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ABSTRACT
Streams are important ecosystems that harbor a high diversity of plant species including bryophytes. Studies suggest streams can function as refugia and/or corridors that buffer against the effects of disturbances. In this study, we sampled five sites along a second-order tropical stream in the Luquillo Experimental Forest. We described the riparian bryophyte community composition in conjunction with the physical structure of the stream to understand what environmental factors influence bryophyte composition in the stream. We identified 56 bryophytes, 33 liverworts and 23 mosses; and we recorded cyanobacteria associated with over half of the species of bryophytes. Rocks were the most frequent and important substrate which supported the highest bryophyte richness. Community composition and species diversity were similar among sites. *Ceratolejeunea cornuta* (Lindenb.) Steph. and *Taxithelium planum* (Brid.) Mitt. were the most frequent species, recorded in all sites. Although stream width varied between sites, all the other environmental variables measured (canopy cover, temperature, humidity, and elevation) were similar. Across plots, species richness increased with bryophyte cover, whereas canopy cover, location in the stream, substrate, site, temperature, and relative humidity showed no clear associations with richness. Bryophyte community composition seems to be shaped by the substrates occupied. We found that similar types of substrates such as branches, trunks, logs and vines, shared more species in common. This is one of the first studies to describe the bryophyte community of a tropical stream and can provide a baseline for future research on the response of bryophytes to increased disturbances and a changing climate.

KEY WORDS
Tropical forest, liverworts, mosses, diversity, drought, disturbances, cyanobacteria, riparian bryophytes, ecology, substrates.

RÉSUMÉ
Composition de la communauté de bryophytes dans un ruisseau tropical de second ordre dans la Forêt expérimentale de Luquillo, Porto Rico.
Les cours d'eau sont des écosystèmes importants qui abritent une grande diversité d'espèces végétales, dont des bryophytes. Des études suggèrent qu'ils peuvent servir de refuges et/ou de corridors pour atténuer les effets des perturbations. Dans cette étude, nous avons échantillonné cinq sites le long

d'un cours d'eau tropical de second ordre dans la forêt expérimentale de Luquillo. Nous avons décrit la composition de la communauté de bryophytes riveraines en conjonction avec la structure physique du cours d'eau afin de comprendre les facteurs environnementaux qui influencent sa composition. Nous avons identifié 56 bryophytes, 33 hépatiques et 23 mousses; et nous avons recensé des cyanobactéries associées à plus de la moitié des espèces de bryophytes. Les roches constituaient le substrat le plus fréquent et le plus important, abritant la plus grande richesse en bryophytes. La composition de la communauté et la diversité des espèces étaient similaires d'un site à l'autre. *Ceratolejeunea cornuta* (Lindenb.) Steph. et *Taxithelium planum* (Brid.) Mitt. étaient les espèces les plus fréquentes, recensées dans tous les sites. Bien que la largeur du cours d'eau ait varié d'un site à l'autre, toutes les autres variables environnementales mesurées (couverture de la canopée, température, humidité et altitude) étaient similaires. Sur l'ensemble des parcelles, la richesse spécifique augmentait avec la couverture de bryophytes, tandis que la couverture de la canopée, la localisation dans le cours d'eau, le substrat, le site, la température et l'humidité relative n'ont montré aucune corrélation claire avec la richesse. La composition de la communauté de bryophytes semble être influencée par les substrats occupés. Nous avons constaté que des types de substrats similaires, tels que les branches, les troncs, les rondins et les vignes, partageaient davantage d'espèces en commun. Il s'agit de l'une des premières études consacrée à la communauté bryophyte d'un flux tropical. Elle peut fournir une base de référence pour les recherches futures sur la réponse des bryophytes aux perturbations accrues et à un climat changeant.

MOTS CLÉS
Forêt tropicale, hépatiques, mousses, diversité, sécheresse, perturbations, cyanobactéries, bryophytes riverains, écologie, substrats.

INTRODUCTION

The neotropics are rich in bryophytes, carrying almost one third of the world's total bryophyte diversity (Gradstein *et al.* 2001). In riparian ecosystems bryophytes are important in controlling erosion, retaining water and nutrients, and as a substrate or for shelter and protection by other organisms, like fish, seedlings of vascular plants, cyanobacteria, and microarthropods (Gradstein *et al.* 2001; Glime 2021). Being poikilohydric organisms, bryophytes can generally withstand desiccation; however prolonged drought and short rain intervals combined with increased temperatures can negatively affect bryophyte survival (Proctor 2000; He *et al.* 2016). With increasing frequency and intensity of disturbances, such as droughts and hurricanes, and changes in the climate including increased temperature, streams in the Caribbean region may face changes in water and nutrient cycling and food chain alteration (Gutiérrez-Fonseca *et al.* 2020).

