes, with ecological specialists and shade species arriving and establishing more slowly. The highest diversity of the fallows is in the understory, contrasting with the highest richness in the canopy of the uncut rainforest. The shift to lower parts of the trees in the fallows corresponds with the greater air humidity there and most likely also with lower temperatures and reduced light intensity.

Return of bryophytes to remnant forests after logging is slow. In subtropical rainforests of Australia, few bryophytes had returned even 25 years after the disturbance (Chapman & King 1983). The same was true in southeastern Brazil (Costa 1999). In Costa Rica, isolated remnant trees (e.g., Figure 43), lacking the dense canopy of the undisturbed forest, had bryophyte diversity reduced by 50% compared to the remaining intact forest.
Much of the land in the tropics has been lost to agriculture before we have even assessed what bryophyte species live there. Sulawesi, Indonesia (Figure 44), is characterized by steep slopes that are often difficult for bryologists to navigate, but logging has nevertheless altered the environment. Ariyanti et al. (2008) investigated the bryophytes on tree trunk bases in the natural forest, selectively logged forest, and cacao plantation (Figure 21) shaded by remnants of the natural forest there. They found that species richness differs little among these forest types. But on close inspection, one finds that the moss richness is lowest in the cacao plantations, but the liverwort richness differs little among the forests. By contrast, the moss cover differs little among the forests, but liverwort cover is significantly less in the disturbed forest. Species composition likewise differs markedly in the cacao plantations compared to the natural forests and selectively logged forests. Drought-sensitive species are notably rare or absent in the cacao plantation, with drought-tolerant species replacing them. Large vs small trees have little effect on bryophyte species composition except in the cacao plantation; the latter phenomenon the researchers attribute to changes in stemflow of precipitation water.

Gradstein and Sporn (2010) compared epiphytic bryophytes from different land use types in several countries of the Neotropics and Indonesia (Sulawesi), including natural rainforests, secondary rainforests, fallows, isolated pasture trees (Figure 20), and cacao agroforests (Figure 21). They found changes in species richness between these disturbed habitats and the various disturbances to vary by 0-10% species loss in the old secondary forest and up to 65-80% loss in young fallows and cacao agroforests. The cacao agroforests lost 75% of their species. In contrast, the remnant forest trees in pastures provide a rich habitat where bryophytes can be conserved. In submontane forests, there were considerable changes in life forms, but these changed little in the montane zones. Sun epiphytes replace shade epiphytes in the deforested areas. The study demonstrates the importance of canopy cover in preserving the rainforest bryophyte vegetation.

Nöske et al. (2008) compared the epiphyte diversity of mature and recovering forest and that in open vegetation in the montane zone of Ecuador. They were unable to discern any pattern of change in species richness among different taxonomic groups (lichen, bryophytes, tracheophytes, and moths) with increasing disturbance. However, richness of epiphytic bryophytes decreased significantly from mature forest through the cline to open vegetation. For some of the taxa, the modified habitats serve to increase overall biodiversity in the Andes.

Benítez et al. (2015) likewise noted the decline of bryophyte and lichen epiphytes in moist tropical montane forests, due to deforestation and habitat loss. Benítez and coworkers investigated 240 trees in primary and secondary forests of southern Ecuador and found that diversity is higher in primary forests and lower in monospecific secondary forest stands. Habitat loss and reduction of canopy cover negatively affect total diversity. This, in turn, modifies the water balance and nutrient cycling of these forests, further complicating the loss of bryophytes and lichens. Shade epiphytes are replaced by sun epiphytes, and species richness diminishes.

In the fragmented Afromontane forests, Malombe et al. (2016) found the diversity of epiphyllous bryophytes exhibits no direct correlation with the distance from forest edge. However, they are affected by microenvironmental variables. These variables include tree species composition, sunlight exposure, and canopy structure, all factors that are typically affected by deforestation, even just thinning.

Cloud forests (Figure 45) are unique ecosystems with high bryological diversity and cover in the northern Andes (Benavides & Gutierrez 2011). But this ecosystem is also one of the most endangered ecosystems in the tropics. Agricultural techniques using slash and burn leave behind isolated individual palms in the middle of newly created grasslands or agricultural fields. This isolates the rare canopy bryophyte species. In Colombia, 72 liverwort species and 21 moss species comprised these epiphytic communities. The researchers found a decrease in the number of species from the forest to the grassland. The diversity likewise decreases from base to canopy of palms, with the more common species appearing an average of 4 m lower on the palms in the grassland when compared to those in the forest. The species remaining tend to be drought-tolerant forest species and species that commonly occur in disturbed sites. Hence, these isolated palms do not serve as suitable refugia for the rarer cloud forest species.

Cordova and del Castillo (2001) conducted a chronosequence study exclusively on tree bases in a tropical montane cloud forest in Mexico (Figure 46). The trees examined were in stands of 15, 45, 75, >90 years old, and a primary forest, and had originally been tropical montane cloud forests. They sampled the trees at 1 dm intervals using a sampling grid, up to 160 cm. Total epiphyte cover increases with forest age, following an S-shaped curve. The highest rate of increase is between 15 and 45 years. Whereas moss and liverwort cover increase with stand age, macro- and microlichens cover appear to be independent of age. Cover of microlichens decreases as cover of mosses and tracheophytes increases. Total epiphyte cover per unit area shows some decrease as the diameter of the tree increases.

Figure 44. Tangkoko National Park, North Sulawesi, Indonesia. Photo by Lip Kee Yap, through Creative Commons.
In an assessment of bryophytic epiphytic diversity in Columbian (Figure 47) forest patches, Orrego (2005) suggested that there is a direct relationship between bryophyte species diversity and the structural heterogeneity of forest fragments. He cautioned that a single index is not adequate to assess the epiphytic bryophyte diversity.

Gradstein (2008) noted that drought-intolerant species suffer more than drought-tolerant ones under the loss of cover due to deforestation. In the South American tropics, disturbance causes high species turnover and the return to the original epiphytic bryophyte flora is slow. Even after 50 years of forest recovery, the bryophyte flora is still very different from the undisturbed flora. Gradstein and Sporn (2010) documented the tropical diversity of epiphytic bryophytes with land use gradients.

