# EFFECTS OF HURRICANES ON THE BRYOLOGICAL AND LICHENOLOGICAL FLORA OF PUERTO RICAN FORESTS

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## Abstract

Hurricanes drastically modify habitat structure and environmental conditions in forests of the island of Puerto Rico. In general, short- and long-term effects of hurricanes on most of the macrofauna and vascular flora in these ecosystems has been well characterized. Unfortunately, the effects of hurricanes on lichens and bryophytes, which are among the most diverse groups in these forests, are much less understood. The present review discusses potential short- and long-term effects of hurricanes on lichen and bryophyte communities on the island. General biological and ecological aspects of these organisms are provided first and are followed by a brief summary of important studies of Puerto Rican bryology and lichenology. We then combine firsthand field observations with current knowledge from the published literature to make inferences about how hurricanes, specifically how hurricanes Irma and María, might have affected lichens and bryophytes in ou r forests. Our work documents the scarcity of studies on hurricane effects on both groups, particularly in lichens. We present questions for future research and argue that properly studying typically overlooked groups, like lichens and bryophytes, will enhance our understanding of how this type of disturbances affect biodiversity on the island.

**Keywords** bryophytes, Caribbean, disturbances, lichens, Natural History, tropics.

## Resumen

Los huracanes afectan drásticamente la estructura de hábitats y las condiciones ambientales en los bosques de la isla de Puerto Rico. Los efectos a corto y largo plazo de los huracanes sobre la mayoría de la macrofauna y la flora vascular en estos ecosistemas han sido bien estudiados. Desafortunadamente, los efectos de los huracanes sobre los líquenes y briofitas, que están entre los grupos más diversos en estos bosques, son mucho menos comprendidos. La presente revisión discute potenciales efectos a corto y largo plazo de los huracanes sobre las comunidades de líquenes y briofitas de la isla. Aspectos generales sobre la biología y ecología de estos organismos es provista inicialmente y es seguida por un breve resumen sobre estudios importantes para la briología y liquenología de Puerto Rico. Luego combinamos nuestras observaciones de campo con conocimiento de la literatura científica para hacer inferencias sobre como los huracanes, en específico los huracanes Irma y María, pudieron haber afectado los líquenes y briofitas en nuestros bosques. Nuestro trabajo documenta la escasez de estudios sobre efectos de huracanes en ambos grupos, particularmente en los líquenes. Presentamos preguntas para investigaciones futuras y argumentamos que si estudiamos adecuadamente grupos típicamente ignorados, como los líquenes y las briofitas, mejorará nuestro entendimiento sobre como este tipo de disturbios afecta la biodiversidad de la isla.

**Palabras clave** briofitas, Caribe, disturbios, líquenes, Historia Natural, trópico.


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## INTRODUCTION

Hurricanes are tropical cyclones that are formed over warm waters in the Atlantic Ocean, and that frequently make landfall in the Caribbean islands. The passage of hurricanes over the Caribbean islands, such as Puerto Rico, is linked to significant physical damage and disruption of biological processes in forests from this region. As a result of exposure over millennia, Caribbean ecosystems are generally adapted to hurricanes. Nevertheless, the effects from these events can pose serious challenges to species inhabiting these ecosystems, particularly over short temporal scales.

Known and potential effects of hurricanes to the biotas and physical elements of these forests were amply reviewed by Lugo (2000) and include, among others, sudden and massive tree mortality, increased opportunities for change in successional direction, high species turnover, and fast biomass and nutrient turnover. Many of these effects can certainly threaten vulnerable elements of these forests (e.g., pushing endangered species to the brink of extinction). However, the periodic passing of hurricanes over Caribbean forests seems to be important for maintaining a diverse mix of succession and climax species at particular sites (Zimmerman et al. 1994; Lugo 1998; Brokaw et al. 2012; Weaver et al. 2013). This suggests that despite their immediate catastrophic impacts, these events are critical for the maintenance of species diversity in these ecosystems (Lugo 1998). Similar observations have also been made for many other biotic elements including birds and amphibians (Waide 1991; Lugo 1998; Lugo 2008), reinforcing the view of hurricanes as important factors influencing biodiversity dynamics in Caribbean forests.

As briefly synthesized above, short- and long-term effects of hurricanes on major plant and animal groups inhabiting Caribbean forests are generally well understood. Little is known, however, about their effects on lichens and bryophytes, which are among the most speciose organisms to be found in these ecosystems (Pérez et al. 2012; Mercado-Díaz et al. 2015). While poorly studied, lichens and bryophytes perform and/or mediate key ecological processes in tropical forests. They are important for soil formation and stabilization, water retention and nitrogen and carbon fixation (Nash 2008; Glime and Gradstein, 2018). These organisms also provide habitat to many invertebrates, serve as the staple diet for many insects and influence, either directly or indirectly, important biological interactions (e.g., potentially reduced predation through crypsis [see Lücking 2010]).

In this review, we will provide a brief description of what lichens and bryophytes are and the important roles they play in Puerto Rican forests. To offer a view on the current state of bryology and lichenology in the island, key studies that have been essential for understanding diversity patterns of these organisms will be summarized. We will combine our more than 20 years of field and research experience with current knowledge within these fields to hypothesize on the effects that hurricanes may have on lichen and bryophyte communities. While lichens and bryophytes grow on diverse substrates and are found in multiple forest ecosystems (see below), our observations focus mostly on epiphytic communities that occur in rainforests and/or other humid forests of the island. Anecdotal observations about potential short- and long-term effects of hurricanes Irma and María on these communities will also be discussed and used to propose questions for future investigation.