Within the forest, riparian areas act as a buffer to climatic change for bryophytes as they provide a constant source of water and protection from extreme elements such as wind (Dynesius *et al.* 2009; Baldwin *et al.* 2012) and reduce the impact of past agricultural land use (Matos *et al.* 2024). Often climate change predictions in the Caribbean focus on the larger view of how overall vascular compositions in a habitat will change over time, but it is also important to understand how the microcommunities, like bryophytes, within a habitat will be impacted (Mercado-Díaz & Merced 2021). Studies about bryophyte communities in tropical streams are scarce. Special attention has been given to rheophilic bryophytes (aquatic in flowing water) in South America, where bryophyte communities are richer and more diverse at higher elevations (including páramos) in areas with lower human impact activities (Linares-C. & Churchill 1997; Lagos *et al.* 2008; Becerra I. *et al.* 2020), which highlights the potential of bryophytes as bioindicators of water quality (Romero 2017; Vásquez *et al.* 2019). Less information is available about riparian bryophyte communities of tropical lower montane ecosystems and their response to disturbances.

The Luquillo Experimental Forest (LEF) in Puerto Rico is a tropical rainforest with multiple streams and rivers, it also hosts the highest number of bryophyte species on the island. Previous studies in the LEF, have shown that bryophytes act as flood-water filters and are important organisms for nutrient retention, including biological nitrogen fixation (Frangi & Lugo 1992; Cusack *et al.* 2009). In relation to disturbances, canopy cover and past land use influence the presence and size of patches of bryophytes in riparian and upland forest (Matos *et al.* 2024). Bryophyte mats on rocks in a stream can interact positively or negatively with the establishment of the miniature orchid *Lepanthes* Sw. in the LEF (García-Cancel *et al.* 2013). However, there are no studies describing the bryophyte communities in streams of this tropical forest or in Puerto Rico.

The objectives of this research are to describe the bryophyte community composition in the second order stream Quebrada Prieta in the LEF, and to assess some of the stream physical structures and environmental variables that may influence the bryophyte species composition in a riparian environment. We predict that bryophyte community composition will be similar throughout the stream, and that bryophyte richness in this riparian environment is influenced by environmental factors such as substrate type, stream width, light and humidity. In addition, we hypothesize that bryophyte communities growing on the same type of substrate will be more similar than those growing on different substrates. This study is the first survey of the bryophyte community in a stream at the LEF and will provide baseline data to understand how bryophyte species composition changes through time and after disturbances.

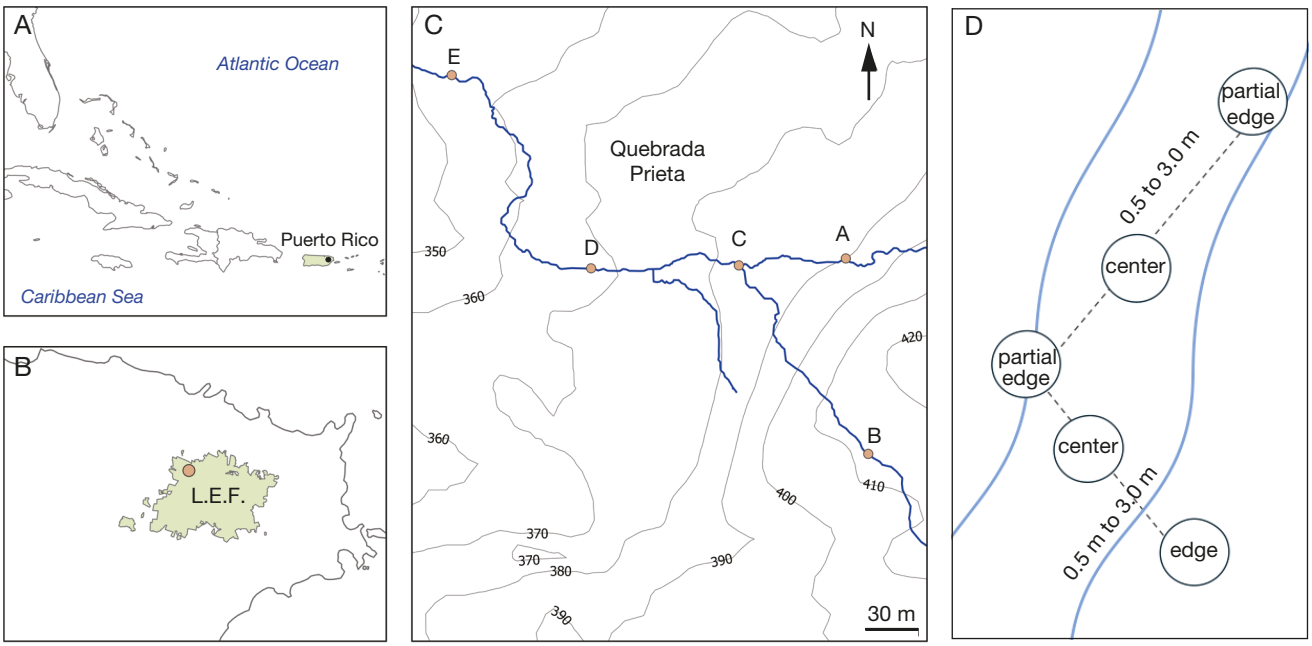

FIG. 1. — **A**, location of the island of Puerto Rico in the Caribbean; **B**, map of the Luquillo Experimental Forest (LEF) and El Verde Field Station (**orange circle**); **C**, the five study sites are located in Quebrada Prieta (locations were adjusted for error in GPS collection), elevation range from 350-420 m; **D**, five plots were sampled across the edge, partial edge and center of the stream; distance between plots was random and ranged from 0.5 to 3.0 m at 0.5 intervals. n = 25.

