

CHAPTER 8-12

TROPICS: ROCKS AND INSELBERGS

JANICE M. GLIME AND TATIANY OLIVEIRA DA SILVA

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Figure 1. Inselbergs in Mozambique, Africa. Photo by Ton Rulkens, through Creative Commons.

Rock outcrops and inselbergs provide unique habitats, usually being more xeric than surrounding habitats. An **inselberg** (Figure 1) is distinguished as "those isolated rock outcrops that stand out abruptly from surrounding plains" (Potembski & Barthlott 2012). The term appears to have been introduced by Bornhardt (1900). Both outcrops and inselbergs can differ in rock types, and this can promote different vegetation groupings. Potembski and Barthlott noted that study of the widespread granite inselbergs has been neglected, yet it is "remarkably" rich in plant life. Porembski (2007) identified the three hot spots of inselberg plant diversity on a global scale as southeastern Brazil, Madagascar, and southwestern Australia; the first two of these are tropical.

Barthlott *et al.* (1993) note that the flora of the inselbergs differs almost completely from that of the surrounding area, behaving like islands. They concluded

that the bare rock is covered almost completely by **Cyanobacteria** in French Guyana, but by lichens in the Ivory Coast. Nevertheless, the life forms are similar in the Palaeotropics and Neotropics. It would be interesting to make these same comparisons for bryophytes.

It is interesting that tracheophytes in such dry habitats may mimic some of the traits of bryophytes. These adaptations include forming **mats** and **poikilochlorophyllous** (lose chlorophyll and cease photosynthesis and transpiration when dry) behavior (Porembski & Barthlott 2000). It is incredible that of the approximately 330 species (in only 13 families) of tracheophytes that are desiccation-tolerant, close to 90% occur on inselbergs.

In Brazil, ironstone rock outcrops provide an adverse environment where daily temperatures vary widely, UV exposure is elevated, constant winds are present, and soils

are impermeable and have low water retention with high levels of iron (Peñaloza-Bojacá *et al.* 2018b). Such conditions favor a very rich and endemic community where xerophilic plants thrive.

Rock outcrops are not just bare rock, even in their earliest stages. These topographic differences include shallow depressions that can fill with water (Figure 2), drainage channels (Figure 3), vertical faces with directional N-S exposures (Figure 4), and horizontal plains (Figure 5). In Guinea, mats of *Afrotrilepis pilosa* (Figure 6) create protected habitats, habitats with extremes (*e.g.* Figure 5) that support ephemeral plants, and areas experiencing flushes that have their own distinct vegetation (Porembski *et al.* 1994). Sandstone outcrops of Fouta Djallon in Guinea (Figure 7) are species-rich and have a large number of endemics. Porembski and coworkers suggested this may be due to the combination of vertical differentiation, large area, long-term climate stability, and isolation. The granite inselbergs and **ferricretes** (hard, erosion-resistant layer of sedimentary rock, usually conglomerate or breccia, cemented into a duricrust by iron oxides), on the other hand, lack local endemics and have a lower species richness. The greatest diversity of inselberg vegetation of tropical Africa seems to occur in Tanzania, Malawi, Mozambique, Zambia, Zimbabwe, and Angola.



Figure 2. Rock outcrop at Pico do Papagaio, Brazil, showing shallow pool in rock in the foreground. Photo courtesy of Tatiany Oliveira da Silva.



Figure 3. Rock outcrop, Pedra da Massa, Brazil, showing drainage channels descending from its crest. Photo courtesy of Tatiany Oliveira da Silva.



Figure 4. Colonizing plants on vertical surface of rock outcrop at Pedra do Cachorro, northeast Brazil. Photo courtesy of Tatiany Oliveira da Silva.



Figure 5. Fully exposed horizontal rock outcrop at Pedra, Brazil. This dark-colored rock is even more formidable because it absorbs heat. Photo courtesy of Tatiany Oliveira da Silva.



Figure 6. *Afrotrilepis pilosa* (grass) on an inselberg in West Africa. Photo by Stefan Porembski, through Creative Commons.



Figure 7. Sandstone rock outcrop at Fouta Djallon, Guinea. Photo by Maarten van der Bent, through Creative Commons.

Inuthail and Sridith (2010) examined the structure of plant communities on the granitic inselberg in Songkhla Province in Peninsular Thailand. They identified seven microhabitat types: rock crevices and clefts (Figure 8), rock falls (Figure 7), shallow depressions (Figure 2), deep depressions, exposed rock slopes (Figure 4), shady flat rocky slopes (Figure 3, Figure 9), and rock platform fringes. They recorded 73 species of tracheophytes, with Orchidaceae, Rubiaceae, and Poaceae predominating. The highest number of plant species occurred on the fringes of the rock platforms where soil conditions and light intensities vary.



Figure 8. Mosses in fissure of rock outcrop, Brazil. Photo courtesy of Tatiany Oliveira da Silva.



Figure 9. Rock outcrop with shade provided by tracheophytes at Sítio Pedra das Moças, Brazil. Photo courtesy of Tatiany Oliveira da Silva.

Although some researchers disagree about which formations belong to the inselberg category, Poremski *et al.* (1997) considered granitic inselbergs to be present in all the climatic and vegetational zones of the tropics. Because of the harsh edaphic and microclimatic conditions, the vegetation of inselbergs differs greatly from that of their surroundings. The habitats on these rocks can be defined by vegetation groups including cryptogamic crusts, rock pools, monocot mats, and ephemeral flush vegetation. **Stochastic** (randomly determined) environmental disturbances promote greater species richness due to prevention of competitive exclusion. Other processes are deterministic, creating high temperatures and light levels and extended periods of drought. Moss cushions are able to take advantage of seepage water. In West Africa, *Bryum arachnoideum* (Figure 10) is able to take advantage of such wet areas (Frahm & Poremski 1994).



Figure 10. *Bryum arachnoideum*, a moss that colonizes wet seepage areas on rock outcrops in West Africa. Photo by Jan-Peter Frahm, with permission.

Sarthou *et al.* (2009, 2017) described tropical inselbergs as rocky outcrops protruding from a plain landscape. These are hot spots of plant and animal biodiversity that result from the high turnover of species between sites and the presence of organisms mostly

restricted to the inselberg habitat. Thus they are isolated patches of tracheophytic vegetation surrounded by bare rock or cryptogamic vegetation (algae, lichens, and bryophytes).

Sarthou and Villiers (1998) remind us that tropical inselbergs are surrounded by rainforest, but that they have their own special vegetation. They describe six such associations on French Guianan inselbergs. These respond to different environmental characteristics, including local relief, insolation, water availability, and soil depth. Species diversity is low in all of these associations. They found striking similarities in the vegetation units when comparing those of South American and African inselbergs.

It is only recently that ecological studies of bryophytes on inselbergs have emerged. Ribeiro *et al.* (2007) provided a comprehensive summary of vegetation on rock outcrops in Brazil and outlined the three needs they considered most urgent for study:

1. inselbergs and high mountains in the Amazon and the Brazilian northeast
2. long-term studies, which are almost totally unavailable, hindering global change monitoring and assessment
3. national and international networking to speed up scientific production about such habitats.

Frahm (2000) summarized early studies in the volume by Barthlott and Porembski on inselbergs. Valente and Pôrto (2006) described the bryophytes from a rocky outcrop in Bahia, Brazil. Even in 2018, Peñaloza-Bojacá *et al.* (2018a, b) commented on the paucity of bryophyte studies on rock outcrops and inselbergs.

To elucidate outcrop vegetation in the northeastern Brazil, Silva *et al.* (2014a, b) looked at both tracheophytes and bryophytes on rocky outcrops there. They noted that for these small plants, the large outcrops served as islands amid a "sea" of soil, resulting in a floristic composition that results from **stochastic processes** (unpredictable events) at a regional scale. However, such stochastic processes did not show any clear relationship with the communities on a local scale.