Gradstein and Sporn (2010) summarize the effects of deforestation on the bryophyte communities of the tropics:

1. Deforestation has a significant impact on the bryophyte diversity in what was once forested land. Old secondary forests still experience 0-10% loss, whereas young fallows and cacao agroforest can have 65-80% loss. Epiphytic bryophytes are more strongly affected than are lichens (Gradstein 1992b), with a 4X turnover of bryophytes compared to lichens (Nöske et al. 2008). In the arid regions, bryophytes are more sensitive to land use changes than are the tracheophytes (Werner & Gradstein 2009).

2. Life form proportions change in the submontane forests, but not in the montane forests. Mats increase in submontane fallows and tufts increase in cacao agroforests; this change is accompanied by a loss of fans, pendants, and tails.

3. Shade epiphytes disappear as more exposure is created, and these are replaced by sun epiphytes. Epiphyte heights on the trees experience a shift to lower locations. The canopies become almost devoid of epiphytes.

4. Canopy closure, microclimate, and host tree characteristics serve as drivers of the epiphytic bryophyte diversity under different land-use types, indicating that canopy cover is necessary to maintain the rainforest diversity (Steffan-Dewenter et al. 2007). As a result, it may take more than 100 years for the bryophyte diversity to fully recover in second-growth forests.
5. Remnant trees in the pastures can provide a rich habitat where bryophyte species can be conserved. However, some agroforests, such as the cacao agroforest, are unable to provide this role (Andersson & Gradstein 2005).

6. Some bryophyte species can serve as indicators of land-use change at the local and regional scales, but not at larger scales. Qualitative and quantitative study of life forms and ecological groups of epiphytic bryophytes promise to provide bioindication of land-use change and rainforest disturbance in the tropics.

**Fragmentation Effects**

Deforestation is creating forest fragments in many areas of the tropics (Figure 1). Zartman (2003) discussed the effects of this habitat fragmentation on epiphyllous bryophyte communities in central Amazonia. He found that regionally common taxa are often reduced in epiphyll diversity in small fragments. On the other hand, rare taxa are often more abundant in fragments than in continuous forest habitat. Larger fragments (100 ha) exhibit higher species richness, abundance, and among site variation than do the smaller fragments (1 & 10 ha).

Silva and Pôrto Assessed effects of fragmentation on bryophytes of decaying logs in the Atlantic Forest remnants in northeastern Brazil. They identified 99 bryophyte species (52 liverworts, 47 mosses). They determined that fragment size is important in determining the community structure on decaying logs. They did not find a correlation between distance from forest edge and bryophyte richness or cover, suggesting that the relationship is non-linear.

Zartman and Shaw (2006) consider the demographic mechanisms causing species loss in the tropics to be greatly under-explored. To contribute to the understanding of the impact of fragmentation, they chose the epiphyllic leafy liverworts *Radula flaccida* (Figure 48) and *Cololejeunea surinamensis* (see Figure 49). They transplanted these two species to study sites with areas ranging 1, 10, 100, up to 110,000 ha. All the transplants exhibited significantly positive local growth with a nearly constant per-generation extinction probability of 15%. In reserves of 100 ha or greater, the colonization rate nearly doubled (to 48%) compared to small reserves (27%). They considered this an indication that epiphyll loss in small fragments was due to reduced colonization.

Bryophytes have relatively fast colonization and extinction rates, making them ideal study organisms for the effects of forest fragmentation (Pharo & Zartman 2007). Nevertheless, they are limited by dispersal, and this somewhat random process helps to explain their observed recolonization patterns.

Nevertheless, edge effects have an impact on community structure, especially where these create abrupt differences in microclimate. Establishment experiments repeatedly indicate dispersal limitation to explain the absence of typical forest species in fragmented habitats (Zartman & Nascimento 2006; Gunnarsson & Söderström 2007).

Younger fragments (<25 yrs), in particular, have lower richness and different species composition than adjacent mature forests (Pharo et al. 2004). Similarly, Snäll et al. (2003) found that age of the trees is more important than size for the moss *Orthotrichum* (Figure 50) on aspen (*Populus*; Figure 51) trees. Older trees support larger colonies.
In southern Veracruz, Mexico, the number of epiphytic tracheophyte species per tree and total estimated biomass correlate most with tree size, measured as diameter at breast height (Hietz-Seifert et al. 1996). When considering this relationship, the number of epiphytes on remnant trees is similar to that in the forest plots. However, the forest plots still differ significantly from each other, a response Heitz-Seifert and coworkers considered might be due to differences in humidity. The number of epiphytes on isolated forest tree species exhibit a negative correlation with distance from the forest border. The researchers also considered that some of the differences exhibited by the remnant trees, which included many figs, may have been due to the attraction of birds and bats that could contribute to seed dispersal. Although the importance of various environmental variables differ between bryophytes and tracheophytes, some of these same variables may affect both, and destruction of bryophytic epiphytes can affect the success of tracheophytic epiphytes and vice versa.

In open, disturbed areas in the Amazonian Andes of northern Peru, contrasting with the larger life forms of the forests, the disturbed and exposed areas comprising secondary forests are characterized by short turf-forming acrocarpous mosses that have a colonist life strategy, a life form not typically found within the developed forests (Kürschner & Parolly 1998; Kürschner et al. 1999).

**Harvesting**

Deforestation isn't the only human danger. Harvesting of bryophytes for commercial use likewise can endanger the bryophytes (Peralta & Wolf 2001). In addition to many Neotropical areas, in India, Japan, and China mats of mosses are peeled from their substrates for use in the horticulture industry (Wuethrich 1993; Peck 2006; Peck & Moyle Studlar 2008). These can greatly reduce cover on the reachable branches and logs.