MATERIAL AND METHODS

STUDY SITE

This study was conducted in the Luquillo Experimental Forest (LEF) in the eastern region of Puerto Rico (18°20'N, 65°49'W) that has one of the longest histories of tropical ecology research (Zimmerman *et al.* 2021). The study site is located within the wet forest and this area receives an average of 3500 mm yr^{-1} of rainfall. The forest floor receives 60% of this precipitation, while the other 40% is intercepted by large vegetation and evaporates (Harris *et al.* 2012).

The sites selected are in a second-order, perennial stream, Quebrada Prieta, that is in the Río Espíritu Santo Watershed. It flows east to west and originates 600 m above sea level and connects to Quebrada Sonadora at 310 m (Leon *et al.* 2021). The chemistry of stream water from the LEF has been taken regularly since the 1980's (McDowell *et al.* 2021). This stream is about 1.5 km long and is primarily composed of boulders, bedrock, and cobble (Masteller & Buzby 1993), and has incised banks which prevent the development of floodplains and flooding (Heartsill-Scalley & Crowl 2021). To the north of Quebrada Prieta past land use is high, this includes land used for agriculture and logging before 1934, while south of Quebrada Prieta marks an area of low past agricultural land use (Heartsill-Scalley & Crowl 2021). Throughout the year, Quebrada Prieta may experience disturbances such as tree falls, landslides, hurricanes, and droughts.

Five study sites within Quebrada Prieta were chosen: Prieta A and B are branches of the stream that merge downstream at site C (also known as QP or Pool 0), sites D and E are further downstream (Fig. 1). Site B is at the highest elevation at 410-420 m, and site E is at the lowest elevation at 350-360 m. Average stream width for Quebrada Prieta is 3 m and average depth is 0.5 m (Heartsill-Scalley & Crowl 2021), average water temperature is 21.89°C ± 1.58 (range 17°-24.9°C) and average pH is 7.04 ± 0.26 (range 6.15-7.78) (McDowell & International Institute of Tropical Forestry, USDA Forest Service 2024). Site B of our study coincides with the location of a flow reduction experiment (Quebrada Prieta B, Fig. 2A) that began in 2021 to reduce half of the stream flow in this part of the stream for three months, during the peak of the dry season, to simulate drought conditions (Luquillo LTER 2021).

DATA COLLECTION AND ANALYSIS

In each study site, five circular plots of 0.90 m in diameter were surveyed for bryophytes, a total of 25 plots were made. The plots were arranged in a diagonal line beginning at the edge of the stream and crossing to the other side so that the edge, partial edge (including the streambank), and the center of the stream had an equal chance of being sampled. The distance between plots was chosen by drawing random numbers ranging from 0.5 to 3.0 m (at 0.5 intervals); if no bryophytes were present in a plot, another random number was drawn (Slack & Glime 1985). A species accumulation curve was done to assess if sampling was representative of the bryophyte community and Chao2 was calculated to estimate the number of species that were not documented. The species accumulation curve was constructed by recording the number of new and unique species observed sequentially in each plot, only the species not previously encountered were added to the cumulative total to reflect the increasing number of unique species observed with each additional plot sampled. The sampling effort was deemed representative when the