Adaptations

Watson (1933) gave an early view of adaptations to terrestrial adaptations of bryophytes. He suggested that these included **cushion** life forms, the arrangement of the leaves to be imbricated or twisted upon drying, hair points or hyaline leaf apices, leaf borders, infolded leaf margins, thickened cell walls, cell size, and papillae. Some store water and others prevent evaporation. Capillarity was accomplished by spaces between leaves, at leaf axils, between leaf folds, and specialized water folds (lobules as in *Frullania*; Figure 11-Figure 12) and storage cells as in *Leucobryum* (Figure 13). Although at that time there was little experimental evidence to support his suggestions, we now find that these traits often describe adaptations of bryophytes of rock outcrops and inselbergs.



Figure 11. *Frullania gibbosa* on rock outcrop in Brazil. Photo courtesy of Tatiany Oliveira da Silva.

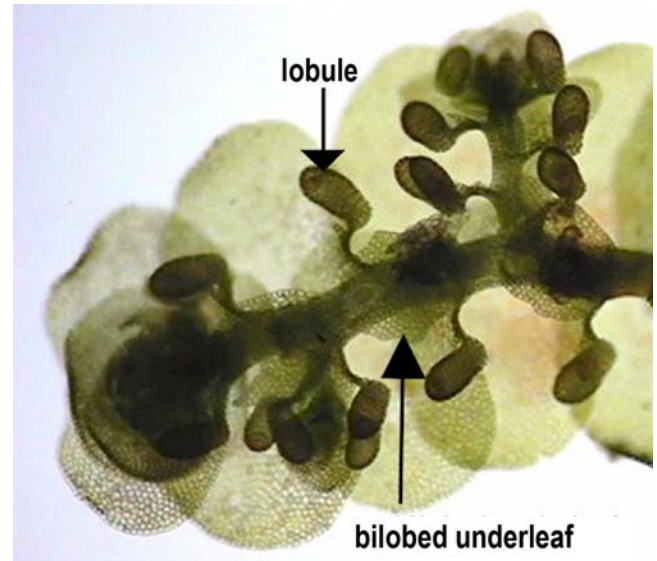


Figure 12. Underside of a *Frullania* branch, showing lobules. Photo by Paul Davison, with permission.



Figure 13. *Leucobryum cf. giganteum* on rock in the Neotropics. Photo by Michael Lüth, with permission.

Life Cycle Strategies

Life cycle strategies can be particularly important in these severe environments. As noted by Benassi *et al.* (2011) for the desert moss *Syntrichia caninervis* (Figure 14), those in the most extreme environments have lower frequencies of sexual expression, fewer sexual branches per individual, and a lower male:female ratio. Sexual reproduction is infrequent. They suggested that male rarity may be due to a lower desiccation tolerance in males. Males have a higher energetic requirement for their sex expression, and this may make them less tolerant to repeated cycles of hydration and desiccation. While rock outcrops and inselbergs are not deserts, many of their microclimate characteristics are similar, so we might expect similar life cycle restrictions.



Figure 14. *Syntrichia caninervis* (Pottiaceae), a xerophytic moss that has lower frequencies of sexual expression, fewer sexual branches per individual, and a lower male:female ratio. Photo by John Game, through Creative Commons.

Frahm (1996) found that bryophytes from the inselbergs he examined in the Ivory Coast and Zimbabwe had a conspicuous lack of both sexual and vegetative propagules. They lacked both the animal and wind dispersal found in inselberg tracheophytes.

Kürschner (2003) found that the life strategy for the *Riccia* liverwort association on thin soil over volcanic rock in Yemen was that of a **shuttle** species. These liverworts produce large spores with short-range dispersal. Disturbances could result in exposure of these spores that have been stored in the diaspore bank. **Geophytes** (plants with short, seasonal lifestyle and some form of underground storage organ) and colonists also occur, but are of only minor importance.

Kürschner (2006) elucidated the ecology of the saxicolous (growing on rocks) *Grimmia ovalis* (Figure 15)-*G. laevigata* (Figure 16-Figure 17)-*G. longirostris* (Figure 18) association on Socotra Island of Yemen. The bryophytes on these sun-exposed, acidic rock formations appear to be mostly endemic and are dominated by *Schlotheimia balfourii* (see Figure 19). The life strategy is that of drought-tolerant **cushions**, **short turf**-forming generative **perennial shuttle species**, **perennial stayers**, and **pauciennial** (short-lived) **colonists**.



Figure 15. *Grimmia ovalis* with capsules, a rock dweller on Socotra Island. Photo by Michael Lüth, with permission.

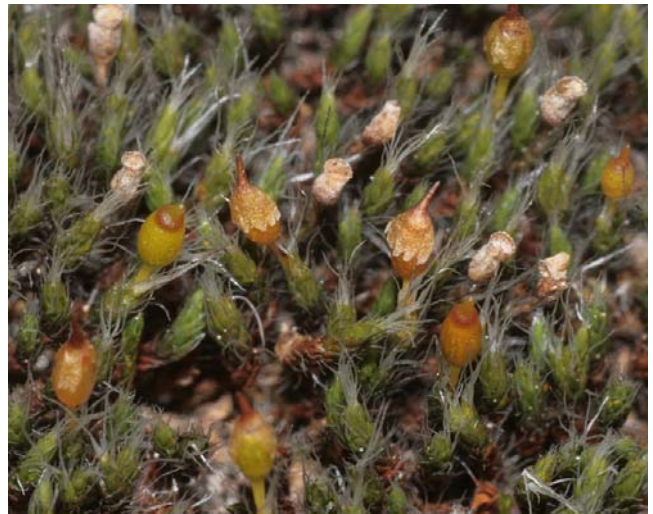


Figure 16. *Grimmia laevigata* with capsules, a rock dweller on Socotra Island. Photo by Hermann Schachner, through Creative Commons.



Figure 17. *Grimmia laevigata*, dry, a rock dweller on Socotra Island. Photo by Janice Glime.



Figure 18. *Grimmia longirostris* with capsules, a rock dweller on Socotra Island. Photo by Hermann Schachner, through Creative Commons.



Figure 19. *Schlotheimia* sp. from the Neotropics; *Schlotheimia balfourii* is a rock dweller on Socotra Island. Photo by Michael Lüth, with permission.

In her study of bryophytes on rock outcrops in Brazil, Silva found that most species were monoicous (26 spp. compared to 20 dioicous species) (Silva 2012; Silva *et al.* 2014b). Nevertheless, the three most frequent species were dioicous. But of these three, two rarely produced sporophytes and one had them only occasionally.

Peñaloza-Bojacá *et al.* (2018a) found that asexual reproduction was important for several of the key species of mosses on Brazilian ironstone outcrops. Surprisingly, dioicous mosses had the highest sexual expression and reproductive success, with most of these species having a female bias. Of the 108 species, 70% were reproducing. A total of 50% of the specimens were reproducing either sexually or asexually. Mosses exhibited mostly asexual reproduction, whereas liverworts mostly exhibited sexual reproduction. Of the asexually reproducing species, 31% had gemmae and 69% had other deciduous propagules. Among the dioicous species, the majority had a female bias.

Pôrto *et al.* (2017) specifically studied the life cycle strategies of the widespread moss *Bryum argenteum* (Figure 20) from a rock outcrop in northeastern Brazil. They noted that despite the severe water constraints of the inselbergs, dioicous mosses are able to colonize rock outcrops and inselbergs. Previous researchers had found

that in northeastern Brazilian rock outcrops, only *Bryum argenteum* frequently had sporophytes (Valente & Pôrto 2006; Silva & Germano 2013; Silva *et al.* 2014a, b). This dioicous species has several asexual strategies – axillary bulbils, rhizoidal gemmae (tubers), and caducous shoot apices (Frey & Kürschner 2011), complemented with numerous small spores when it reproduces sexually (Söderström 1994). Despite its asexual options, 93% of the rock outcrop colonies were expressing sex (Pôrto *et al.* 2017). Although there was a slight female bias, the ratio was only 56:44 female to male. The relationship of number of sporophytes to male:female sex ratio is shown in Figure 21.