## THE LICHENOLOGICAL PERSPECTIVE

### Lichen Biology, Ecology, and Diversity Patterns

Lichens are traditionally defined as symbiotic associations between fungi and at least one photosynthetic partner (i.e., algae and/or cyanobacteria) (Figure 1). Most fungal partners, or mycobionts, are members of the phylum Ascomycota, but nearly one percent of the species form associations with Basidiomycetous

Figure 1. Growth forms of different lichens from Puerto Rico. (A) Crustose – *Thalloloma rubromarginatum* from El Yunque National Forest (EYNF); (B) Foliose – *Sticta tainorum* from Bosque Estatal de Toro Negro, central Puerto Rico; (C) Fruticose – *Cladonia robusta* from Reserva Natural Laguna Tortuguero, northern Puerto Rico.

fungi (Nash 2008). Algae that are found in lichens usually belong to the genera *Trebouxia* and *Trentepohlia*, whereas lichenized cyanobacteria most commonly belong to the genus *Nostoc* (Friedl and Büdel 2008). Work by Spribille et al. (2016), Mark et al. (2020), and others, however, have begun to challenge the notion of lichens as static systems with fixed numbers of essential symbionts. This current view of lichens as more dynamic systems was elegantly summarized in the most recent definition of lichens provided by Hawksworth and Grube (2020): "A lichen is a self-sustaining ecosystem formed by the interaction of an exhabitant fungus and an extracellular arrangement of one or more photosynthetic partners and an indeterminate number of other microscopic organisms."

Lichens are present in every major terrestrial biome and are capable of colonizing nearly every substrate (e.g., rocks, leaves, bark) available in those ecosystems (Nash 2008). In forests, lichens are known to contribute to soil formation and stabilization and therefore facilitate primary succession (Brodo et al. 2001). They potentially influence nutrient dynamics as many species are also capable of fixing atmospheric nitrogen (Forman 1975; Antoine 2004; Elbert et al. 2012). Lichens are also believed to play critical roles in the maintenance of water cycles (Green and Lange 1991; Beckett 1995; Zotz et al. 1998) and constitute an important staple in the diet of many animals in those ecosystems (Brodo et al. 2001; Storeheier et al. 2002). Close to 20,000 species of lichens have been formally recognized (Lücking et al. 2017). However, estimates indicate that global diversity might reach 28,000 species (Lücking et al. 2009), suggesting that nearly one-third of extant species in the planet are still to be discovered (Lücking et al. 2009).

While it was initially believed that lichens were more diverse in temperate ecosystems, recent work suggests that at smaller spatial scales, species diversity increases towards the tropics (Lücking et al. 2011). In fact, half of the estimated global number of species is predicted to be found in this biome (Lücking et al. 2009; Sipman and Aptroot 2001; Lücking et al. 2011).

Epiphytic lichens, which are lichens that depend on vegetation surfaces to grow, dominate the lichen flora in tropical humid and rainforests (Sipman and Harris 1989). Epiphytic lichen communities in these ecosystems are influenced by factors such as substrate characteristics (e.g., pH, degree of bark shedding, among others) and microclimate (Cáceres et al. 2007). Community composition of these organisms within these forests, on the other hand, vary along different spatial and temporal axes. Most variation, at least in short spatial scales, is possibly found between vertical forest layers (i.e., canopy *versus* understory) (Komposch and Hafellner 2000; Normann et al. 2010). Environmental conditions in the canopy have high diurnal variation, alternating between periods of high or low temperature and humidity, and increased solar radiation or shadiness. Due to these conditions, species in this layer likely have broader environmental tolerances if compared to those in the understory. Some families commonly found in this layer are Asterothyriaceae, Parmeliaceae, Strigulaceae, Trypetheliaceae and the non-thelotremoid Graphidaceae (Sipman and Harris 1989; Komposch and Hafellner 2000; Lücking 2008). Understory communities, on the other hand, are exposed to less variable conditions. Most species are shade-tolerant and are adapted to high humidity conditions with the Pyrenulaceae, Coenogoniaceae, Porinaceae, Bacidiaceae and most thelotremoid Graphidaceae frequently found in this layer (Sipman and Harris 1989; Komposch and Hafellner 2000; Rivas-Plata et al. 2008). Canopy and understory communities also vary in the distribution of growth forms, the former containing a higher proportion of fruticose and foliose species, and the latter characterized by a high diversity of crustose and squamulose species (Forman 1975; Cornelissen and Ter Steege 1989; Komposch and Hafellner 2000). Together with bryophytes, lichens represent conspicuous elements of the non-vascular flora present in tropical forests. However, in comparison to their vascular counterparts, these organisms remain poorly characterized in tropical regions.

Although studies on the lichens of Puerto Rico are still scarce, the lichen flora of Puerto Rico is possibly the best known among the islands in the region (Mercado-Díaz and Santiago Valentín 2010). Ongoing inventory efforts based on published literature, information from online herbarium databases and collections from the first author indicate that nearly 1,500 species names have been recorded for Puerto Rico (Mercado-Díaz, unpublished). While this amount of species is similar to a previous estimate (~1,600 species, Lücking et al. 2009), the nomenclatural status of these names has not been revised, hinting that this number of species is likely inflated due to synonymy issues (see Dubois 2008 for an interesting discussion on this topic). This suggests that at least a small portion of the flora still awaits discovery.

## Lichen Studies in Puerto Rico

Mercado-Díaz and Santiago-Valentín (2010) provided the first historical account of lichen studies that have shaped our understanding of lichen species richness in Puerto Rico. Two of the works cited in that review are notable in this respect. The first is Ismael Landrón-Concepción Ph.D. thesis on the genus *Ramalina* Ach. (Landrón-Concepción 1972). Landrón-Concepción is the first native Caribbean lichenologist, and his work represents the first formal taxonomic treatment for any lichen group in the region. Harris (1989) working keys to the lichen-forming fungi of Puerto Rico represents the second milestone. Besides providing keys to identify species within most micro- and macro-lichen genera present in the island, this work is of particular relevance to tropical lichenology as it constitutes the "first attempt to treat all the lichen-forming fungi in any tropical region" (Harris 1989). It also provided the first rough estimate of lichen species present in the island (i.e., 750 spp.).