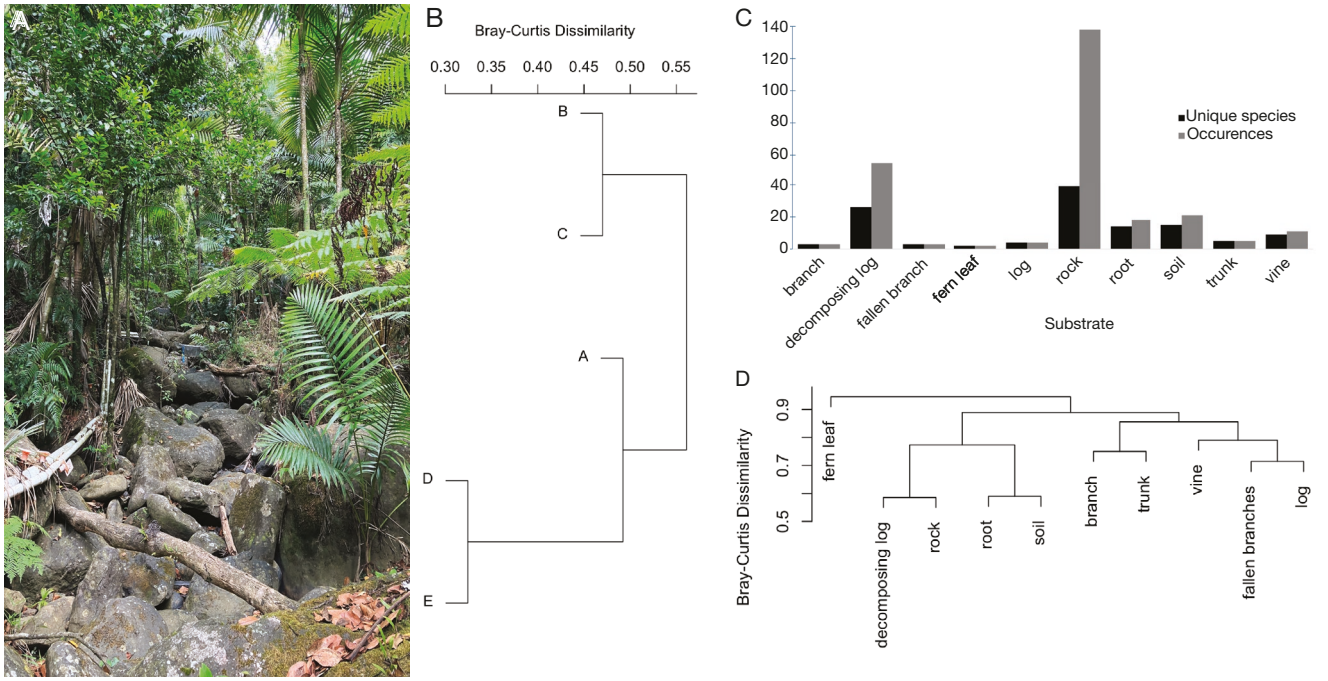

FIG. 2. — **A**, section of Quebrada Prieta showing the typical composition of the sites; **B**, similarities in community composition by site (0 = same species composition, 1 = do not share any species); **C**, bryophyte richness and occurrence by substrate; **D**, similarities in species composition by substrate (0 = same species composition, 1 = do not share any species).

curve approached an asymptote and no novel species were encountered. The curve started to level off at our third site and continued to plateau through the fourth and fifth sites.

All species were recorded in each plot and samples were collected for identification, especially those that could not be identified in the field. The substrate type (substrate group) was documented as: rock, decomposing log, soil, root, vine, trunk, log, branch, fallen branches, and fern leaf. Canopy cover was measured with a spherical convex densiometer (Model A, Forestry Suppliers) placed at the center of each plot. Environmental variables for temperature and relative humidity were recorded for four of the five study sites every six hours for five days using a HOBO Weatherproof Temperature and Relative Humidity Data Logger (Onset MX2301A) placed on the edge of the stream above the water in sites A, B, C and E. Environmental data were collected from four sites to represent different sections of the stream. Measurements of stream physical structure taken were the stream width and wet channel width. This research was conducted in June of 2023 where precipitation was minimal thus the wet channel width was smaller than the historical stream width.

Samples were identified to species and voucher specimens for some species were deposited in the Herbarium of the Biology Department at the University of Puerto Rico, Río Piedras (UPRRP) (Appendix 1). Species that could not be identified were treated at the generic level. Bryophytes were identified using the checklists and keys published in Crum & Steere (1957), Miller & Russell (1975), Gradstein (1989), Sastre-D. & Buck (1993), Reese (1993), Buck (1998) and Gradstein *et al.* (2001). Nomenclature of species follows that presented in The Bryophyte Nomenclator (Brinda & Atwood 2025; Tropicos.org 2025). While identifying the samples under the compound microscope, we documented the presence of cyanobacteria growing with the bryophyte plants.

Richness and abundance of bryophyte species was calculated for each plot and site. Bryophyte cover was visually estimated as the percentage of the plot occupied by bryophyte patches. For each species we calculated three measurements of abundance: frequency is the total number of times the species was documented, percent frequency is the percent of plots (n = 25) in which a species was present, and constancy is the number of sites (n = 5) in which the species was present (Evans *et al.* 2012). Alpha diversity index, Shannon's Species Diversity Index (H'), Effective Number of Species (exp(H')) and Evenness were calculated for each site and for each substrate for the entire bryophyte community and separately for mosses and liverworts. We modeled plot-level richness using generalized linear models (GLMs; Poisson, log link). For predictors measured at all five sites (A-E), the model included bryophyte cover, canopy cover, location in the stream (edge, partial edge, center), substrate group, site, elevation, stream width and wet channel width. A second model used the four sites where microclimate data was available (i.e. A, B, C, E) and added site-mean temperature and relative humidity; to estimate these effects without collinearity, site D was omitted from this four-site model. Dispersion (Pearson χ^2/df) supported Poisson fits ($\phi \approx 0.6$-0.7). We report Type-II likelihood-ratio tests for each term, exponentiated coefficients (rate ratios) with 95% CIs, and estimated marginal means for channel position. For categorical predictors, we obtained estimated marginal means and multiplicity-adjusted pairwise comparisons (Tukey), with predictions averaged over other factors as

TABLE 1. — List of bryophyte species found in Quebrada Prieta, Puerto Rico, species total frequency, percent frequency and consistency. For each species an "**x**" in the last column marks the presence of cyanobacteria. n = 25.