In the monarch butterfly biosphere reserve, Sierra Chincua, Michoacan, Mexico, mats of bryophytes are harvested, packed, and sold in Mexico City for ornamental use. One family alone (about 10 members) harvested 50 tons (fresh weight) of bryophytes in one collecting season. This created a mosaic of gaps of bare soil in the mossy layer, with an average gap size of 0.48 m². This moss removal consequently caused the removal of 11,000 Abies (fir) seedlings that were growing with the mosses.

In the montane tropical oak-bamboo forests in Costa Rica, pendent bryophytes are a locally valuable resource subject to commercial harvesting (Romero 1999). Thus, logging that destroys the habitat of these taxa is of local concern. These harvestable bryophytes include the mosses *Pilotrichella flexilis* (Figure 52-Figure 53), *Phyllogonium viscosum* (Figure 54), *Zelometeoriun* sp. (Figure 55), and *Squamidium leucotrichum* (Figure 56) and other *Frullania* species. These pendent life forms are important in water interception and thus might be expected to have an important effect on the hydrological balance in these forests. However, nine years after careful selective logging in a montane oak-bamboo forest, there were no detectable negative impacts on the biomass of these bryophytes at commercially available heights (1-3 m). Unfortunately, there is no comparable study in Costa Rica to show the impact of bryophyte harvesting on their successful return. In Africa, Jacobsen (1978) found that epiphytes require a minimum of 7-10 years to regenerate after harvesting from the forest.
Figure 53. Close view of *Pilotrichella flexilis*, a pendent bryophyte that is used locally in Costa Rica as a forest product. Photo by Claudio Delgadillo Moya, with permission.

Figure 54. *Phylogonium viscosum*, a pendent bryophyte that is used locally in Costa Rica as a forest product. Photo by Jan-Peter Frahm, with permission.

Figure 55. *Zelometeorium patulum* from the Neotropics, a pendent bryophyte in a genus that is used locally in Costa Rica as a forest product. Photo by Michael Lüth, with permission.

Figure 56. *Squamidium leucotrichum* from the Neotropics, a pendent bryophyte that is used locally in Costa Rica as a forest product. Photo by Michael Lüth, with permission.
Industrialization and Air Pollution

Escocia Ariza (1998) reported losses of epiphyllous and epiphytic bryophyte species in the 20th century. The industrial district in particular has lower coverage, sexual reproduction, diversity, and a lower index of community vigor. Chlorosis (loss of green color of chlorophyll) indicates stress. *Lejeunea trinitensis* (Figure 58) emerged as a stress-tolerant species, whereas *Leptolejeunea exocellata* (Figure 59) is a sensitive species that disappears from the industrialized area. The species present in the polluted area are colonists, particularly on rocks. The colonization is a slow process. Species with both sexual and asexual reproduction are more successful at establishment.

Vareschi (1953) was one of the earliest researchers on tropical air pollution in Venezuela. These studies were actually the reverse of most, looking at the influence of the forests and parks on the air quality of the city of Caracas. Rebelo et al. (1995) reported on the epiphytic bryophyte communities under the effects of air pollution in Brazil.

In 1992, Durán et al. used the Index of Air Purity (IAP) to evaluate the responses of epiphytic mosses to air pollution in Mexico City, Mexico. They were able to demonstrate a significant negative correlation ($p<0.5$) between these IAP values and $SO_2$, $NO_2$, $NO_x$, and Pb (lead). On the other hand, there were significant positive correlations with ozone. This relationship is manifest in the gradual decrease in frequency and cover of epiphytic mosses in Mexico City.

Bryophytes in temperate zones are well known for their ability to accumulate heavy metals (e.g. Faus-Kessler et al. 2001). But the behaviors of tropical bryophytes are less well known. Based on many temperate studies showing that bryophytes were good accumulators of heavy metals, Lisboa and Borges (1995) examined the potential use of bryophyte diversity as an indicator of pollution in Belém, in the lower Amazon region of Brazil.
Jayasekera and Rossbach (1996) conducted one of the few tropical species to address this issue. They examined background levels of heavy metals and their differences in plants of different taxonomic groups, including bryophytes, in a montane rainforest in Sri Lanka. They found that when a lichen (*Usnea barbata*; Figure 60), an epiphytic club moss (*Huperzia selago*; Figure 61), an epiphytic fern (*Pleopeltis lanceolata*; Figure 63), an epiphytic orchid (*Bulbophyllum elliae*; see Figure 64), a large dicotyledonous tree (*Actinodaphne ambigua*; see Figure 65) and a moss [*Pogonatum* sp. (Figure 66)] were compared for their heavy metal content, the levels were essentially homogeneous for Cd, Cu, Pb, and Zn. The moss *Pogonatum* had the highest degree of homogeneity for lead. The primitive taxa, the lichen *Usnea* and moss *Pogonatum* seem to have higher accumulation levels of As, Cd, Co, and Pb than do the tracheophytes.

Figure 60. *Usnea* from Cumbre Vieja, Canary Islands, a genus used locally in Costa Rica as a forest product. Photo by Fährtenleser, through Creative Commons.

Figure 61. *Usnea barbata*, a fruticose lichen with higher accumulations of Cd, Cu, Pb, and Zn levels than surrounding tracheophytes. Photo from MO Observers, through Creative Commons.

Figure 62. *Huperzia selago*, a tracheophyte with less accumulation of Cd, Cu, Pb, and Zn than the associated moss and lichen tested. Photo by Malcolm Storey, DiscoverLife, with online permission.

Figure 63. *Pleopeltis lanceolata*, a tracheophyte with less accumulation of Cd, Cu, Pb, and Zn than the associated moss and lichen tested. Photo by Robbin Moran, with permission.
Figure 64. *Bulbophyllum guadense*; *Bulbophyllum elliae* is a tracheophyte with less accumulation of Cd, Cu, Pb, and Zn than the associated moss and lichen tested. Photo by USDA & GPEPP, through Creative Commons.

Figure 65. *Actinodaphne angustifolia*; *Actinodaphne ambigua* is a tracheophyte with less accumulation of Cd, Cu, Pb, and Zn than the associated moss and lichen tested. Photo by Dinesh Balke, through Creative Commons.