Figure 20. *Bryum argenteum* with capsules on rock outcrop in Brazil. Photo of Tatiany Oliveira da Silva.

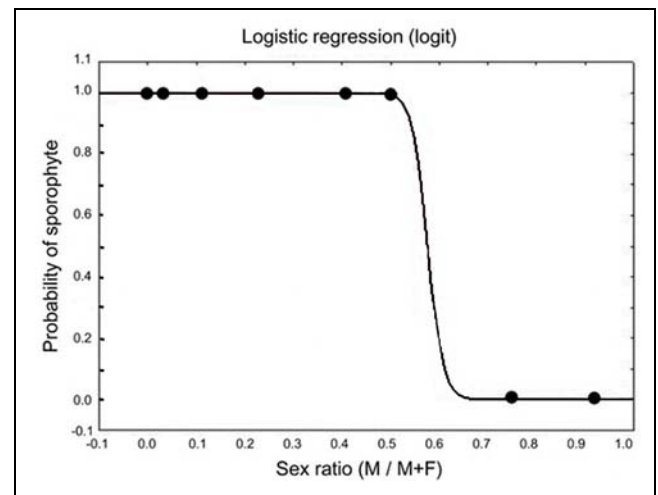


Figure 21. Probability of sporophytes based on sex ratio in *Bryum argenteum*. Modified from Pôrto *et al.* 2017.

So why is *Bryum argenteum* (Figure 20) so productive with sporophytes on the rocks when most other dioicous species are unable to succeed on these rocks? Cronberg *et al.* (2006, 2008) may have the answer. They found that mites are able to disperse the asexual propagules and that springtails (*Collembola*; Figure 22) and possibly mites as well facilitate fertilization. Another factor that may contribute to the success of *B. argenteum* on the rocks and

elsewhere is the ability of antheridia to survive desiccation and rehydration, then to release viable sperm (Shortlidge *et al.* 2012; Stark *et al.* 2016).

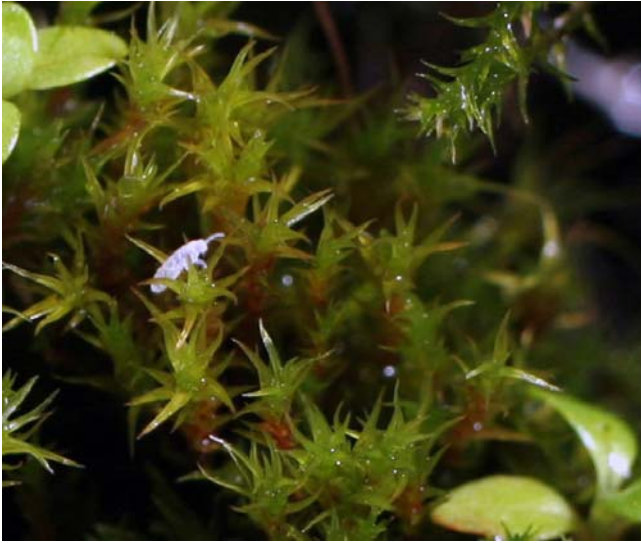


Figure 22. *Folsomia candida* (Collembola) on *Ceratodon purpureus* in fertilization study. Photo courtesy of Erin Shortlidge.

Dispersal

Dispersal can limit the species that reach inselbergs because the surrounding vegetation is of a completely different type (Burke 2002a). Frahm and Porembski (1994) considered the inselbergs of western Africa to be refugia for dry-adapted bryophyte species. Burke (2002a) investigated the role of inselbergs in Namibia as refugia for tracheophyte species. These inselbergs are considered to have a high recolonization potential and a high diversity relative to the landscape. Burke found that gene flow and nutrient flow occur from the inselbergs to the surrounding lowlands. The granite inselbergs support longer-lived species of stable communities, whereas the dolerite inselbergs support transient communities of short-lived species. Regional differences relate to climate, with differences in climate and geology contributing. Altitude is likewise an important variable. Species of granite inselbergs are more closely allied to the surrounding habitats than are those of dolerite inselbergs. Burke concluded that conserving groups of inselbergs is more important to conserving their unique species than conserving isolated mountains. "Stepping stone" inselbergs have greater potential for conserving those species with short dispersal ranges.

These principles should likewise apply to bryophytes, but most likely at a greater distance scale. One way that bryophyte dispersal is facilitated to boulders and inselbergs is having a large number of propagule sources nearby. This can be other boulders and inselbergs, but for many species, it is the ability to grow on other types of substrates. Pócs (1982) demonstrated that many of the tropical species of **Meteoriaceae** (Figure 69-Figure 70), **Neckeraceae** (Figure 23-Figure 24), **Pterobryaceae** (Figure 25), **Plagiochila** (Figure 26), and **Lejeuneaceae** (Figure 37) that are typically corticolous (growing on bark) may also be abundant on rocks.



Figure 23. *Neckera* on rock. Photo by Michael Lüth, with permission.



Figure 24. *Neckera urnigera* from the Neotropics. Photo by Michael Lüth, with permission.



Figure 25. *Calyptothecium duplicatum* (Pterobryaceae) from the Neotropics. Photo by Michael Lüth, with permission.



Figure 26. *Plagiochila* sp. from the Neotropics. Photo by Michael Lüth, with permission.

Desiccation Recovery

One area of adaptations that was usually ignored in early studies was physiological adaptations. Lüttge *et al.* (2008) reported strong quenching of chlorophyll fluorescence in the three desiccated bryophytes in their study of three poikilohydric, homiochlorophyllous moss species from sun-exposed rocks of a Brazilian tropical inselberg. Using *Campylopus savannarum* (Figure 27-Figure 28), *Rhacocarpus fontinaloides* (see Figure 29), and *Ptychomitrium vaginatum* (see Figure 30), they concluded that these species have photo-oxidative protection that permits them to live on exposed rocks that experience high light intensity. They achieve this by a reduction of the base chlorophyll fluorescence to nearly zero. Upon rewetting there is a rapid recovery to higher values in the first 5 minutes, requiring more than 80 minutes to reach equilibrium. These adaptations help to define their niches, with *C. savannarum* forming an inner belt and *R. fontinaloides* forming an outer belt around the vegetation. *Ptychomitrium vaginatum*, on the other hand, lives in small cushions on bare rock. Nevertheless, these three species differ little in their reduction of fluorescence or rewetting recovery and have only slight differences in photosynthetic capacity. The researchers suggest that CO₂ acquisition is a greater problem in *P. vaginatum* than in the other two species, with water films causing limitations in CO₂ uptake.



Figure 27. *Campylopus savannarum* and *C. pilifer* in fissure of rock outcrop in Brazil. Photo by courtesy of Tatiyan Oliveira da Silva.



Figure 28. *Campylopus savannarum*, a species that has photo-oxidative protection that helps to adapt it to living in exposed rock habitats. Missouri Botanical Garden, through Creative Commons.

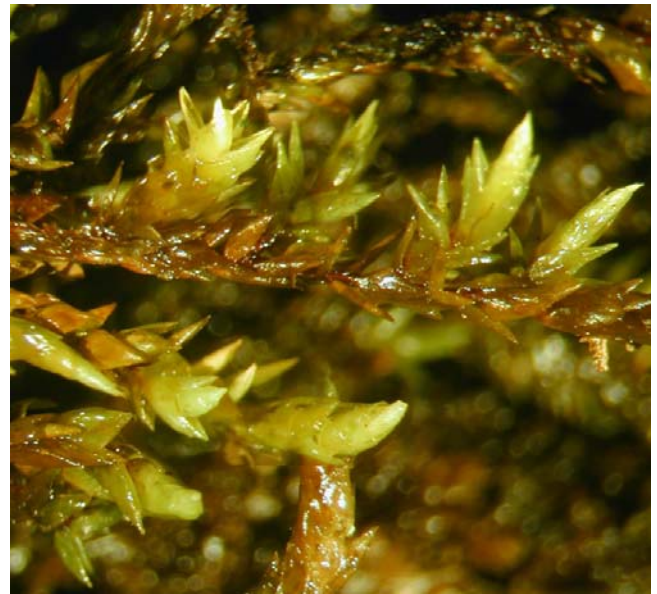


Figure 29. *Rhacocarpus inermis* from the Neotropics; *Rhacocarpus fontinaloides* has photo-oxidative protection that permits it to live on exposed rock surfaces. Photo by Michael Lüth, with permission.