Family	Species	Frequency (total)	Percent frequency % (total/25)	Consistency	Presence of cyanobacteria
Marchantiophyta					
Aneuraceae H.Klinggr.	*Riccardia schwaneckei* (Steph.) Pagan	6	24	5	x
Calypogeiaceae Arnell	*Mnioloma crenulatum* (Bischl.) R.M.Schust.	1	4	1	
Frullaniaceae Lorch	*Frullania kunzei* (Lehm. & Lindenb.) Mont.	4	16	3	x
	Ceratolejeunea sp. (Spruce) J.B.Jack & Steph.	1	4	1	
	Ceratolejeunea cornuta (Lindenb.) Steph.	14	56	5	x
	Cheilolejeunea holostipa (Spruce) Grolle & R.L.Zhu	1	4	1	
	Cheilolejeunea rigidula (Nees ex Mont.) R.M.Schust.	2	8	1	x
	Cheilolejeunea xanthocarpa (Lehm. & Lindenb.) Malombe	2	8	1	x
	Cololejeunea cardiocarpa (Mont.) A.Evans	2	8	2	
	Cyclolejeunea accedens (Gottsche) A. Evans	3	12	3	x
	Cyclolejeunea convexistipa (Lehm. & Lindenb.) A.Evans	10	40	5	x
	Drepanolejeunea crucianella (Taylor) A.Evans	2	8	2	x
	Drepanolejeunea evansii Bischl. ex L. Söderstr., A.Hagborg & von Konrat	3	12	1	x
Lejeuneaceae Cas.-Gill	*Harpalejeunea tridens* (Besch. & Spruce) Steph.	1	4	1	x
	Harpalejeunea uncinata Steph.	1	4	1	x
	Lejeunea caracensis Lindenb.	2	8	2	
	Lejeunea deplanata Nees	4	16	1	
	Lejeunea glaucescens Gottsche	10	40	5	x
	Lejeunea minutiloba A. Evans	8	32	3	
	Leptolejeunea elliptica (Lehm. & Lindenb.) Besch.	3	12	2	x
	Leptolejeunea exocellata (Spruce) A.Evans	1	4	1	x
	Microlejeunea acutifolia Steph.	13	52	4	x
	Schiffneriolejeunea polycarpa (Nees) Gradst.	1	4	1	x
	Stictolejeunea squamata (Willd. ex F.Weber) Schiffn.	7	28	5	x
	Symbiezidium sp. Trevis.	1	4	1	
	Symbiezidium transversale (Sw.) Trevis.	1	4	1	
Lepidoziaceae Limpr.	*Telaranea diacantha* (Mont.) J.J.Engel & G.L.Merr.	3	12	1	x
Lophocoleaceae Müll. Frib. ex Vanden Berghen	*Lophocolea bidentata* (L.) Dumort.	1	4	1	
Marchantiaceae Lindl.	*Dumortiera hirsuta* (Sw.) Nees	2	8	2	
Metzgeriaceae Klinggr.	*Metzgeria lechleri* Steph.	1	4	1	
Plagiochilaceae (Jörg.) Müll.Frib. & Herzog	*Plagiochila* (Dumort.) Dumort. spp.	10	40	5	
Radulaceae Müll.Frib.	*Plagiochila dichotoma* (P. Beauv.) Nees & Mont.	1	4	1	x
	Radula pallens (Sw.) Nees ex Mont.	7	28	4	x
Bryophyta					
Calymperaceae Kindb.	*Calymperes erosum* Müll. Hal.	1	4	1	
	Calymperes palisotii Schwägr.	11	44	5	x
	Syrrhopodon incompletus Schwägr. var. *incompletus*	1	4	1	
Daltoniaceae Schimp.	*Actinodontium pygmaeum* W.R.Buck	1	4	1	x
Dicranaceae Schimp.	*Leucoloma serrulatum* Brid.	5	20	2	x
Fissidentaceae Schimp.	*Fissidens* Hedw. spp.	10	40	4	
Hypnaceae Schimp.	*Vesicularia vesicularis* (Schwägr.) Broth.	3	12	1	x
	Ectropothecium leptochaeton (Schwägr.) W.R.Buck	1	4	1	x
Leucobryaceae Schimp.	*Leucobryum martianum* (Hornsch.) Hampe ex Müll. Hal.	2	8	1	
Leucomiaceae Broth.	*Leucomium strumosum* (Hornsch.) Mitt.	4	16	2	
Neckeraceae Schimp.	*Neckeropsis undulata* (Hedw.) Reichardt	1	4	1	x
Octoblepharaceae A.Eddy ex M.Menzel	*Octoblepharum albidum* Hedw.	1	4	1	
Orthotrichaceae Arn.	*Groutiella apiculata* (Hook.) H.A.Crum & Steere	2	8	2	
	Callicostella belangeriana (Besch.) A.Jaeger	5	20	2	x
	Callicostella pallida (Hornsch.) Ångstr.	2	8	2	
Pilotrichaceae Kindb.	*Callicostella rivularis* (Mitt.) A. Jaeger	1	4	1	
	Crossomitrium epiphyllum (Mitt.) Müll. Hal.	8	32	2	x
	Crossomitrium patrisiae (Brid.) Müll. Hal.	1	4	1	
Pylaisiadelphaceae Broth.	*Taxithelium planum* (Brid.) Mitt.	27	108	5	

Table 1. — Continuation.