Figure 66. *Pogonatum urnigerum*, a species that has a high degree of homogeneity for absorbing lead. Photo by David Holyoak, with permission.

Faus-Kessler et al. (2001) used biannual collections of epiphytic *Hypnum cupressiforme* (Figure 67) to determine changes in accumulations of trace metals.

Figure 67. *Hypnum cupressiforme*, a species used for determining accumulations of trace metals. Photo by Aconcagua, through Creative Commons.

On the other hand, bryophytes have been used to help clean the air and remove pollutants (Vareschi 1953). Bryophytes greatly expand the available surface area for trapping and immobilizing both water and ions from the atmosphere (Coxson 1991).

**Radiation**

Although the studies on radiation effects on tropical bryophytes are limited, the extensive study at El Verde, Puerto Rico (Figure 68), did include bryophytes (Odum et al. 1970). High levels of radiation fallout retention were present in the epiphytic mosses in the mossy forest (Figure 69) of the Luquillo Mountains in 1962. The algae-moss-liverwort encrustations had the highest levels of radiation, with massive moss colonies being second. Bromeliads and rooted plants had less. Radioactivity in tree leaves was in proportion to the epiphyllous growths on them, and that growth was related to leaf age.

Figure 68. Rainforest of El Yunque, Puerto Rico, where the El Verde radiation study site is located. Photo by Alessandro Cai, through public domain.
Man-made Habitats

Many forested areas have been replaced by man-made habitats. These provide greater variety in available habitats. In the tropics, one can find *Diplophyllum obtusatum* (Figure 70), *Solenostoma sphaerocarpum* (Figure 71), and *Schistochilopsis incisa* (Figure 72) in man-made habitats (Gradstein & Vána 1987). It appears that these Laurasian species have spread relatively recently through human activities.

In Alto Beni, Bolivia, corticolous bryophytes on trees in the primary rainforest decreased significantly in the fallows as measured after 4-15 years (Cabby et al. 2003). But liverwort diversity barely changed except in the 4-year-old forest. Smooth mats had a significantly higher percentage (72%) in the fallows, perhaps due to the warmer, drier microclimate. But even in the 10-15-year-old fallows, only about half the species had returned, mostly generalists and sun epiphytes. Whereas species richness is highest in the undisturbed canopy, in the fallows it is highest in the understory, with rough mats, fans, and tails shifting to lower heights on the trees, most likely due to changes in air temperature and air humidity.

If sufficient natural forest is retained, artificial forests can increase the diversity by providing new niches. Petit and Symons (1974) reported 28 bryophyte species from 17 artificial woodlands planted with *Cupressus* (Figure 73-Figure 74) and *Acacia* (Figure 22) in Burundi, Africa. In these woods, the litter layer is covered with bryophytes and the flowering plants are almost absent.
Sillett et al. (1995) compared bryophyte diversity in Ficus tree crowns from the cloud forest and a pasture in Costa Rica. In the lower montane wet forest, they found 127 bryophyte species (50 mosses, 76 liverworts, 1 hornwort) in the inner crowns of only six Ficus tuericxheimmi trees. Of these, 52 were found only in the intact forest, whereas only 18 species occurred exclusively in the isolated trees of the pasture. One of the factors contributing to the differences was a moisture gradient that diminished away from the intact forest.

In the northern Andes, roadside habitats in humid locations can be invaded by canopy liverworts from the montane forest (Gradstein 1992b). These include such liverwort species as Dicranolejeunea axillaris, Frullania brasiliensis (Figure 75), Frullania convoluta (Figure 57), Frullanoides densifolia (Figure 76), Herbertus acanthelius (see Figure 77), Jamesoniella rubricaulis (Figure 78), Omphalanthus filiformis (Figure 79), and Taxilejeunea pterigonia (see Figure 80). In such locations these liverworts behave as pioneers.
Climate Change

Benzing, in 1998, stressed the vulnerabilities of tropical forests to climate change, and even more so to that of their bryophytic inhabitants. Noting the complexity of these systems, he pointed to the narrow set of circumstances that define the habitats for these bryophytes. This raises the concern of their often underestimated role in both hydrology and mineral cycling, added to their ability to support a wide diversity of smaller organisms such as salamanders, arthropods, fungi, and micro-organisms, makes them major contributors to the ecosystem. Yet their vulnerability in tropical forests under climate change is great.

Many bryophytes in the tropics are approaching their limits of tolerance to the high temperatures that increase their rate of respiration (see Microclimate above). Hence, as considered by Zotz and Bader (2009), "rising temperatures could have disastrous effects." Moving farther away from the equator may provide a refuge for some species, but the authors suggest that epiphytes may be "particularly threatened" because the cloud forest habitats are likely to be the most seriously affected. And these are species-rich habitats where "exceptional" species occur. They furthermore are often isolated, requiring long-distance dispersal to reach a suitable climate.

Durán et al. (1992) used the IAP values to demonstrate that higher rainfall and relative humidity helped to account for higher bryophyte diversity values. Climate changes can affect these parameters, making some areas drier. Furthermore, bryophyte IAP values exhibit a negative correlation with temperature.

Climate change studies in the tropics are of utmost importance in a region where many species are already limited by temperature. Jácome et al. (2011) summarized what we know about the effects on the epiphytic bryophyte communities of simulated climate change in the tropics. Based on a translocation experiment in the upper montane forest in Bolivia they showed that exposure to air temperature increases of 1.5-2.5°C had a measurable effect on the structure of epiphytic bryophyte communities of the tropical montane forest within two years. The results confirm the sensitivity of non-tracheophytic epiphytes to atmospheric changes and predict that changes in the climatic regimes of tropical montane forests will rapidly affect the rich non-tracheophytic epiphyte communities.

Epiphytes seem to be particularly vulnerable to climate change because they must survive "at the interface of vegetation and atmosphere" (Zotz & Bader 2009). Furthermore, land use exacerbates the problem by decreasing the suitability of the environment. On the other hand, some drought-resistant species may benefit. They projected that new assemblages would form among bryophytes and lichens. But rising temperatures can be very destructive for both bryophytes and lichens. This will most likely be most detrimental to the habitats in the tropics with exceptional species richness, in particular, the cloud forests.