Figure 30. *Ptychomitrium* sp. with capsules; *Ptychomitrium vaginatum* has photo-oxidative properties that help to permit it to live on exposed rocks. Photo by Paul Wilson, with permission.



Figure 31. *Cyanotis lanata*, a species that seems to improve the rock outcrop environment for the moss *Archidium acanthophyllum*. Photo by Anya Quinn, through Creative Commons.



Figure 32. *Archidium ohioense*; in southwestern Nigeria, *Archidium acanthophyllum* occurs on rock outcrops. Photo by Li Zhang, with permission.

Interactions with Other Plants

As noted by During and van Tooren (1990) as a general principle, bryophyte habitats can be defined by not only the physical environment, but also the tracheophyte vegetation associated with it. Nevertheless, at that time few studies had analyzed the functionality of these interactions.

Tracheophytes on boulders and inselbergs collect soil, provide shade, and retain moisture for longer times than unvegetated areas. Protection by the monocot *Cyanotis lanata* (Figure 31) permits *Archidium* (see Figure 32) to survive on savannah rock outcrops in southwestern Nigeria (Egunyomi 1984; Oluwole & Adetunji 2010). [The naming of this *Archidium* has been problematic, with Egunyomi naming it *Archidium ohioense*, then Frahm and Porembski (1994) determining it to be *Archidium globiferum* in West Africa. However, currently it seems to be considered to be *Archidium acanthophyllum*.] During the rainy season, the annual mosses *Bryum argenteum* (Figure 20) and *Pelekium gratum* (Figure 33) may also appear in this association (Egunyomi 1984).



Figure 33. *Pelekium cf. gratum*, a species that often accompanies *Archidium acanthophyllum* on rock outcrops in southwest Nigeria. Photo by Shyamma L., through Creative Commons.

On these southwestern Nigerian inselbergs, there is a three-member association that illustrates relationships among the moss *Archidium acanthophyllum* (see Figure 32), tracheophyte *Cyanotis lanata* (Figure 31), and lichen *Diploicia canescens* (Figure 34) (Oyesiku & Amusa 2010). Oyesiku and Egunyomi (2004) found a frequency of 50% of occurrences of *Archidium acanthophyllum* with *Cyanotis lanata*, whereas only 20% grew alone and 30% grew with other plants, suggesting some benefit from its association with *C. lanata*. But these two species grow best in somewhat different optima. For *C. lanata*, the optimum pH is 6.7, whereas it is 7.7 for *A. acanthophyllum*. *Cyanotis lanata* density increases and *Archidium acanthophyllum* decreases from March to September, whereas both the *A. acanthophyllum* and *C. lanata* decrease from September to December (Figure 35). This is likely due to the strong increase in temperature of the substrate to 39.6°C in December. Both plants are harmed at temperatures above 50°C. In June and September, the relative humidity above the vegetation increases significantly, with a mean of 79% during the study. Data indicate that *C. lanata* and *A. acanthophyllum* facilitate each other. As noted in other ecosystems (e.g. Richardson 1958; Edward & Miller 1977), thick bryophyte growths can serve as insulation to buffer the temperature of the underlying substrate. Richardson (1958) also noted that bryophytes could reduce evaporation. Both of these properties provide a more favorable environment for the roots of tracheophytes. Oyesiku and Egunyomi (2004) verified that these relationships are true for bryophytes on inselbergs.



Figure 34. *Diploicia canescens*, a lichen that occurs on rock outcrops in southwestern Nigeria. Photo by Jymm, through public domain.

On these inselbergs in southwestern Nigeria, the lichen *Diploicia canescens* (Figure 34) maintains a consistent density throughout the year (Oyesiku & Amusa 2010). On the other hand, the monocot *Cyanotis lanata* (Figure 31) and the moss *Archidium acanthophyllum* (see Figure 32) coexist, but in this relationship, the density of *A. acanthophyllum* decreases as that of *Cyanotis lanata* increases from March to September (Figure 35). From September to December, both species decrease (Figure 35). Whereas the moss and monocot seem to facilitate each

other, the lichen is inhibited by growth of these two species.

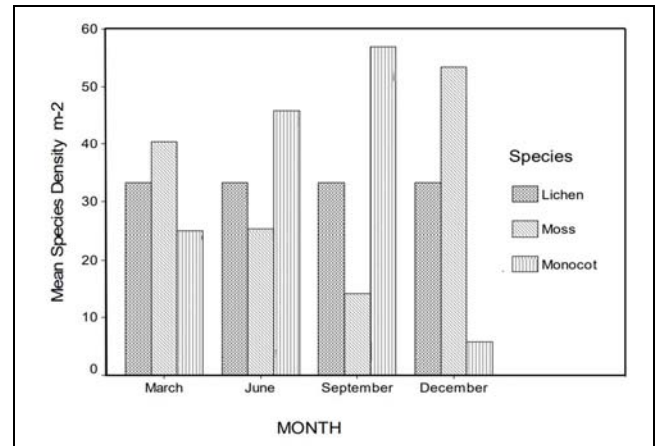


Figure 35. Quarterly density dominance of three interacting plants and lichens on the Baasi Inselberg, Nigeria. Modified from Oyesiku and Egunyomi 2004.

The bryophytes and tracheophytes can also have nutrient cooperation. Bryophytes collect dust and runoff that contain nutrients. These can later be transferred to the tracheophytes. Oyesiku (2018 in press) investigated these relationships between *Archidium acanthophyllum* (see Figure 32) and *Cyanotis lanata* (Figure 31).

Lava Flows

Tropical lava flows provide unique rock habitats. Ah-Peng *et al.* (2007) investigated the altitudinal differences on a recent lava flow (19 years old) on Réunion Island. Because of the uniformity of the lava flow, it is easier than in most habitats to isolate variables such as altitudinal effects. They surveyed bryophyte communities from 250 to 850 m asl using the three substrates of ground and rachises of two fern species. As in many other altitudinal studies, bryophyte diversity increased with altitude. They identified 70 species of bryophytes in the study, with diversity related to microhabitats. The lava flows support a high number of pioneer organisms that are able to colonize remnant lowland rainforest.

Richness and Diversity

Rocky outcrops and inselbergs form islands amid the surrounding soil vegetation (Silva *et al.* 2014a, b), although Silva and coworkers did not compare the flora of the inselbergs with the surrounding vegetation. If they are correct, the species that arrive there must often come from a distance and must rely on **stochasticity** (unpredictable events). Silva and coworkers demonstrated that such processes are the major factors determining species clustering at a regional scale. Such a relationship was not clear at the local level.

Later, Sarthou *et al.* (2017) provided us with evidence that the surrounding forest, regional climate, and inselberg features including altitude, shape, habitats, summit vegetation, epiphytism, and fire events contribute to shifts in the distribution of species and functional traits. These factors determine the floristic patterns on inselbergs in French Guiana and demonstrate that the surrounding forest

can contribute to the inselberg vegetation. This is probably even more likely for bryophytes.

Ribeiro *et al.* (2007) often found xerophytes and hydrophytes (of the tracheophytes) side-by-side on the boulders due to the small scale environmental heterogeneity. Such conditions also support the great variety of bryophytes on these rocks.