While Puerto Rican lichenology remained inactive for nearly 20 years (1989–2009), the last decade witnessed an increase in the number of studies focusing on the ecology, taxonomy, systematics, and phylogenetics of these organisms. Four new species in the genus *Coenogonium*, all potentially endemic to Puerto Rico, were described by Mercado-Díaz and collaborators (Mercado-Díaz et al. 2013). Their findings have major conservation implications as these species were found in two threatened ecosystems (i.e., *Pterocarpus* wetlands and Non-calcareous dry forests), prompting the need to protect these habitats better. Mercado-Díaz et al. (2014) generated, on the other hand, one of the first studies to suggest that lichen endemism in islands is likely higher than previously assumed. This work resulted in two new genera and twelve new species in the family Graphidaceae, all apparently endemic to the Luquillo Mountains. The work by Mercado-Díaz et al. (2015) is particularly relevant as is the first to assess lichen diversity from an ecosystem-level perspective. Together with useful information for implementing forest health bioindication studies, Mercado-Díaz et al. (2015) provided general descriptions for lichen communities present in eight major ecosystem types in the island. Lastly, recent work by Mercado-Díaz et al. (2020) is the first to combine traditional taxonomic approaches with molecular methods to elucidate diversity patterns of a lichen group in the Caribbean. Focusing on the genus *Sticta*, researchers found that species assemblages in the island resulted from multiple colonization events. They also suggest that nearly 70 percent of the species (eight newly described in that work) are endemic to the island, further supporting the idea suggested in Mercado-Díaz et al. (2014) that endemism in the Caribbean islands is probably underestimated.

## Effects of Hurricane Disturbances on Lichens

Lichens are often seen as "hardy" organisms mostly because many species are present in some of the most hostile environments in the planet (e.g., Antarctica). However, like any other species, lichens found in these environments adapt over evolutionary time to the specific conditions found in those areas. In this sense, lichens are also "fragile" because minimal alterations to the natural conditions of the preferred habitats in which they evolved can have detrimental effects on populations and communities. Since lichens are an association between two compatible (but usually unrelated) species, a specific set of environmental conditions are typically required for these species to develop and sustain a new individual. Disturbances, both non-anthropogenic and anthropogenic, could therefore pose major threats to the health, growth and survival of many species (Matthes and Feige 1983; Gries 1996; Tripp et al. 2019).

Only a handful of studies mention hurricanes and cyclones as a potential factor influencing organismal and species diversity patterns in lichens. Some of these hypothesize that these disturbances might serve as long-distance dispersal agents allowing species to expand their geographical ranges (Smith et al. 1997; DeLange and Galloway; 2015; Mercado-Díaz et al. 2020). Hurricanes along the US Gulf Coast might help maintain gaps in the shrub canopy, thereby benefiting the endangered species *Cladonia perforata*, which requires an open habitat structure to thrive (Yahr 2000). In contrast, a study evaluating hurricane effects on survival and resprouting of Florida rosemary (*Ceratiola ericoides*) in that same region, linked dense coverage of reindeer lichens (*Cladonia* sp.) with longer hurricane return intervals (Bertz and Brewer 2013). These authors suggested that these lichens might be swept away or buried by widespread storm surge due to hurricane-induced overwash. Similar observations were made by Allen and Lendemer (2016) on their study on the effects of sea-level rise in coastal lichen biodiversity in the Mid-Atlantic Coastal Plain. According to these authors, hurricanes can drive the migration of barrier islands, which contain maritime forests that support distinct lichen communities. They anticipate that failure of maritime forests to migrate at the same rate as the barrier islands could result in negative consequences to lichens and other unique organisms that distinguish this habitat type.

At least in the short term, hurricanes most likely affect lichen communities in Puerto Rican forests indirectly by reducing canopy cover and increasing mortality of host trees. These structural changes can stimulate significant temperature increases and cause reductions in humidity and moisture. They should also reduce available substrates for colonization and result in higher solar radiation reaching the forest floor. Responses from lichen communities will be inextricably linked to these factors, and other more direct effects such as physical removal from substrates due to wind abrasion, as they can trigger increases in mortality and affect growth and survival rates in all groups. For instance, expected responses from these changes include reductions in species richness, abundance and diversity. In the short term, these changes will likely be more pronounced on canopy communities as these will lose more individuals due to defoliation, debranching, and tree-felling. Changes in understory communities will probably be most linked to environmental and microclimatic alterations resulting from structural effects on forests. Consequently, these will most likely be detected months or even years after an event.

Effects at the ecosystem level are also expected. For instance, because there is a higher proportion of foliose and fruticose growth forms in the canopy (Forman 1975), higher losses in lichen biomass are likely to be more pronounced in that layer. Decreases in moisture and shade associated with hurricane passage over the forest are also detrimental to cyanobacterial species, which are known to potentially fix 1.5–8 kg of nitrogen per hectare per year in tropical forests (Forman 1975). Increased mortality associated with canopy changes could therefore diminish potential nutrient influx that might result from nitrogen fixation by cyanolichens.

## THE BRYOLOGICAL PERSPECTIVE

### Bryophyte Biology, Ecology, and Diversity Patterns

Bryophytes are distinct lineages of non-vascular plants that are closely related and include mosses, liverworts, and hornworts. As the group sister to the ancestor of the rest of land plants, bryophytes disperse by sexually produced spores and require water for reproduction. In bryophytes, as in all plants, two generations alternate to produce gametes (gametophyte) and to produce spores (sporophyte). The dominant photosynthetic and long-lived generation of a bryophyte is the gametophyte while the sporophyte is short-lived and dependent on the gametophyte (Figure 2A). Bryophytes are usually associated with humid environments but are found in a wide variety of substrates, in aquatic to terrestrial habitats, and from arctic to deserts. In these ecosystems, bryophytes play an important role in water storage, nutrient uptake from the rain, soil protection and succession, and provide habitats for animals and other plants (Frahm et al. 2003; Glime and Gradstein 2018).