Family	Species	Frequency (total)	Percent frequency % (total/25)	Consistency	Presence of cyanobacteria
Sematophyllaceae Broth.	*Brittonodoxa subpinnatum* (Brid.) W.R.Buck, P.E.A.S.Câmara & Carv.-Silva	17	68	5	x
	Trichosteleum sentosum (Sull.) A.Jaeger	1	4	1	x
Stereophyllaceae W.R.Buck & Ireland	*Eulacophyllum cultelliforme* (Sull.) W.R.Buck & Ireland	1	4	1	
Thuidiaceae Schimp.	*Thuidium urceolatum* Lorentz	25	100	5	x

appropriate. Reference levels were "center" (location), "soil" (substrate), and "site A". Similarity in species composition between sites and by substrate were analyzed using Bray-Curtis dissimilarity index calculated with the vegdist function in the vegan package in R, cluster analyses were performed using hclust and the results visualized as dendrograms. Analyses were performed with R 4.3.3 (R Core Team 2024).

RESULTS

Bryophyte richness and diversity

Across the five study sites in Quebrada Prieta, we recorded 260 occurrences of bryophytes, all growing above water, and identified 56 bryophytes (52 to species) in 25 families, 33 were liverworts and 23 species were mosses (Table 1). The Chao2 estimator predicted an asymptotic richness of 96.6 (± 22.3 SE), suggesting that sampling captured about 58% of the species estimated. From the identified liverwort species, the most common family found was Lejeuneaceae Rostovzev with 23 species, and the most common moss family was Pilotrichaceae Kindb. with four species. Some samples of *Plagiochila* (Dumort.) Dumort. spp. and *Fissidens* Hedw. spp. were identified to genus, and two specimens, *Ceratolejeunea* (Spruce) J.B.Jack & Steph. sp. and *Symbiezidium* Trevis. sp. could not be identified to species because there was not enough material. Most of the species were recorded only in one site (29 species) or two sites (11 species), three species were recorded on three and four sites each, and ten species were recorded in all five sites (consistency values in Table 1). We observed cyanobacteria on 12 moss species and 20 liverworts species (Table 1).

Bryophyte species richness for the five sites was highest in sites A and B, with 28 species (53 occurrences) and 33 species (52 occurrences) respectively (Table 2). These two sites were also found to harbor the highest species diversity; the Shannon's diversity index for site A was 3.12 and for site B 3.25, while the effective number of species was 22.56 for A and 25.80 for B. For the five sites, high species richness was related to high diversity. Although species richness and diversity increase together, species evenness was dispersed throughout all the sites, with values above 0.92 (Table 2).

In the five-site Poisson GLM, plot-level richness increased with bryophyte cover (rate ratio = 2.57, 95% CI 1.00-6.60; LR $\chi^2(1) = 3.81$, $p = 0.051$), whereas canopy cover (LR $\chi^2(1) = 0.19$, $p = 0.659$), location in the stream (LR $\chi^2(2) = 1.36$, $p = 0.508$), substrate group (LR $\chi^2(3) = 2.41$, $p = 0.492$), and site (LR $\chi^2(4) = 6.27$, $p = 0.180$) were not significant. Adjusted pairwise comparisons among positions were non-significant in the five-site model (center vs partial edge $p = 0.844$; center vs edge $p = 0.488$; partial edge vs edge $p = 0.776$; Fig. 3A). Effect sizes for all predictors are shown in Figure 3B.

Taxithelium planum (Brid.) Mitt. was the most frequent moss species recorded, it was found in all sites and as the most abundant bryophyte in sites C and B (Table 1). *Thuidium urceolatum* Lorentz followed by *Brittonodoxa subpinnatum* (Brid.) W.R.Buck, P.E.A.S. Câmara & Carv.-Silva were also abundant and found in all sites. *Thuidium urceolatum* was most prominent in sites A and D, and as abundant as *Fissidens* spp. in site E. The most frequent liverwort found was *Ceratolejeunea cornuta* (Lindenb.) Steph. and was present in all sites. *Microlejeunea acutifolia* Steph. was the second most frequent liverwort, found in sites A, B, C, and E. *Cyclolejeunea convexistipa* (Lehm. & Lindenb.) A.Evans was the third most frequent liverwort; however, we observed that when this species was present, it was the most abundant and/or formed the largest patches in the plot. Species composition ranged from similar to intermediate among sites (Bray-Curtis Dissimilarity between 0.3-0.55, Fig. 2B). Sites D and E have more species in common and together they are more similar to site A; and species composition of sites C and B are more similar.