Sometimes human interference resulting in local climate change actually helps bryophytes. Kautz and Gradstein (2001) found that the critically endangered Spruteanthus theobromae (Lejeuneaceae; Figure 19) grows on the trunk bases of Theobroma cacao (Figure 20- Figure 21) in 12 plantations that had minimal management. In fact, the researchers felt that it should instead be considered as a near-threatened species and removed from the World Red List.

Recovery

Hallingbäck and Tan (1996) bemoaned the loss of species worldwide, citing reduction, fragmentation, and isolation of their habitats, in addition to damaging pollution. They noted the value of designating certain bryophytes as key species to protect because of the associated plants and animals that would also be protected. But if areas already impacted are allowed to recover, what can we expect?

Gradstein and Sporn (2010) found that canopy closure, microclimate, and host tree characteristics are important in determining epiphytic bryophyte diversity. Preservation of the canopy, therefore, is important in maintaining this diversity. Recovery of bryophyte communities after clear-cutting is very slow and may take more than 100 years.

Recovery following deforestation requires the presence of viable plant parts or reproductive units. Olarinmoye (1986), working in Nigeria, examined survival strategies in
three species during re-establishment after a period of drought. *Hyophila involuta* (Figure 81-Figure 82) is able to re-establish through spores, with its sporophyte production appearing to give it a competitive advantage compared to *Barbula indica* (Figure 83) and *Fissidens asplenioides* (Figure 84). The latter two species were similarly wide-spread, using vegetative regrowth from rhizoids, shoot bases, apices, or the main stem, with rhizoids contributing the most regrowth.

![Figure 81. Hyophila involuta, a species that can recolonize disturbed areas. Photo by Shyamal L., through Creative Commons.](image1)

![Figure 82. Hyophila involuta, a species that can colonize by spores after disturbance. Photo by M. C. Nair, K. P. Rajesh, and Madhusoodanan, through Creative Commons.](image2)

![Figure 83. Barbula indica, a species that can colonize deforested areas by vegetative means. Photo by Michael Lüth, with permission.](image3)

![Figure 84. Fissidens asplenioides, a species that can colonize deforested areas by vegetative means. Photo by David Tng, with permission.](image4)

Liu *et al.* (2007) elaborated the species on the forest floor and on the tree trunks in the forest of Heishiding Nature Reserve, Guandong, China. They found that species composition of the mature forest was similar to that of the mixed pine and broad-leaved forest, and to young secondary forest, but community structure of the mature forest was quite different from that of the secondary forest. Most of the bryophytes occurred on the tree trunks (40 species), with only 24 species on the forest floor. Bryophyte cover was low on both substrata. Species richness of forest floor bryophytes in 2,500 m² quadrats ranged 8 to 13 with 0.59% to 1.12% cover. Slope and microenvironment were the primary determinants of species distribution and richness on the forest floor. Epiphytes, on the other hand, exhibited 12 to 20 species with a mean cover of 0.63 to 1.63% in these plots. The researchers concluded that bryophytes in 30-year-old secondary broad-leaved forest had returned to the level of the mature broad-leaved forest.

Corrales *et al.* (2010) recorded 151 terrestrial bryophyte species in secondary and planted montane forests in the northern portion of the Central Cordillera of Colombia. Secondary montane forests have a higher weighted species richness than do the pine plantations. Weighted species richness is higher in secondary montane forests and cypress plantations than in pine plantations. Cypress plantations have the highest bryophyte abundances, although Detrended Correspondence Analysis indicates a high floristic similarity among the various forest types. Differences seem to relate to soil pH, slope, and light availability. Regional patterns depend on continuous dispersal of propagules.

Serrano (1996) found 37 species of mosses in 25 genera in disturbed areas in the municipality of Bayamon, Puerto Rico. *Fissidens* is the most species-rich genus. The most frequent of all species is *Fissidens zollingeri* (see
Figure 84), occurring at all study sites. It is an indicator of disturbed areas. Urbanization further reduces the number of species present. One mechanism accounting for the spread of the species is spore production. Of the 37 species, 18 were observed with capsules and these species tended to occur more frequently when their sporophytes were more frequent. Only 7 species exhibited special vegetative reproductive structures. Among the pleurocarpous species, those with the greatest frequency in collections were those colonizing the greatest number of substrates.

Conservation Issues

Gradstein (1992a, b) and Pócs (1996) emphasized that conservation of epiphytes "can only be achieved through the rigorous protection of the forests."

Plantations seem to have positive and negative effects on bryophyte diversity. One problem they create is a reduction in the number of niches (Ramovs & Roberts 2005; Yan et al. 2013). Their reduction in substrates includes absence of rotten logs and tip-up mounds, substrates that typically have at least some differences in species from typical epiphytic habitats.

Deforestation (Figure 85) has greatly reduced diversity of bryophytes, as one might expect. The loss of the high canopy has forced species that typically occupy the canopy to appear as low as the base of the tree (Gradstein 2002). This change in position correlates with the microclimate of the canopy in the mature forest, with the microclimate in the fallows matching closely the humidity and air temperature of the mature canopy. Such is not the case with the microclimate of the tree bases under the mature canopy.

Henderson et al. (1991) reported that approximately 90% of the South American tropical mountain forests had been converted into pastureland or other non-forest use. Bryophyte losses are greater among mosses than among liverworts (Jácome et al. 2011). Shade species are more affected than drought-tolerant canopy species. The latter species are able to grow in lower positions on the remaining trees. A dense canopy is important in maintaining high diversity (Steffan-Dewenter et al. 2007; Sporn et al. 2009). Despite the negative impact, in Costa Rica the secondary forests may have up to 40% of their epiphytic species exclusively in the secondary forest.