Bryophyte species composition at a small geographical scale depends on the types of forests, microhabitats and substrates available, and the phylogenetic diversity of the region (Frahm et al. 2003). Elevation, annual temperature, and humidity influence species richness in tropical forests (Frahm and Gradstein 1991; Vitt 1991). Other aspects of the landscape also influence the distribution and abundance of species such as forest interior to forest edge differences (Jiang et al. 2018) and distance from stream banks (Chinea et al. 1993). The principal drivers of epiphyte diversity in tropical forests with different land-uses are canopy cover, microclimate, and the characteristics of host trees such as bark structure and chemistry (Gradstein and Sporn 2010).

Global diversity of bryophytes is around 20,000 species making it the second-largest group of land plants. The most abundant are the mosses with an estimate of 12,700 species, followed by 6,000 to 8,000 liverwort species and 100 to 150 species of hornworts (Shaw 2009). Bryophyte species richness does not necessarily increase as latitude decreases, as observed for other organisms (Shaw 2009). Mosses are as diverse in tropical forests as in broadleaf, tundra, and boreal forest (Geffert et al. 2013). However, liverworts species richness is higher near the equator; it is hypothesized that tropical taxa have higher diversification rates than non-tropical taxa (Laenen et al. 2018). In fact, tropical America contains one-fourth of the total diversity of liverworts, with leafy liverworts being the most diverse, including the family Lejeuneaceae with hundreds of species (Gradstein et al. 2001). Hornworts are the least studied group of bryophytes and the one with fewer species. The highest diversity of species within this group are found in the tropics in India, Asia, and the Americas (Villarreal et al. 2010). In general, bryophyte species have a broader geographical range than flowering plants, probably due to their capacity for long distal dispersal (Patiño and Vanderpoorten 2018).

In Puerto Rico, bryophytes are represented with 526 species, in 217 genera and 69 families (Gradstein 1989; Sastre-D.J. and Buck 1993). Mosses and liverworts have the highest diversity with 284 and 237 species, respectively. Only five species of hornworts in 3 families are represented in the bryophyte flora of Puerto Rico. No endemic mosses are reported for Puerto Rico, and the

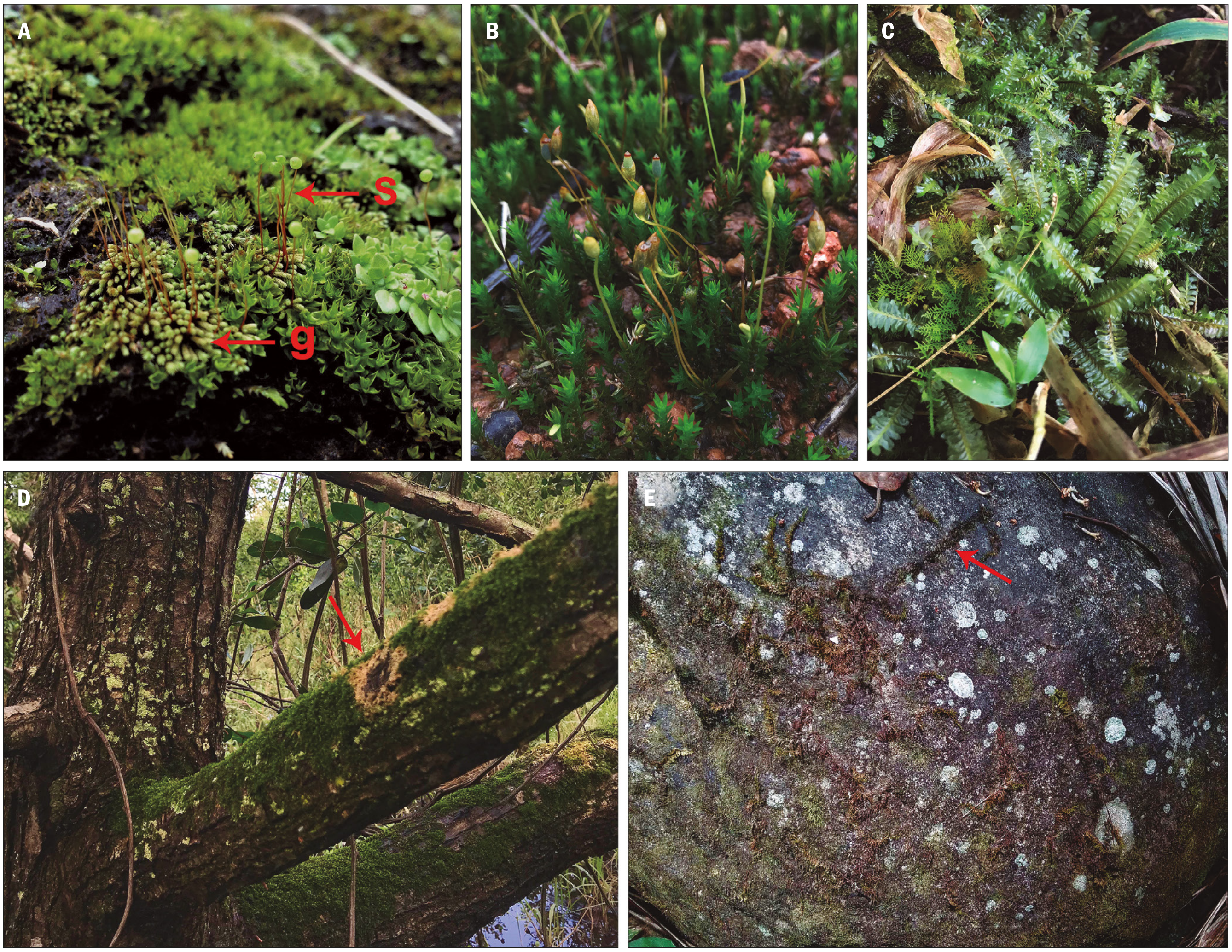


Figure 2. (A) *Philonotis* with sporophytes, five months after hurricane Maria near La Coca Falls, El Yunque National Forest (EYNF). (B) *Pogonatum* with sporophytes growing on exposed soil from a landslide, Trade Winds Trail at EYNF. (C) The liverwort *Plagiochila* growing among grasses in the understory at EYNF. (D) Patches of "burned" or decolored moss in a branch of a tree a year after the hurricane, Cienagás Las Cucharillas, Cataño, northern Puerto Rico. (E) Possible remains of *Thuidium* on a rock in a stream at El Verde Field Station, EYNF, two years after the hurricane. s = sporophyte; g = gametophyte.

number of endemic liverwort and hornworts is unknown (Sastre-D.J. and Santiago-Valentín 1996a). Considering that few phylogenetic studies include specimens from Puerto Rico and the Caribbean, the number of endemic and cryptic species might be higher.