Stream composition and bryophyte community

In all the plots, canopy cover measurements were over 85%. In the four-site GLM that included microclimate (A, B, C, E; Site D omitted), bryophyte cover showed a positive trend (rate ratio ≈ 2.46, 95% CI 0.88-6.90; LR $\chi^2(1) = 2.97$, $p = 0.085$), while canopy cover (LR $\chi^2(1) = 0.31$, $p = 0.579$), location (LR $\chi^2(2) = 0.40$, $p = 0.818$), substrate group (LR $\chi^2(3) = 1.62$, $p = 0.656$), temperature (LR $\chi^2(1) = 0.10$, $p = 0.756$), and relative humidity (LR $\chi^2(1) = 0.55$, $p = 0.458$) were not significant. Average relative humidity of the four sites was 92.42% (± 0.38), the highest relative humidity was in site E with 93.3% while site B had the lowest with 91.8%. Predicted richness by position was center ≈ 7.67 (95% CI 4.51-13.0), partial edge ≈ 8.47 (5.30-13.5), and edge ≈ 9.40 (6.36-13.9); Pairwise comparisons among positions were also non-significant in the microclimate model (center vs partial

TABLE 2. — Alpha diversity indices for bryophyte communities in each site at Quebrada Prieta, Puerto Rico.

Sites	Richness	Shannon's Index (H')	Effective number of species (exp(H'))	Evenness
A	28	3.116	22.56	0.935
B	33	3.250	25.80	0.930
C	22	2.837	17.07	0.918
D	18	2.684	14.75	0.929
E	21	2.867	17.6	0.942

TABLE 3. — Alpha diversity indices of bryophyte communities by substrate in 25 plots at Quebrada Prieta, Puerto Rico.

Substrate	Richness	Shannon's Index (H')	Effective number of species (exp(H'))	Evenness
Branch	3	1.099	3	1
Decomposing log	25	3.072	21.58	0.954
Fallen branches	3	1.099	3	1
Fern leaf	2	0.693	2	1
Log	4	1.386	4	1
Rock	37	3.199	24.50	0.886
Root	14	2.582	13.23	0.978
Soil	15	2.574	13.11	0.950
Trunk	5	1.609	5	1
Vine	9	2.14	8.55	0.98

edge $p = 0.944$; center vs edge $p = 0.812$; partial edge vs edge p = 0.904; Fig. 3A).

Elevation of sites ranged between 350 m to 420 m, sites A and B were at the highest elevation, and site D at the lowest elevation. Across sites, variation in microclimate and elevation was minimal relative to the within-stream plot conditions, which likely limited detectable site-scale effects on richness (Appendix 2). The width of the stream at the sites ranged from 3.2 m to 11 m. However, wet channel stream width varied from 2 m (Site A) to 6.5 m (Site B) and average wet channel stream width was 3.56 m (± 1.8). Consistent with the models, richness patterns tracked local bryophyte cover rather than channel width metrics (Fig. 3A).

Substrate and community composition

Rock was the dominant substrate in 92% of the sites, followed by decomposing logs, roots and vines (Fig. 2C). Most bryophyte species (37) were found on rocks. Rock as a substrate had a high diversity (H' = 3.20, exp(H') = 24.50) and the greatest richness with 138 occurrences (Fig. 2C). Site D contained two plots without rocks, and the dominant substrate occupied by bryophytes was decomposing logs, soil, and roots.

Decomposing logs was the second dominant substrate with more diversity of bryophytes (H' = 3.07, exp(H') = 21.58) and 55 occurrences. The least diverse substrate was fern leaf, recorded once in the plots. Fern leaf had a very low value for Shannon's diversity index (H' = 0.69), effective number of species (exp(H') = 2) and a species richness of 2. The base of tree trunks had low diversity (H' = 1.61, exp (H') = 5) with a highly even (E' = 1) community of bryophyte species (Table 3). This substrate had the greatest value for evenness; however, all the substrates, besides rock, had an evenness value of over 0.95. This riparian community is fairly distributed with a slight dominance of one or more species on the rock substrate. Species composition between substrates ranged from intermediate to very distinct (Bray-Curtis Dissimilarity between 0.5-1). The bryophyte community on the "fern leaf" is more dissimilar to the communities in all other substrates; species composition on rocks is more similar to those on decomposing logs, and bryophyte communities on roots and soil are more similar. Bryophyte communities on branches, trunks, fallen branches, logs and vines share more species and are grouped together (Fig. 2D).