When the cacao (Figure 20-Figure 21) culture was expanded by 230% by converting tropical rainforests, there was little effect on the overall species richness, but plant biomass and carbon storage were reduced by approximately 75% (Steffan-Dewenter et al. 2007). Species richness of forest species was reduced by approximately 60%. More intense agriculture and reduced shade by agroindustry of cacao plantations reduced shade cover from 80% to 40%, but only minor quantitative changes occurred in biodiversity. Unfortunately for the forests and their bryophytes, unshaded systems increased income by 40%. Intermediate levels of canopy cover seemed best for species richness of herbs, bees, wasps, and their antagonists. On the other hand, bryophytes, canopy beetles, and ants lack any significant correlation with canopy cover. This may be because only a small fraction of the forest herb, bryophyte, and beetle species were also able to colonize the agroforestry systems.

When epiphytes were transplanted to lower elevations in the Bolivian Andes, the cover became more even and dominance of individual species decreased (Jácome et al. 2011). The researchers concluded that as the climate changes the individual species responses will differ, resulting in new community relationships. They warn that short-term responses might not be indicative of long-term responses.

Pócs (1989) reported that epiphytes are much rarer in disturbed forests than they are in undisturbed forests in submontane rainforests in the East Usambara Mountains of East Africa. Rather, the species in the disturbed forests are sun species and occur on the lower parts of trunks of Maesopsis (umbrella tree; Figure 86). In the undisturbed forests, these same species occur in the canopy. Pócs has also found a decline in epiphytes in the "undisturbed forest." He attributed this to the drying climate.

Hallingbäck and Hodgetts (2000) contend that the negative impact of habitat loss has already gone too far in the tropical lowlands. Forested land has been cleared continuously for the expansion of the human population and the agriculture to support it (Hyvönen et al. 1987).

Hodgetts et al. (2016) raised concern about the very diverse tropical Atewa Forest in the Eastern Region of Ghana. This area is highly threatened by human activities, including illegal mining, farming, and hunting, as well as thread from industrial bauxite mining. Little is known of its bryophyte flora, and it could be lost before it can be explored adequately. A single survey in March 2014 revealed 164 species, with 58 new to Ghana and 1 new to science.

Costa and Faria (2008) noted conservation priorities for bryophytes in the state of Rio de Janeiro, Brazil. Recognizing the high degree of biological diversity, with an estimated 1,040 species of bryophytes, they cautioned that most of the inventories have focussed on the montane rainforest and coastal region. Among those bryophytes that have been recorded, 14% are considered vulnerable or threatened in the region. They considered the old-growth Atlantic forests to be among most important habitats needing conservation, citing reduction, fragmentation, and isolation as causes for concern. Although 13% of the land
area of the state is protected, these protected areas are mostly montane and upper montane Atlantic rainforests. Alvarenga et al. (2009b) likewise reported a highly significant loss of richness as a result of habitat loss in a Brazilian Atlantic forest. The most conserved fragments have more than 10 times the species richness of the least conserved fragment. In non-conserved fragments, the epiphytes do not colonize the lower trunks (2.1-10 m) or higher zones. Instead, they are restricted to the lowest 2 m at the tree base and clearly exhibit an altered floristic composition. Specialists of sun or shade are impacted more than generalists. The generalists decrease in richness in non-conserved habitats, but their proportion increases due to the loss of specialists. The habitats that retain their rich epiphyte flora are greater than 300 ha in size – an uncommonly large size in the Brazilian Atlantic rainforest.

Figure 86. *Maesopsis eminii* (umbrella tree) providing shade for a coffee plantation. Photo by Aniruddha Dhamorikar, through Creative Commons.

Holz and Gradstein (2005) found that total species richness of bryophytes and lichens differs little between primary and early or late secondary upper montane *Quercus copeyensis* forests (Figure 87) of Costa Rica. The high richness in the secondary forest is most likely due to the high humidity under the closed canopy. Nevertheless, species composition differs markedly. After 40 years of recovery, 46 (one-third) of the species still had not become re-established. Of all recorded species, 40% (68 species) occur exclusively in the secondary forests.

Figure 87. *Quercus copeyensis* forest wherein species richness differs little between primary and secondary forest, but the kinds of species differ. Photo through Creative Commons.

In addition to habitat loss, pollutants can destroy canopy bryophytes. Bryophytes are scavengers of atmospheric nitrogen as they collect the dust from the atmosphere. In this way, they are able to serve as bio-indicators of nitrogen pollution. Shi et al. (2017) examined epiphytic bryophytes from a subtropical montane cloud forest in southwest China. The critical load of nitrogen deposition there was estimated at 18 kg N ha⁻¹ yr⁻¹. The bryophytes become nutrient pools in these circumstances. These high levels are detrimental to the bryophytes, with a significant decrease in cover when the nitrogen input is only 7.4 kg ha⁻¹ yr⁻¹. The study site had a nitrogen deposition rate of 10.5 kg ha⁻¹ yr⁻¹. The researchers suggested that the high N levels not only did direct damage, but caused the leakage of magnesium and potassium, both essential nutrients for cellular metabolism.

In addition to habitat loss, pollutants can destroy canopy bryophytes. Bryophytes are scavengers of atmospheric nitrogen as they collect the dust from the atmosphere. In this way, they are able to serve as bio-indicators of nitrogen pollution. Shi et al. (2017) examined epiphytic bryophytes from a subtropical montane cloud forest in southwest China. The critical load of nitrogen deposition there was estimated at 18 kg N ha⁻¹ yr⁻¹. The bryophytes become nutrient pools in these circumstances. These high levels are detrimental to the bryophytes, with a significant decrease in cover when the nitrogen input is only 7.4 kg ha⁻¹ yr⁻¹. The study site had a nitrogen deposition rate of 10.5 kg ha⁻¹ yr⁻¹. The researchers suggested that the high N levels not only did direct damage, but caused the leakage of magnesium and potassium, both essential nutrients for cellular metabolism.