## Bryological Studies in Puerto Rico

The bryophyte flora of Puerto Rico has been extensively studied. Early explorations by Europeans and US Americans described new species and records of bryophytes to the island (Pagán 1939; Crum and Steere 1957). Checklists and species descriptions were done separately for mosses but combined for liverworts and hornworts. New York Botanical Garden scientists led surveys that included collections of bryophytes by Elizabeth Britton, a recognized bryologist and first female scientist to conduct research in the Luquillo Mountains and throughout Puerto Rico, and her husband, Nathaniel Britton (Sastre-D.J. and Santiago-Valentín 1996a,b). During this period Alexander W. Evans published the "Hepaticae of Puerto Rico" describing the Lejeuneaceae (Evans 1902–1912). In the 1930-40s the first Puerto Rican bryologist, Francisco M. Pagán, published a list of liverworts and hornworts of Puerto Rico that included the collections of A. W. Evans. Pagán also described a new species of hornwort for Puerto Rico (Pagán 1942). The preliminary list reported 244 species of liverworts, including eight hornworts, and expanded the localities previously reported and added new records for the island (Pagán 1939). For mosses, the number of species increased with the publication of "The mosses of Porto Rico and the Virgin Islands" by Howard Crum and William C. Steere (Crum and Steere 1957). These authors reported 268 species of mosses, with 11 new species and provided the first comprehensive treatment of the mosses of Puerto Rico with keys and descriptions. Pagán was working on a similar treatment for the liverworts but was not completed because of his passing (Steere 1942).

Bryological work continued in the 1970s with studies of the liverworts (Fulford et al. 1970,1971) and epiphytic mosses (Russell and Miller 1977) of the elfin forest in Luquillo Experimental Forest/El Yunque, and the development of a guide to the genera of the mosses of Puerto Rico (Miller and Russell 1975). Ecological studies and inventories in the Luquillo Experimental Forest included bryophytes, such as the irradiation experiments (Steere 1970), the flora of Bisley (Chinea et al. 1993) and the nutrient content and biomass of bryophyte communities on wooden posts (Frangi and Lugo 1992). Studies of moss taxonomy and biogeography of the Caribbean by William Buck in the 1980s were important for creating the checklist of mosses of Puerto Rico (Sastre-D.J. and Buck 1993), the key for Pleurocarpous Mosses of the West Indies (Buck 1998), and motivated more bryological work in the island. A period of high bryological activity started in the late 1980s until recently; as Puerto Rican bryologist Inés Sastre-De Jesús began collecting, identifying and developing projects that included ecology, restoration, genetics, morphology and taxonomy of bryophytes, primarily of mosses. In addition, I. Sastre-De Jesús mentored students from Puerto Rico and Latin America, who were involved in projects that contributed to our understanding of the flora of Puerto Rico and the Caribbean. She invited bryologists from around the world to give workshops and develop materials for identification of species on the island. A result of one of those collaborations is the key for the liverworts and hornworts of Puerto Rico published by Gradstein (1989) that included 237 species and is the most recent guide available for this group in Puerto Rico.

Floristic inventories of protected and non-protected forests around the island, have increased the number of species documented in these areas but did not significantly increase in the number of species for Puerto Rico (Reyes-Colón and Sastre-DJ 1998, 2000; Galva et al. 2008; Pérez and Sastre-De Jesús 2009; Pérez et al. 2012). Many species are only known from the original collections, and about 12 percent of the mosses listed to the island are now extinct. By the beginning of the 20th century, island-wide deforestation peaked, and most-likely caused the extinction of these species (Sastre-D.J. and Tan 1995).

## Effects of Hurricane Disturbances on Bryophytes

Disturbances such as hurricanes likely affect bryophyte communities by modifying or eliminating their microhabitats. Bryophytes are susceptible to changes in humidity, light intensity, and temperature (Glime and Gradstein 2018); all of these environmental factors can dramatically change after a hurricane. Bryophytes are tolerant to desiccation, but the degree, duration, and frequency of hydration/dehydration will have an effect on their recovery. When bryophytes dry and rehydrate, carbon and nitrogen are released to the surroundings. Plants adapted to dry environments are expected to experience less cellular injury and less nutrient loss than those of mesic or wet places (Slate et al. 2019). Higher resistance to desiccation occurs in tropical forests with low humidity and species in the canopy are more resistant to drying than those of the understory and can retain their photosynthetic capacity after longer periods of low humidity (Pardow and Lakatos 2013; Glime and Gradstein 2018). An increase in light intensity and temperature also affect bryophytes, changes in coloration are noted with higher solar radiation, and with an increase of temperature above 25 °C, net productivity decreases (Glime and Gradstein 2018). This suggests that changes in canopy opening after a hurricane, can alter the microenvironmental conditions and potentially increase the frequency of hydration/dehydration cycles, thus affecting bryophytes' physiology.

Not many studies address the effects of hurricanes or storms to the bryophyte flora of the tropics. The strong winds of Hurricane Hugo's removed bryophytes from trees, but parts remaining from the surviving patches were left on the trees and probably facilitated recolonization and new growth (Glime 2019). A fertilization experiment to measure the effects on the vegetation of the influx of nutrients expected from leaf-litter and debris after Hurricane Hugo found that bryophyte biomass decreased three-fold after adding fertilizer every three months for three years (Walker et al. 1996). Bryophytes were measured only in one of the sites, Pico del Este, where *Sphagnum* is a major component of the terrestrial bryophytes, although *Marchantia*, *Philonotis*, and *Fossombronia* are also common. The decline in biomass is not surprising because bryophytes are sensitive to high levels of nutrients and can be outcompeted by vascular plants in those conditions (Glime 2017a).