Africa

The inselbergs of West Africa are geologically old and typically dome-shaped monoliths (Porembski & Barthlott 1996). The vegetation differs starkly from that of the surrounding vegetation. The inselbergs provide a severe climate with extreme temperatures and light intensity. Nevertheless, ~600 tracheophyte species occur among these inselbergs, predominately in the grasses (Poaceae), sedges (Cyperaceae), and legumes (Fabaceae). The rocks provide such habitats as cryptogamic crusts, rock pools, monocotyledonous mats, and ephemeral flush vegetation that can be distinguished based on physiognomy (Porembski *et al.* 1997). The ephemeral flush vegetation is the richest in species (Porembski & Barthlott 1996). Moss cushions, particularly those of *Bryum arachnoideum* (Figure 10), can establish where seepage water is sufficient (Frahm & Porembski 1994).

The tracheophytes on Ivory Coast inselbergs exhibit low **beta diversity** – that is, the flora is relatively uniform across the country (Porembski & Barthlott 1996). Higher beta diversity occurs in the small habitats like rock pools, presumably due to stochasticity. Diversity decreases from savannahs toward the rainforest zone. In the drier areas in the northern part of the Ivory Coast, the growing conditions are less favorable, permitting weak competitors to have a better chance.

On the tropical inselbergs of the Ivory Coast (Côte d'Ivoire) (Figure 36) and Zimbabwe, Frahm and coworkers found that the number of bryophyte species does not correlate with either size of inselberg or elevation (Frahm 1996; Frahm *et al.* 1996). In the Ivory Coast, species richness is greater when the inselberg is in the savannah compared to those in rainforest regions. In the Ivory Coast, they found total species richness of inselbergs to be 31, whereas in Zimbabwe it was only 25. Only 3 families are represented. These researchers found that inselberg bryophytes have larger distribution areas and no endemic species compared to tracheophytes on them. Eight species are common to both. One interesting feature is that these bryophytes typically lack sexual reproduction, but have "conspicuous" vegetative reproduction.

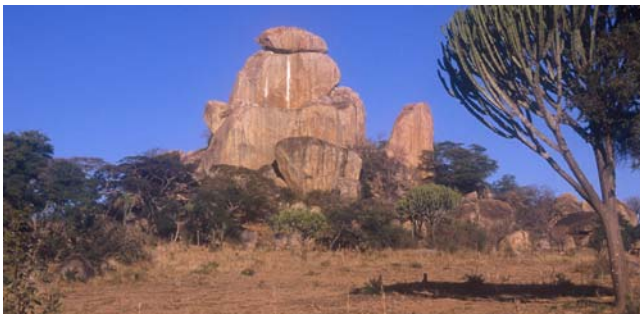


Figure 36. Inselberg (kopje) in Marada Hills, Zimbabwe. Photo by Kevin Walsh, through Creative Commons.

The highest number of bryophyte species from African inselbergs was in the Côte d'Ivoire with 31 species, contrasting with the lowest number of 16 in the Seychelles. This can probably be explained by the location of Côte d'Ivoire in the rainforest as well as in the savanna belt, widening the surrounding vegetation types. Most of the species of bryophytes are acrocarpous mosses, with only *Sematophyllum fulvifolium* and *Erythrodonium squarrosus* representing the pleurocarpous mosses.

Frahm and Porembski (1997) visited the small tropical African country of Benin. They identified 8 liverworts and 10 mosses from inselbergs. Of these, 5 liverworts [*Acrolejeunea emergens* (Figure 37), *Riccia atropurpurea* (Figure 38), *R. congoana* (Figure 39), *R. discolor*, *R. moenkemeyeri*] and all of the mosses [*Archidium ohioense* (possibly *A. acanthophyllum*; Figure 32), *Brachymenium acuminatum* (Figure 40), *B. exile* (Figure 41), *Bryum arachnoideum* (Figure 10), *B. argenteum* (Figure 20), *Bryum depressum*, *Garckea moenkemeyeri* (see Figure 42), *Hyophila involuta* (Figure 43-Figure 44), *Philonotis mniobryoides* (see Figure 58) and *Weissia cf. edentula* (Figure 45)] proved to be new records for the country. This may relate more to lack of studies than to uniqueness of the inselbergs.

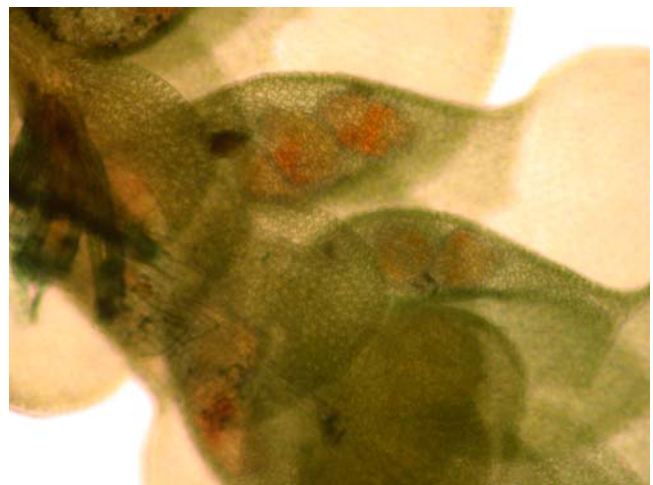


Figure 37. *Acrolejeunea emergens* (Lejeuneaceae) with liverworts (reddish). Photo courtesy of Claudine Ah-Peng.



Figure 38. *Riccia atropurpurea*, a liverwort that occurs on inselbergs in Benin, Africa. Photo from Missouri Botanical Garden, through Creative Commons.



Figure 39. *Riccia congoana*, a liverwort that occurs on inselbergs in Benin, Africa. Photo from Missouri Botanical Garden, through Creative Commons.



Figure 40. *Brachymerium acuminatum*, a moss that occurs on inselbergs in Benin, Africa. Photo by Jan-Peter Frahm, with permission.



Figure 41. *Brachymerium exile*, a moss that occurs on inselbergs in Benin, Africa. Photo by Show Ryu, through Creative Commons.



Figure 42. *Garckea flexuosa*; *Garckea moenkemeyeri* is a moss that occurs on inselbergs in Benin, Africa. Photo by Manju C. Nair, through Creative Commons.



Figure 43. *Hyophila involuta* habitat in India. Photo by Michael Lüth, with permission.



Figure 44. *Hyophila involuta*, a moss that occurs on inselbergs in Benin, Africa. Photo by Michael Lüth, with permission.



Figure 45. *Weissia edentula* with capsules, a moss that occurs on inselbergs in Benin, Africa. Photo by Louis Thouvenot, with permission.

Burke (2002b) found that in Namibia, soil properties do not seem to have an important role in the arid environments. Furthermore, parameters such as slope aspect and angle play a minor role. The grassland and shrubland plant communities relate primarily to general habitat, elevation, size of inselberg, and geology. The inselbergs are able to harbor plant species from neighboring higher rainfall areas, thus providing a propagule source for recolonization.

Burke (2003) found that granite inselbergs in Namibia are more closely related to mountain habitats than are the dolerite ridges. And as expected, higher inselbergs are more closely related to mountain habitats than are lower inselbergs. Many species, especially those with broad habitat requirements, are common to both inselbergs and mountain habitats. On the other hand, the short-lived transient species are more similar between the dolerite ridges and the "mainland." Thus, the granite inselbergs can be important sources of remnant populations from a wetter past, whereas the dolerite ridges can form species pools for the rangeland.

Kürschner (2003) extended our knowledge of rock outcrops in the Jabal Arays area of Yemen. Here they found communities of *Riccia jovet-astiae* (see Figure 38-Figure 39) and *Riccia argenteolimbatæ* on the thin soils overlying volcanic rock outcrops in monsoon areas where woodlands are characterized by *Sterculia africana* (Figure 46). These are typically accompanied by *Mannia androgyna* (Figure 47) and *Barbula unguiculata* (Figure 48-Figure 49). The shallow soils generally have large numbers of riccioid and marchantioid liverworts, with *Riccia atromarginata*, *R. albolimbata* (Figure 50-Figure 51), and *R. argenteolimbatæ* characterizing the association.