Plantations seem to have both positive and negative effects on bryophyte diversity. One problem they create is a reduction in the number of niches (Roberts et al. 2005). Their reduction in substrates includes absence of rotten logs and tip-up mounds, substrates that typically have at least some differences in species from typical epiphytic habitats.
Deforestation (Figure 1, Figure 85) has greatly reduced diversity of bryophytes, as one might expect. The loss of high canopy has forced species that typically occupy the canopy to appear as low as the base of the tree (Gradstein 2002). This change in position correlates with the microclimate of the canopy in the mature forest, with the microclimate in the fallows matching closely the humidity and air temperature of the mature canopy. Such is not the case with the microclimate of the tree bases under the mature canopy.

When epiphytes were transplanted to lower elevations in the Bolivian Andes, the cover became more even and dominance of individual species decreased (Jácome et al. 2011). The researchers concluded that as climate changes, individual species responses will differ, resulting in new community relationships. They warn that short-term responses might not be indicative of long-term responses.

Pócs (1989) reported that epiphytes are much rarer in disturbed forests than they are in undisturbed forests in submontane rainforests in the East Usambara Mountains of East Africa. Rather, the species in the disturbed forests are sun species and occur on the lower parts of trunks of *Maesopsis* (Figure 86). In the undisturbed forests, these same species occur in the canopy. Pócs has also found a decline in epiphytes in the “undisturbed forest.” He attributed this to the drying climate.

Climate change studies in the tropics are of utmost importance in a region where many species are already limited by temperature. Jácome et al. (2011) summarized what we know about the effects on the epiphytic bryophyte communities to simulated climate change in the tropics.

Jacobsen (1978) found that epiphytes require a minimum of 7-10 years to regenerate after harvesting of the forest. In any case, deforestation leads to local extinction of species (Gradstein 1992b). Shade epiphytes are the most easily affected by disturbance.

Hällingbäck and Hodgetts (2000) contend that the negative impact of habitat loss has already gone too far in the tropical lowlands. Forested land has been cleared continuously for the expansion of the human population and the agriculture to support it (Hyvönen et al. 1987). In India, Japan, and China mats of mosses are peeled from their substrates for use in the horticulture industry (Peck 2006).

Alvarenga et al. (2009b) likewise reported a highly significant loss of richness as a result of habitat loss in a Brazilian Atlantic forest (Figure 88). The most conserved fragments had more than 10 times the species richness of the least conserved fragment. In non-conserved fragments, the epiphytes did not colonize the lower trunks (2.1–10 m) or higher zones. Instead, they were restricted to the lowest 2 m at the tree base and clearly exhibited an altered floristic composition. Specialists of sun or shade were impacted more than generalists. The generalists decreased in richness in non-conserved habitats, but their proportion increased due to the loss of specialists. The habitats that retained their rich epiphyte flora were greater than 300 ha in size – an uncommonly large size in the Brazilian Atlantic rainforest.

In addition to habitat loss, as seen above, pollutants can destroy canopy bryophytes. Bryophytes are scavengers of atmospheric nitrogen as they collect the dust from the atmosphere. In this way, they are able to serve as bio-indicators of nitrogen pollution. Shi et al. (2017) examined epiphytic bryophytes from a subtropical montane cloud forest in southwest China. The critical load of nitrogen deposition there is estimated at 18 kg N ha⁻¹ yr⁻¹. The bryophytes become nutrient pools in these circumstances. These high levels are detrimental to the bryophytes, with a significant decrease in cover when the nitrogen level is only 7.4 kg ha⁻¹ yr⁻¹. The study site had a nitrogen deposition rate of 10.5 kg ha⁻¹ yr⁻¹. The researchers suggest that the high N levels not only do direct damage, but cause the leakage of magnesium and potassium, both essential nutrients for cellular metabolism.

Figure 88. Atlantic Forest, Antonina Bay, Brazil. Photo by Deyvid Setti and Eloy Olindo Setti, through Creative Commons.

The International Association of Bryologists has representation on the IUCN (International Union for Conservation of Nature). To quote Söderström et al. (1992), “The conservation process involves recognizing and listing rare and decreasing species, recording their distribution, biology and specific threats, proposing conservation programmes, and executing these programmes.” But they point out that the large gaps remaining in our knowledge about bryophytes complicate conservation practices. They list areas needing further study, including taxonomy, bryogeography, habitat demands, natural dynamics, dispersal ability, population structure, and genetics. They stress the importance of focussing on conservation of habitats and sites where species can survive on their own.

In this regard, Villaseñor et al. (2006) gathered data on the rich moss and *Senecio* (Figure 89) flora in the Trans-
Mexican volcanic belt. They were able to identify 11 hotspots that are beneficial to the rich species composition of both groups. They conclude that 18 "cells" in this range would conserve the total diversity of both mosses and Senecio species in these species-rich hotspots.

Figure 89. Senecio toluccanus, a common species of the Trans-Mexican volcanic belt. Photo by Juan Carlos Pérez Magaña, through Creative Commons.

Twenty years ago, our knowledge of tropical bryology was quite meager, making conservation efforts problematic. Sastre de Jesus and Tan (1995) noted the problems in Puerto Rico and the Philippines. As noted by Streimann (1994) for Australia, conservation programs must be preceded by a good knowledge of the bryophytes. In absence of those data, he recommended that at least for those areas that are poorly known for bryophytes, those areas conserved for vascular plants, including national parks and forest reserves, would in most cases be adequate to conserve bryophytes as well.

The bryophyte flora of Mexico was somewhat better known, with more than 900 species, including 98 endemic taxa (Delgadillo 1996). Even so, many areas still need to be explored. Meanwhile, habitat destruction may be destroying some taxa forever. Delgadillo bemoaned the fact that there still was no legislation to protect the habitats of any Mexican mosses.

As in Mexico, moss diversity in the tropical Andes is extensive, with 2,058 species known in 1995. Although this number is probably inflated due to the same species being named multiple times in different locations, the presence of 343 genera and 75 families is still an indicator of the high diversity. Churchill et al. (1995a) estimate the actual number to be 1,500-1,700. They contend that the tropical Andes are eight times as rich in moss species as the Amazon basin. Churchill (1996) summarized the status of our knowledge of moss diversity and conservation in the Andes, noting the needs to prepare for the future.