A study describing the effect of hurricane Georges to the cryptogram flora of Toro Negro Commonwealth Forest found that effects to terrestrial plants (mostly ferns) were lower than to epiphytes (i.e., bryophytes and ferns; Rosado 2000). Visible hurricane effects to mosses and liverworts include yellowing (chlorosis), changes in color was evident in 9 (of 39) genera of liverworts and 6 (of 30) genera of mosses; while drying and reduction in plant size or abundance was found in one genus of liverwort and three genera of mosses. Death of individual plants was recorded for three genera of liverworts and one genus of moss, but the effects were not the same in all sites, and not all genera had the same responses. Before the hurricane, the most abundant and diverse groups were leafy liverworts from the Lejeuneaceae and Plagiochilaceae, and mosses in the families Pilotrichaceae and Sematophyllaceae. After the hurricane, some genera remained abundant such as liverworts of the genus *Plagiochila* and the mosses *Leucoloma* and *Lepyrodontopsis*. In contrast, taxa with more visible effects were thallose liverworts Aneureaceae and Metzgeriaceae, and leafy liverworts in the Lejeuneaceae. Rosado (2000) speculated that mosses appear to be more tolerant to hurricanes than liverworts and that most of the effects occurred to the microhabitats. A study from Honduras found that bryophyte cover was significantly lower in trees located in areas more affected by hurricanes, years after the hurricanes (Batke and Kelly 2015). From these studies, we can hypothesize that hurricanes can reduce species richness and abundance at a small scale, such as in a specific microhabitat or phorophyte and not necessarily at a larger scale or forest area and that effects of hurricane disturbance on bryophyte communities can be long-lasting.

## LESSONS FROM OTHER EPIPHYTES

Many lichens and bryophytes are epiphytes; organisms that grow on other plants. Epiphytes in tropical forests also include bromeliads, orchids, species within the family Araceae, and ferns (Batke and Kelly 2015). Responses of other epiphytes to hurricanes can reasonably be extrapolated to lichens and bryophytes because life-history strategies among these groups are similar. One aspect to consider is the endurance of epiphytes to remain attached to their host tree. A study on the effects of Hurricane Hugo on the epiphytic orchid *Comparettia falcata* in Toro Negro found that about 70 percent of the plants had no meaningful damage (the rest of the individuals were detached from their host tree) and that less than 10 percent of the phorophytes were destroyed (Rodríguez-Robles et al. 1990). A recent inventory found that over 600 plants of the miniature orchid *Lepanthes eltoroensis* survived after Hurricane María, half of which were already recorded, and the rest were new records (Endangered and Threatened Wildlife and

Figure 3. Views of a rainforest understory in El Verde Field Station, El Yunque National Forest (EYNF), northeastern Puerto Rico, before (A) and after (B) hurricanes Irma and Maria.

Plants 2020). Most of the effects to populations were due to loss or host trees being knockdown; 30 percent of the individuals were still attached to fallen trees. These studies show that while hurricane winds can detach epiphytes from their hosts and destroy phorophytes, their effects are likely transient. The level of damage to the epiphytic community is contingent on the level of structural effects on the host tree and changes in the microenvironment. Many epiphytes can be observed growing with patches of lichens and bryophytes. After hurricanes, bryophyte cover and branch surface area influence epiphyte composition and diversity among tree branches (Batke and Kelly 2015). It is evident that bryophytes and lichens are important components of epiphytic communities and are key for the establishment and recolonization of other epiphytes. More studies will be needed to understand the scope of these interactions fully.

## POTENTIAL EFFECTS OF HURRICANES IRMA AND MARÍA TO BRYOPHYTE AND LICHEN COMMUNITIES

Very few studies document the effects of hurricanes on bryophytes and lichens. Furthermore, it is difficult to generalize or predict effects to lichens and bryophytes based on those studies because hurricane effects on vegetation vary by location (exposure) in the landscape and by hurricane strength (López-Marrero et al. 2019). While lichens and bryophytes differ in many aspects of their organismal biology, both groups share similar habitats and growth forms and rely on similar ecological and physiological strategies to disperse, reproduce, and survive, hinting that responses to hurricanes might be similar. We have visited on a regular basis several natural protected areas of Puerto Rico after hurricanes María and Irma with the goal of determining how these events affected lichen and bryophyte floras and assessing similarities/differences in responses (Figure 3). The main attributes of these communities were well understood as these areas had been visited numerous times before these events. This allows us to hypothesize how large-scale effects of hurricanes might influence survival, growth, and reproduction of bryophytes and lichens in our forests.

### Ecological and Organismal Responses

High short-term mortality of individuals in both canopy and understory communities was likely the main response of lichens and bryophytes to hurricane disturbance. Populations of canopy species seem to have been diminished as a result of major debranching, defoliation, and wind abrasion caused by hurricane winds. Understory populations, particularly those of ground-dwelling species, were consequently affected as many were buried under the large quantities of leaf litter and other organic debris that covered the forest floor. Spatial data from G-LiHT (Goddard's Lidar, Hyperspectral and Thermal Imager) estimated that about 40 to 60 percent of the trees in forests of the island were snapped or uprooted by these events, and the average canopy height of the Luquillo Experimental Forest/El Yunque National Forest (EYNF) was reduced by one third (NASA/Goddard Space Flight Center 2018). The visible effects caused by Hurricane María exceeded those of other hurricanes in recent years. At one experimental area in El Verde Field Station/Luquillo Experimental Forest, Uriarte et al. (2019) reported that twice as many trees died during Hurricane María compared to hurricane Hugo, while breaking of branches and stems was on average tripled and uprooting of trees was widespread. Defoliation and canopy cover loss, which were exacerbated in higher elevations, were among the most visible and immediate effects that Hurricane María had on our forests (Munroe et al. 2018).