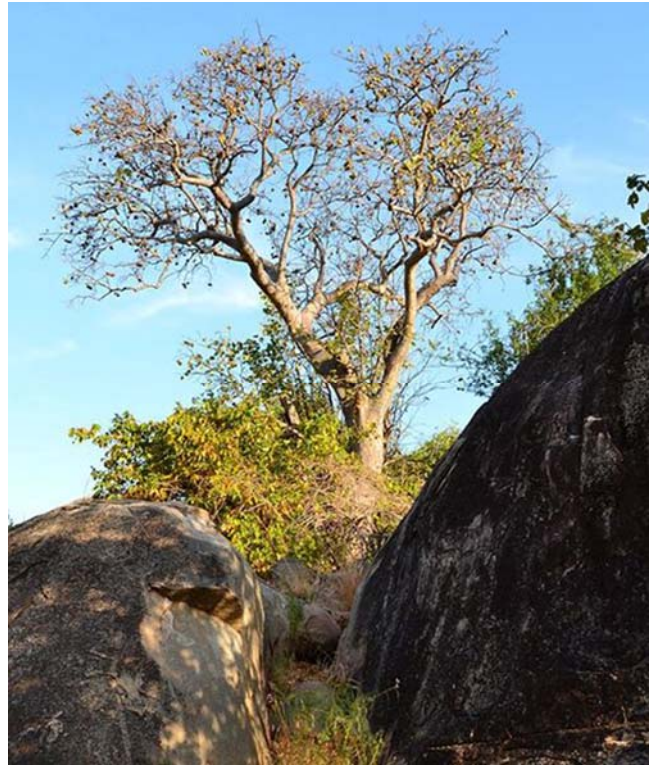


Figure 46. *Sterculia africana* in Malawi. Photo by Jinge Norvall Andrews, through Creative Commons.



Figure 47. *Mannia androgyna*, a species of rock outcrops in the Jabal Arays area of Yemen. Photo by Valter Jacinto, through Creative Commons.



Figure 48. *Barbula unguiculata* (dry), a species of rock outcrops in the Jabal Arays area of Yemen. Photo by Bob Klips, with permission.



Figure 49. *Barbula unguiculata* with capsules (wet), a species of rock outcrops in the Jabal Arays area of Yemen. Photo by Michael Lüth, with permission.



Figure 50. *Riccia albolimbata* (dry), a species of rock outcrops in the Jabal Arays area of Yemen. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

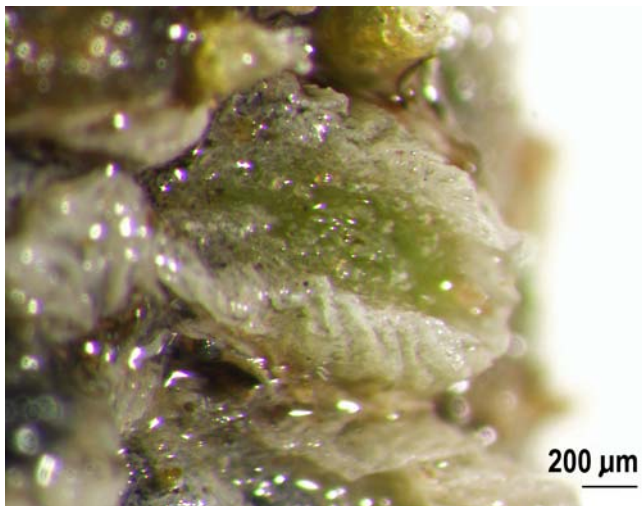


Figure 51. *Riccia albolimbata* (wet), a species of rock outcrops in the Jabal Arays area of Yemen. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

In the Drakensberg area of South Africa, Hodgetts *et al.* (1999) found that lowland sandstones support common and widespread species that can survive long drought periods. More species are present where there is more moisture, as in ravines, rock crevices, and on stream banks. A different suite of species occur on shaded sandstone cliffs and rocks. A third type of community occurs in flushes. Exposed rocks generally have few species, with *Grimmia pulvinata* (Figure 52) and *Ptychomitrium cucullatifolium* (Figure 53) being common here. On the basalt rocks, at about 3,000 m asl, most species are restricted to crevices, on boulders, and in the turf below the cliffs. *Quathlamba debilicostata* (in narrow cracks) and *Orthotrichum oreophilum* (in cushions on inner vertical and overhanging surfaces of wider cracks; Figure 54) seem to occur only in vertical cracks in the basalt cliffs.



Figure 52. *Grimmia pulvinata* with capsules, a species of exposed rocks in tropical South Africa. Photo by Michael Becker, through Creative Commons.



Figure 53. *Ptychomitrium polyphyllum* with capsules; *Ptychomitrium cucullatifolium* is a species of exposed rocks in tropical South Africa. Photo by David T. Holyoak, with permission.



Figure 54. *Orthotrichum* sp. on vertical rock; *Orthotrichum oreophilum* occurs on the inner vertical surfaces of wide cracks of inselbergs. Photo by Algirdas, through public domain.

Neotropics

Porembski *et al.* (1998; Porembski 2007) defined **inselbergs** as "mostly" dome-shaped rock outcrops in all climatic and vegetational zones of the tropics. In Brazil, these consist of Precambrian granites and gneiss that form ancient and stable landscape elements. Because of their exposure, they create harsh conditions of microclimate. These strikingly different conditions result in strikingly different vegetation. One of the most characteristic communities is one of monocotyledonous mats. These can provide cover and retain moisture that permits some bryophytes to survive there. Porembski and coworkers, studying tracheophytes, found that the alpha diversity (community diversity) of the mats differed little among the six outcrops studied. However, beta diversity (regional) differed greatly between sites. The Brazilian rock outcrops demonstrate a higher diversity compared to those of West African inselbergs, with the appearance of more endemics in the Brazilian communities. However, some species considered endemics at that time may have proved to be synonyms of more widespread species since then. Nevertheless, the diversity is high, perhaps due to the large species pool.

Silva (2012) studied the rock communities in the state of Pernambuco, Brazil. She divided the microhabitats on the outcrops into exposed rock, fissure, soil island, and **cacimba** (rock pools – pit in wet or marshy ground, collecting the water present in the soil that accumulates in it by condensation). Substrates also differed: rock, live

trunk, dead trunk, and soil. She identified 49 species in 36 genera and 20 families. Of these, 34 were mosses, 15 were liverworts. The most species-rich families were the leafy liverworts **Lejeuneaceae** (Figure 37) (7 spp) and **Frullaniaceae** (Figure 55) (4 spp), and the moss families **Bryaceae** (Figure 20) (6 spp), **Dicranaceae** (Figure 27-Figure 28, Figure 56) (4 spp), and **Pottiaceae** (Figure 14) (4 spp), comprising 53% of the species. The liverwort genus *Frullania* (Figure 55) and moss genus *Campylopus* (Figure 56) had the highest species richness. The most common species were the mosses *Brachymerium exile* (Figure 57), *Bryum argenteum* (Figure 20), *Campylopus pilifer* (Figure 56), *C. savannarum* (Figure 27-Figure 28), *Philonotis hastata* (Figure 58), and *Syrrhopodon gaudichaudii* (Figure 59-Figure 60), and the liverworts *Frullania kunzei* (Figure 55) and *Riccia vitalii* (Figure 61); frequencies are in Table 1. Two of the less common species, *Atrectylocarpus brasiliensis* (see Figure 62) and *Riccia taeniiformis* (Figure 63), are endemic to Brazil. **Turf** comprised 74% of the life forms. The most species richness (37 spp., 89%) occurred on soil islands that were 1.0 and 4.9 cm deep, whereas only 12 species occurred on rock. Approximately half the species had a wide distribution pattern. Similarity among sites was less than 50%.