One of the problems with conserving bryophytes in Neotropical cloud forests (Figure 45) is that they are typically surrounded by xeric habitats unsuitable for their survival (Churchill et al. 1995b).

The Neotropics are not the only tropical area experiencing serious species loss. Turner et al. (1994) reported extinction of 594 of the 2,277 tracheophyte species in the Republic of Singapore. Epiphytic species have suffered 62% loss. These losses are due to deforestation (99.8% of primary forest) and disturbance, with the mangrove epiphytic flora disappearing completely. These losses will necessarily impact the losses of bryophytes through loss of substrate, shade, and sufficient humidity.

Holz and Gradstein (2005) considered that genera and species of bryophytes and macrolichens that are exclusive to the primary (uncut) forests could be used as indicator taxa and that these species and their forests should be conserved.

In French Guiana, water availability affects the bryophyte life forms. When Pardow et al. (2012) compared the life forms of the lowland cloud forests with those of the other lowland forests, they concluded that life forms could indicate lowland cloud forests that are appropriate for conservation. This would permit conservation of a rich bryophyte flora with higher biomass and cover.

With 1,000 epiphyllous liverworts worldwide, these tiny plants represent a group that is also endangered worldwide (Pócs 1996). Of these, 504 are in Asia and 375 in the Americas. They are by far the most species rich in the tropical and subtropical rainforests, but as these forests disappear, so do the epiphylls.

Newer tools may help us to process the data in meaningful ways to understand environmental impacts. In summarizing the symposium and priorities for future research, presented at the first IAB and IAL Symposium on Foliicolous Cryptogams, Gradstein and Lücking (1997) noted that multivariate statistical methods were useful in analyzing the foliicolous community data.

With the inevitability of global climate change, bryophytes living in tropical mountain habitats are clearly in danger. Zhang (2001) found a linear increase in number of species per forest plot with an increase in altitude. As those areas become warmer, those species may not have the time needed for significant dispersal to distant areas with a similar cool climate.

Gradstein and Pócs (1992a) advised that protection of as much as possible of the remaining natural tropical rainforest area seems the best approach to the conservation of the tropical bryophyte flora. This seems to be working in the Wet Tropics of northern Queensland, Australia.
Current Status

In 1982, Schultze-Motel referred to the crisis in tropical bryology. Part of this crisis is the loss of habitats and species before we have even explored to determine what is there to be lost. Even worse, we know little of their role in these sensitive, disappearing ecosystems, even today.

In 1992, Motito et al. recognized the need for bryological study in Cuba (Figure 90). At that time 383 infrageneric bryophyte taxa were known, and studies had begun on phytochemistry and antibiosis. However, it seems that little progress has been made since then on protection of species or of understanding their ecology.

Figure 90. Montane moist forest, Pico Turquino, Cuba. Photo by Male Gringo, through Creative Commons.

In Brazil, biological diversity is high, particularly in the state of Rio de Janeiro (Figure 91). In this area, there are many bryophyte endemics with a total species number estimated at ~1,040 species. Of these, 150 species are classified as vulnerable or threatened. Unfortunately, many of the 1,040 species are in the "data deficient" category, so their abundance is not known, nor do we know what conditions are needed to maintain them. Fortunately, almost 13% of Rio de Janeiro is protected land, but it is mostly in the montane and upper montane Atlantic rainforests. The remaining old-growth Atlantic rainforests are in need of greater conservation.

Figure 91. Rio de Janeiro Tijuca Forest, Brazil. Photo by Pierre André, through Creative Commons.

It appears that the Wet Tropics of Australia may be among the best protected areas with rare and endemic species (Streimann 2000). Most of these areas are in national parks, national estates, world heritage sites, and flora reserves. Even so, they are impacted by tourism.

Summary

Natural disturbances such as El Niño, hurricanes, fire, volcanoes, and animal activity can dislodge bryophytes or provide conditions unsuitable to their continued growth. Some rare and threatened species thrive in these altered conditions, but in general these are potential sources of species losses.

Disturbance is a major cause of loss of species and populations in the tropics. Approximately half of the bryophyte taxa lost on fallow land can become re-established in 10-15 years; most of these are ecological generalists and sun-loving epiphytes. For others it can take 100 years. Sufficient fragment size is important in maintenance and re-establishment of species.

The highest diversity of the fallows is in the understory, contrasting with the highest richness in the canopy of the uncut rainforest. This difference is the result of light penetration, and in some cases moisture.

Human harvesting of bryophytes for horticulture and other human uses not only reduces the bryophyte cover, but also removes habitat for numerous invertebrates and many amphibians.

Industrialization can raise nitrogen levels beyond the limits of tolerance. Heavy metals accumulate in the bryophytes and reach lethal levels. On the other hand, the bryophytes can serve as filters to remove these pollutants from the air, in some cases after the bryophytes die.

Man-made habitats displace natural habitats, but they do increase the number of niches. Some species thrive in these new niches. For example, the leafy liverwort *Spruethanthus theobromae* is currently known from the bark of cacao on plantations.

Many bryophytes have narrow temperature, light, and moisture requirements. Changing climate can not only destroy the forests where they live, but change the microclimate so that it is no longer suitable for them.

Bryophyte recovery can take a long time. In particular, those species living on mountain tops may not have any suitable propagule source without intervening unsuitable habitats. Even in restored lowland rainforests, recovery of bryophyte diversity can require more than 100 years.

The most pressing issues seem to be massive losses of habitat due to agriculture and forestry management for trees only. But climate change is likely to be a close second in the loss of tropical bryophytes in the tropics.

Current practices are beginning to recognize that some species can be conserved by maintaining larger fragments, keeping more trees where trees are cut, anddesignating more land to conservation.
Acknowledgments

My appreciation goes to Robbert Gradstein for his efforts to make this subchapter complete and up-to-date. His many publications, his contribution of images, his mentoring of students, and his helpful comments on a very early version of the chapter kept me going on this part of the world I know so little about.

Literature Cited


Orrego, O. 2005. Ecological indexes and mathematical models as tools for evaluating the epiphytic bryophyte diversity in...