Three types of phenotypic responses, which are most likely linked to environmental changes induced by these hurricanes, were seen in several lichen groups after these events. The first is known as chorophyll bleaching (Gauslaa and Solhaug 1996). Bleaching manifests as a general whitening of the thallus and can have detrimental effects on individuals as it occurs after photosynthesis is severely inhibited by light stress (Gauslaa and Solhaug 1996). This response to light stress most likely occurred in green algal species such as *Chapsa thallotrema* (Figure 4A) and *Coenogonium leprieurii* (Figure 4B). The second response could be termed "spotting". A thallus affected by spotting is easily distinguishable as it has discrete, white-to-beige


Figure 4. Presumed phenotypic responses of lichens to effects caused by environmental changes induced by hurricanes. (A) Signs of "bleaching" in the thallus of the otherwise dark-green species *Chapsa thallotrema*, El Verde Field Station, El Yunque National Forest (EYNF). (B) An individual of *Coenogonium leprieurii* (a normally bright-green filamentous species) affected by "bleaching", El Verde Field Station, EYNF. (C) Individuals of *Sticta densiphyllidiata* from El Verde Field Station, EYNF and (D) Mt. Britton trail, EYNF, showing signs of "spotting" effects.

colored patches that appear to lack photobiont cells. This type of effect has so far been detected in *Sticta densiphyllidiata* (Figure 4C, D), but presence in green algal species and other cyanobacterial species is also likely. The third type of response is a general browning of the thallus, which is likely caused by the deposition of melanin in the outer layer of the upper cortex in light-stressed lichens (Gauslaa and Solhaug 2001). Browning has been recently seen in individuals from scattered populations of the newly described endemic species *Sticta tainorum* (Mercado-Díaz et al. 2020). Similar to our observations, these authors suggest that browning is likely a result of hurricane defoliation and concomitant increases in solar radiation. We suspect that damage from bleaching, spotting and browning may lead to long-term detrimental effects on populations of susceptible species. Additional studies are needed to understand causal links between hurricane-induced environmental conditions and these physiological responses.

Dead or dry mosses and liverworts was a recurrent observation from visitors to the forest after Hurricane María. In contrast to other plants, most bryophytes can withstand long periods of drying. When water is available, bryophytes will be physiologically active and photosynthesizing, and when the humidity of the atmosphere drops, they will dry and become dormant. However, drying combined with a rapid increase in temperatures and sunlight intensity resulting from canopy loss would increase the stress to the plants, thus reducing their survival (Glime and Gradstein 2018; Pardow and Lakatos 2013). In this novel environment, we can expect bryophytes to dry more frequently, for which they may not be adapted to, than in the previous humid forest. This could explain why parts of bryophyte patches were 'burned' after the hurricane and other parts survived (Figure 2D). Although sunlight exposure increased after Hurricane María, bryophytes of open areas such as *Philonotis* and *Plagiochila* seem to be unaffected and continued to grow and reproduce (Figure 2A,C).

## Responses to Changes in the Landscape and Effects on Riparian Communities

Landslides, which are largely caused by heavy rainfall during hurricane events, can dramatically change the landscape and result in significant modification of the habitat of many species. The highest density of landslides after Hurricane María was reported in the central mountain region (Bessette-Kirton et al. 2017), which has a high diversity of lichen and bryophyte species. Massive movement of rocks and soils associated with these events affected lichen- and bryophyte-covered areas and triggered reductions in populations from both groups. Paradoxically, landslides are likely important for the persistence of many species in these ecosystems. For bryophytes, bare areas resulting from landslides will eventually be colonized by groups like *Pogonatum* (Figure 2B) or members of the Pottiaceae, both of which have species that can be considered ruderal or early colonizers. Soil propagule banks can facilitate recolonization of disturbed or bare areas for a fraction of the mosses, particularly for acrocarpous mosses (Pasiche-Lisboa and Sastre-De Jesús 2014). Landslides are believed to be important for the persistence of many lichen species, including the genus *Stereocaulon*, which is found almost exclusively in roadcuts and areas where bare soil have been recently exposed (Walker and Shiels 2012; Mercado-Díaz et al. 2015). Heavy rainfall associated with hurricanes could also have affected lichen and bryophyte communities in riparian zones. Large amounts of water entering rivers at high speeds can detach individuals from rock surfaces and affect species inhabiting those areas (Figure 2D). Fortunately, some bryophytes can remain alive underwater for periods of time and resume growth if at least parts of individuals remain attached to rocks (Glime 2017b). For instance, medium to large patches of *Thuidium* persisted on rocks in the forest understory and in riparian zones of the El Verde Field Station in the Luquillo Experimental Forest/El Yunque National Forest two years after

Hurricane María. In this moss, changes in coloration from light green to brown orange were observed in plants under different light conditions. In contrast, many lichens in riparian zones (excluding those in surrounding vegetation) are endolithic and cannot be detached from rock surfaces by moving water. For these lichens, mortality will mostly be associated with individuals growing on rocks that could have been turned upside down during a flood event.

## Responses by Forests Types and Modifications in Forest Structure and Composition

The effects of hurricanes Irma and María on lichen and bryophyte communities were potentially variable within and among different forest types. High elevation forests, which host a high diversity of lichens and bryophytes (Sastre-D.J. and Buck 1993; Mercado-Díaz et al. 2015), were more affected as hurricane winds were generally stronger in these areas (Munroe et al. 2018). We have noted that in general, many species in both groups are able to recolonize and reestablish, suggesting they are likely adapted to these changes. Mercado-Díaz et al. (2020) suggested that *Sticta harrisii*, a relatively uncommon species in Luquillo Experimental Forest/El Yunque National Forest before 2017, might have increased in cover after these two hurricanes. Unfortunately, communities in other forests might face higher threats, particularly because hurricane effects are exacerbated by other types of disturbances. For example, conversion to agricultural, urban or industrial land uses has, and is still reducing the habitat available for lichen and bryophytes species in lowland forests, which host diverse species assemblages in both groups (Perez and Sastre De-Jesus 2009; Perez et al. 2012; Mercado-Díaz et al. 2015). The effects of land-use history on tree species composition remain evident after hurricanes and influence the recovery of the forests (Zimmerman et al. 1995; Lugo 2008). Effects from compounded pressures from these disturbances will pose major challenges to already vulnerable elements in these communities, such as species with heightened risks of extinction that might exist in these forests.