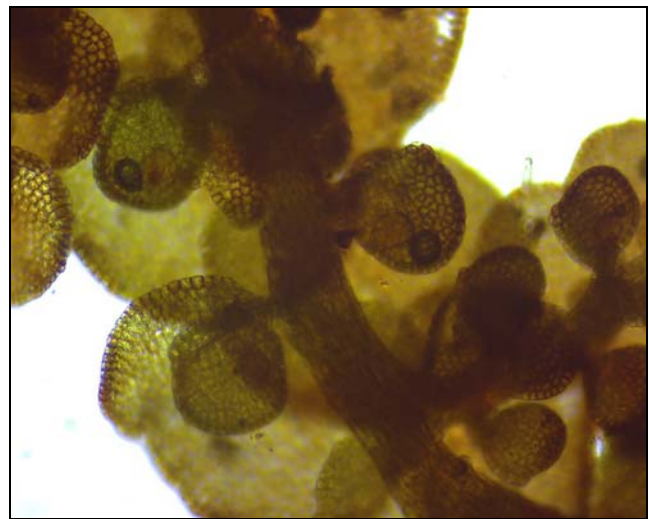


Figure 55. *Frullania kunzei*, a frequent rock outcrop species in Brazil. Photo by Y. Inturias, through Creative Commons.



Figure 56. *Campylopus pilifer* on rock outcrop in Brazil. Photo courtesy of Tatiany Oliveira da Silva.



Figure 57. *Brachymerium exile*, one of the most common species on rock outcrops in Brazil. Photo by Show Ryu, through Creative Commons.

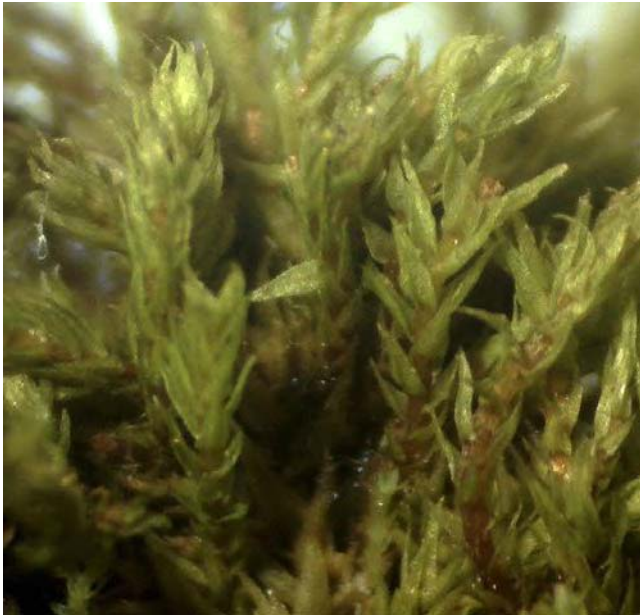


Figure 58. *Philonotis hastata*, a common species on rock outcrops in Brazil. Photo by Y. Inturias, through Creative Commons.



Figure 59. *Syrrhopodon gaudichaudii*, on a rock outcrop in Brazil. Photo courtesy of Tatiany Oliveira da Silva.



Figure 60. *Syrrhopodon gaudichaudii* demonstrating the leaf curling that helps it conserve water on exposed rocks. Photo by Juan David Parra, Creative Commons.



Figure 61. *Riccia vitalii*, a common liverwort on rock outcrops in Brazil. Photo courtesy of Tatiany Oliveira da Silva.



Figure 62. *Atractyllocarpus madagascariensis*; *Atractyllocarpus brasiliensis* occurs on rock outcrops in Brazil, where it is endemic. Photo by Jan-Peter Frahm, with permission.



Figure 63. *Riccia taeniiformis* on rock outcrop in Brazil. Photo courtesy of Tatiany Oliveira da Silva.



Figure 65. *Barbula indica*, a common species on rock outcrops in Brazil. Photo by Jan-Peter Frahm, with permission.

Table 1. The most common bryophyte species on rock outcrops in Brazil (Silva 2012).

Species	Frequency
<i>Campylopus savannarum</i> (Figure 27-Figure 28)	97
<i>Campylopus pilifer</i> (Figure 56)	52
<i>Bryum argenteum</i> (Figure 20)	30
<i>Frullania kunzei</i> (Figure 55)	15
<i>Philonotis hastata</i> (Figure 58)	14
<i>Syrrhopodon gaudichaudii</i> (Figure 59-Figure 60)	14
<i>Barbula indica</i> (Figure 64-Figure 65)	13
<i>Brachymenium exile</i> (Figure 57)	13
<i>Riccia vitalii</i> (Figure 61)	12
<i>Octoblepharum albidum</i> (Figure 66)	10



Figure 66. *Octoblepharum albidum*, a common species on rock outcrops in Brazil. Photo courtesy of Tatiany Oliveira da Silva.



Figure 64. *Barbula indica* on rock in Bareilly India. Photo by Michael Lüth, with permission.

Like Silva (2012), when studying Brazilian ironstone outcrops Peñaloza-Bojacá *et al.* (2018a) found the greatest bryophyte diversity on soil, but also on the rocks. They identified 108 species of bryophytes (42 liverworts and 66 mosses). In Cangas sites, Peñaloza-Bojacá *et al.* (2018b) reported 96 bryophyte species from Brazilian ironstone outcrops. These were comprised of 56 mosses and 40 liverworts, with 68 of the species associated with tree microhabitats and 67 species with bark substrates. The ironstone sites seem to harbor more species than other types of rock outcrops in the country.

Silva and Germano (2013) studied rock outcrops in the caatinga biome in the state of Paraíba, Brazil, from February 2010 to May 2011 and identified 21 bryophyte species, 6 liverworts and 15 mosses. They were able to identify three species clusters. These were **generalist** species that required high light. Their leaf structures generally permitted them to withstand drying environmental conditions.

In their study of the campos rupestres of Chapada Diamantina, Bahia, Brazil, Bastos *et al.* (2000) identified 65 taxa (41 moss species, 24 liverwort species) comprising a total of 20 families. Most of these taxa seem to be restricted to the Chapada Diamantina and are not known from other parts of the state.

Sarthou *et al.* (2009) examined the factors that have a role in the seral stages on the inselbergs in French Guiana. The environment is harsh, with violent storms, intense runoff, and lightning strikes, destroying vegetation cover and organic matter. They considered the vegetational changes to be truly successional, not conditioned by slope. The vegetation experienced cyclic changes that were reinitiated by fire (lightning), wood-destroying fungi, and termites that destroyed the vegetation.

In her inselberg succession studies, Sarthou and coworkers (2009, 2017) found that where the aerial parts of *Clusia minor* (Figure 67) have been destroyed, the ground frequently is covered with mosses and lichens. Their rhizoids capture and retain soil particles, preventing them from being flushed away by water.



Figure 67. *Clusia minor*, an inselberg species that is replaced by mosses and lichens when it is destroyed by fire or other disturbance. Photo by David J. Stang, through Creative Commons.

Sarthou *et al.* (2017) compared 22 inselbergs in French Guiana. They found that the spatially dictated environmental gradient was a primary driver in the floristic composition on these inselbergs. Southward communities have more drought-adapted plants. The northern group has high endemism. The north-south gradient is driven by regional climate (annual rainfall), forest matrix (canopy openness), and inselberg features (altitude, shape, habitats, summit forest, degree of epiphytism, fire events).