The recovery and recolonization of bryophyte and lichen communities will also be linked to hurricane-induced changes in tree composition. Species like Palma de sierra (*Prestoea montana* syn. with *P. acuminata*), Yagrumo hembra (*Cecropia schreberiana*) and shrub species will be major woody components of the open-canopy vegetation during the first few years in high elevation forests (Heartsill-Scalley et al. 2010; Weaver 2013). These plants grow relatively fast but have straight stems and relatively homogeneous barks which would support less diversity of bryophytes (although possibly a higher diversity of lichens [Rosabal et al. 2013]). In addition, many bryophytes and lichens might be outcompeted due to the inevitable arrival of fast-growing herbs and vines. These species will temporarily displace the local flora but will eventually be replaced by bryophytes, lichens, and other native plants as the composition of the forest changes and the cover of the canopy increases.

## Responses as a Function of Hurricane Frequency and Intensity

The effects of hurricanes on lichen and bryophyte communities will ultimately depend on hurricane frequency and intensity. More frequent and severe storms will certainly alter forest species composition and the size assemblage of trees (Uriarte et al. 2018), and therefore the habitats in which lichens and bryophytes thrive. Yet, positive feedbacks on species richness and diversity at local scales could also be expected and will likely be maximized when these events are moderate in strength and frequency. For example, a high diversity of Cladoniaceae that has been noted in Laguna Tortuguero is likely explained by frequent canopy openings that are characteristic of this coastal scrub habitat and are possibly maintained by periodic hurricanes. Similar to what has been observed for *Cladonia perforata* (Yahr 2000), maintenance of these openings might be critical for the survival of *Cladonia robusta*, a potentially endangered species that is endemic to this habitat. In the cloud forest, *Sphagnum portoricense* is abundant near trails and open disturbed areas, environmental modifications caused by hurricanes probably provide opportunities for this moss to expand its range and colonize new areas (Karlin 2006). Unfortunately, empirical data from lichen and bryophyte communities to test these ideas are lacking; therefore they should be taken as working hypotheses.

Work on the effects of hurricane disturbances on tropical tree species diversity has shown that beyond the frequency and magnitude of disturbances, the intensity in the spatial extent of damage is an important force driving patterns of species richness (Vandermeer et al. 2000). This observation hints that responses from lichen and bryophyte communities will vary depending on the spatial scale they are being analyzed. Thus, spatially explicit approaches to evaluate potential impacts will ultimately be needed to efficiently interpret and understand how responses relate to the frequency and intensity of these events.

## CONCLUSION

In this work, we synthesized general biological and ecological aspects of lichens and bryophytes in tropical forest ecosystems, briefly reviewed key bryological and lichenological literature from Puerto Rico and provided insights about potential effects of hurricanes, particularly hurricanes Irma and María, on lichens and bryophytes from the island. The dearth of literature about the effect of this type of disturbances in these organisms was evident but was more pronounced in lichens. Considering the high levels of endemism documented in lichens (Mercado-Díaz et al. 2014,2020), this scarcity of studies is troubling, and more studies are sorely needed to understand better short- and long-term effects of hurricanes in these organisms.

Because lichens and bryophytes are present in all forest types of the island, their abundance and diversity can serve as indicators of ecological continuity and forest health (Frego 2007; Rivas-Plata et al. 2008). We understand forest health as the production of current and future sustainable forest conditions, considering the interplay between human needs and the ability of ecosystems to persist, recur, and be resilient to disturbances. Useful guidelines on how to carry out studies of this type and evaluate forest health using lichen communities from the island are provided in Mercado-Díaz et al. 2015. Similar tools for bryophytes are currently being developed by the second author and are certainly an exciting avenue for future research.

Other areas of research also remain understudied with respect to the effects of hurricanes on lichen and bryophyte communities. Some important questions that should be investigated include: 1) What are the short-term physical and physiological changes, and phenotypic responses that occur to bryophytes and lichens after a hurricane? 2) How do species richness, abundance, and diversity change in the short- and long-term at the local and regional scales? 3) How does community succession operate in the new, modified microhabitats? 4) How hurricane effects on lichens and bryophytes affect ecosystem dynamics in terms of biomass, nutrient, and water cycles? 5) How do hurricanes alter between/within-species relationships of organisms that interact at the bryophyte/lichen community scale? 6) Are hurricanes important drivers of species diversity dynamics in lichens and bryophytes in these forests? The inclusion of lichens and bryophytes in after-hurricane surveys and long-term projects will give us a better understanding of the recovery process of the forest and of the organisms that depend on them.

The future of lichen and bryophyte communities will be further hindered by changes occurring at global scales, such as climate change. The intensity of hurricanes and tropical storms in the Atlantic has incremented since the 1970s (Mann and Emanuel 2006).

This increase is due to both longer and more intense storms and has been linked to rising sea surface temperatures in the Atlantic (Mann and Emanuel 2006; Lugo 2008). It remains to be seen how these changes will affect survival and subsistence of lichen and bryophyte communities on the island. Likewise, as in many tropical countries, biodiversity loss in Puerto Rico is strongly linked to changes in land-use and habitat fragmentation. We can hypothesize that in conjunction with frequent hurricane disturbances, anthropogenic-induced changes will also lead to further reductions in available habitats, and consequently, to potential losses in lichen and bryophyte species. Increased conservation efforts and accumulated knowledge on lichens and bryophytes will certainly play a critical role in buffering these effects. However, societal and political willingness will ultimately determine how effective we will be in addressing these pressing issues.

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