Breen (1953) studied bryophytes in subtropical Florida, USA. She found that a number of tropical species occurred exclusively on limestone in subtropical Florida (and in many cases other southern states). Tropical *Jaegerinopsis* (Pterobryaceae), *Vesicularia* (Hypnaceae; Figure 68), *Meteoriopsis* (Figure 69), *Papillaria* (Figure 70), and *Syrrophodon* (Figure 59-Figure 60) are restricted mostly to hammocks, usually on bark of 1-2 species of hardwoods. In swamps, *Cyclodictyon* (Figure 71) and some tropical *Fissidens* (Figure 72) occur. But the limestone regions hold the most bryologically interesting species. Most of the coastal land in the Caribbean and in the West Indies is of limestone origin. She found 11 Neotropical species that in Florida are restricted to limestone. *Luisierella barbula* is a tiny species easily overlooked, but is relatively widespread in Central America and Brazil. *Hyophiladelphus agraria* (see Figure 73) is widespread in both the Neotropics and subtropics. *Weissia*

jamaicensis (Figure 74) occurs in some Central American countries as well as Florida; it is sterile in Florida. This species typically occurs there with *Marchantia paleacea* (Figure 75). *Hypopterygium tamarisci* (Figure 76) is a tropical relic in Florida, also known from both Central and South American tropics. *Leptodictyum riparium* (Figure 77), also a Floridian limestone dweller, is more widespread in aquatic habitats, but is known from Mexican tropics. *Gymnostomiella vernicosa* (Figure 78-Figure 79) is also in Jamaica, Haiti, and Mexico. *Plaubelia sprengelii* (Figure 80) also occurs in the West Indies, Mexico, and Central America, whereas *Syrrophodon prolifer* (Figure 81) occurs in these locations plus South America, typically on thin layers of soil over limestone in protected pockets. *Taxiphyllum cuspidatum* (see Figure 82) occurs on boulders. *Hyophila involuta* (Figure 43-Figure 44) is a common tropical rock dweller, but is again restricted to limestone in Florida. *Fissidens hallianus* (see Figure 72) is restricted in the USA to Florida. The other species Breen found on the Floridian limestone are not tropical.



Figure 68. *Vesicularia vesicularis* var. *vesicularis* from the Neotropics. *Vesicularia* occurs on limestone rocks in Florida, USA. Photo by Michael Lüth, with permission.



Figure 69. *Meteoriopsis squarrosa*; the genus *Meteoriopsis* is restricted mostly to bark in hammocks in Florida. Photo by Manju Nair, through Creative Commons.



Figure 70. *Papillaria crocea*; *Papillaria* is restricted mostly to bark in hammocks in Florida. Photo by Peter Woodard, through public domain.



Figure 73. *Hyophiladelphus* sp. with capsules; *H. agraria* is a Neotropical species that in Florida is restricted to limestone. Photo by Fred Essig, with permission.



Figure 71. *Cyclodictyon albicans* with capsules, in a tropical genus that also occurs in Florida, USA. Photo by Claudio Delgadillo Moya, with permission.



Figure 72. *Fissidens asplenioides* from the Neotropics, in a genus found in swamps in Florida. Photo by Michael Lüth, with permission.



Figure 74. *Weissia jamaicensis* on limestone rock bands, Uige Province, Angola, a species that also occurs on limestone rocks in Florida, USA, and the Neotropics. Photo by T. Lautenschläger, through Creative Commons.



Figure 75. *Marchantia paleacea*, a species that occurs on limestone rocks in Florida, USA, and the Neotropics. Photo by David Long, with permission.



Figure 76. *Hypopterygium tamarisci*, a species that occurs on limestone rocks in Florida, USA, and the Neotropics. Photo by Peter Woodard, through Creative Commons.



Figure 77. *Leptodictyum riparium*, a species that occurs on limestone rocks in Florida, USA, and the Neotropics. Photo by Michael Lüth, with permission.



Figure 78. *Gymnostomiella vernicosa tenerum*, a species that occurs on limestone rocks in Florida, USA, and in the Neotropics. Photo by Sean Edwards, with permission.



Figure 79. *Gymnostomiella vernicosa tenerum* gemma, a species that occurs on limestone rocks in Florida, USA, and in the Neotropics. Photo by Sean Edwards, with permission.



Figure 80. *Plaubelia sprengelii*, a species that occurs on limestone rocks in Florida, USA, and in the Neotropics. Photo by Jan-Peter Frahm, with permission.

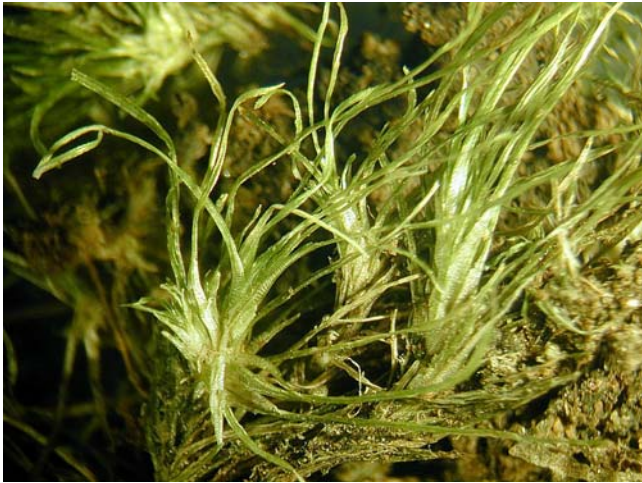


Figure 81. *Syrrhopodon prolifer* var. *scaber* from the Neotropics, a species that occurs on limestone rocks in Florida, USA, and in the Neotropics. Photo by Michael Lüth, with permission.



Figure 82. *Taxiphyllum taxirameum* with capsule; *Taxiphyllum cuspidatum* occurs on limestone rocks in Florida, USA, and in the Neotropics. Photo by Bob Klips, with permission.

Conceição and Pirani (2005) noted the lack of quantitative studies in tropical cave habitats. They compared outcropping, intertidal, and trench habitats, and found that when different types of habitats are contiguous, there is greater heterogeneity of both strata and life forms in a restricted area, supporting more species. Their study was not based on bryophytes, but it would be interesting to test this hypothesis on the bryophytes.

Summary

Inselbergs (abrupt rock outcrops) and other rock formations are typically xeric and have unique vegetation surrounded by vegetation of a different type, often isolating them like an island. Temperatures and water availability can vary widely, and exposure to high light intensity is common. The bryophytes, and even the tracheophytes, are typically **poikilochlorophyllous mats**). Differing niches are created by fissures and crevices, pockets where water collects, tracheophyte shade, and vertical faces that are shaded or exposed.

Limited competition permits **stochastic** processes to determine communities. Surprisingly, inselberg vegetation units of South America and Africa are similar.

Moss **cushions** are common. Adaptations such as hyaline tips and awns protect against UV light during dry periods. Leaves often twist when dry, have infolded leaf margins, thickened cell walls, small cells, and papillae to protect against UV damage and to retain water longer. Lobules help to store water in some leafy liverworts. Mosses such as *Leucobryum* have hyaline cells that store water and protect the chlorophyll. Sexual reproduction is infrequent. Photo-oxidative protection protects chlorophyll from UV light when dry. *Riccia* species on thin soil produce large spores with short-range dispersal and storage in diaspore banks, permitting them to be **shuttle** species. Other bryophytes are drought-tolerant **cushions**, **short turf-forming perennial shuttle species**, **perennial stayers**, and **pauciennial colonists**. Mosses are more likely to have asexual reproduction, whereas liverworts mostly exhibit sexual reproduction. *Bryum argenteum* is a common rock resident that frequently has sporophytes, perhaps due to sperm dispersal by springtails and mites. It is important to conserve groups of inselbergs to facilitate stepping stone dispersal. For others (e.g. **Meteoriaceae**, **Neckeraceae**, **Pterobryaceae**, *Plagiochila*, and *Lejeuneaceae*), having other suitable substrates increases dispersal potential.

In some cases the bryophytes retain moisture and collected nutrients that provide for the tracheophyte roots, whereas the tracheophyte provides shade that cools the bryophytes and protects from UV damage, as seen in the moss *Archidium globiferum* and the shrub *Cyanotis lanata*.

In Africa, inselbergs surrounded by savannah have a higher species richness than when forests surround them. Inselbergs can harbor recolonization sources for surrounding disturbed dry habitats. Asexual reproduction predominates. Leafy liverworts seem to be more common on the Neotropical rock outcrops than on the African inselbergs. *Riccia* species are common on thin soils in both areas. Having trees and shrubs to provide shade can greatly increase the diversity. Limestone areas in subtropical Florida, USA, provide similar habitats and harbor a number of tropical species.

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