Taxithelium planum was the most frequent moss species (Table 1), mostly growing on rocks but was found in all other substrates except fern leaves. *Thuidium urceolatum* the second most frequent moss, found mostly on rock and decomposing logs but also on soil, logs, roots, and fallen branches. The most frequent and abundant liverwort species were found on rocks but also on other substrates. *Microlejeunea acutifolia* was predominantly found on rocks, but also on branches, decomposing logs, and tree trunks. *Ceratolejeunea cornuta* was mainly found on rocks, but it was also found on vine, decomposing log, root, and fern leaves. *Lejeunea glaucescens* Gottsche was equally found on decomposing logs and rocks. *Cyclolejeunea convexistipa* was found on rocks. *Vesicularia vesicularis* (Schwägr.) Broth. and *Callicostella pallida* (Hornsch.) Ångstr. were two moss species found only on decomposing logs. *Frullania kunzei* (Lehm. & Lindenb.) Mont. and *Drepanolejeunea evansii* Bischl. ex L.Söderstr., A.Hagborg & von Konrat, two liverwort species, were only found on rocks. *Drepanolejeunea evansii* was only found in plot A, and *Frullania kunzei* was found in sites A, B, and C.

DISCUSSION

The bryological flora of Puerto Rico consists of approximately 520 species; 284 mosses, 232 liverworts and five hornworts,

55% of those are found in the Luquillo Experimental Forest (LEF) (Sastre-D. & Tan 1995). The LEF is the most bryophyte rich forest in Puerto Rico, this tropical forest has five Holdridge life zones and contains diverse microhabitats. In this study, we focused on a section of a second order stream, Quebrada Prieta, in the lower montane wet forest; the 56 bryophytes documented represent about 18% of the total bryophytes in the LEF. No similar studies have been carried out in streams of any other tropical forest in the Caribbean region. Although streams were not surveyed, Russell & Miller (1977) documented 23 epiphytic mosses in the elfin forest in the LEF, and Fulford *et al.* (1971) reported 156 species of liverworts in ten areas of the LEF but only five species were present in all the areas. Two of those species, *Ceratolejeunea cornuta* and *Cyclolejeunea convexistipa*, were also present in all our study sites and had some of the highest frequencies (Table 1).

The presence and abundance of bryophytes is connected to the external environment that shapes the unique microhabitats they inhabit. As predicted, bryophyte community composition was similar throughout the stream and species diversity was similar among sites. Plot-level richness tracked bryophyte cover, and we found that other environmental and stream-structure variables provided little additional explanatory power for richness. Instead, bryophyte composition appeared to be shaped by location in the stream and by the presence and diversity of substrates. The most abundant mosses were pleurocarps and almost all liverworts were leafy in this section of Quebrada Prieta. Ten bryophyte species were present in all sites but most of the species were rare and found only in one or two sites, this pattern might reflect habitat availability, and/or particular substrate preferences and dispersal mechanisms of bryophytes (Heinlen & Vitt 2003). We found that the most abundant species of mosses and liverworts occur across multiple substrates which could indicate a generalist strategy. Although our sampling may not fully represent the overall bryophyte community of the stream, this is the first study to describe any tropical stream bryophyte community and the importance of substrates in structuring these communities.

Humidity, temperature, and canopy cover were broadly uniform among sites and showed no clear association with plot-level richness; canopy cover and relative humidity values were over 90%. This likely reflects the limited among-site contrast in canopy and humidity, which were uniformly high. Canopy cover seems to be an important factor for riparian bryophyte communities (Tessler *et al.* 2014); bryophyte species richness has been found to be higher near streams with closed canopies and declines in areas with more open canopy (Lagos *et al.* 2008; Baldwin *et al.* 2012; Romero 2017). A preference for open canopy was found for *Thuidium urceolatum* in riparian zones of the LEF (Matos *et al.* 2024). It is possible that this species can tolerate a wider range of light intensity and desiccation conditions than some of the other bryophytes documented, which can explain its high abundance. Although bryophytes are desiccation tolerant, they are sensitive to humidity and canopy cover change (Benítez *et al.* 2015); if humidity levels go below 75% some species, particularly understory species, are unable to recover (Pardow & Lakatos 2013; Glime 2021).

Location of microhabitats (edge, partial edge, center) along the stream structured habitat availability and community composition, but it did not produce consistent differences in richness across locations (Appendix 3). A greater variety of substrates away from the center likely contributes to higher bryophyte cover near the edges, which can coincide with higher richness in some plots. Although we did not find aquatic bryophytes, some patches could be temporarily submerged with flooding; water chemistry, current velocity, and bryophyte position in relation to water level influence bryophyte presence in streams (Glime & Vitt 1987; Monteiro & Vieira 2017). Bryophyte species documented in our study occupy a wide range of available microhabitats, although not all sites are equal because of differences in substrates available (Kimmerer & Driscoll 2000). Many species are shared between the stream communities, but different types of substrates have less similar bryophyte communities.

Bryophyte communities growing on rocks and decomposing logs had more species in common, these substrates also have the highest richness. Vegetative substrates (i.e. branches, trunks, vines, logs), except roots, share more species among them, while bryophyte communities on roots and soil were more similar (Fig. 2D). Rocks were the dominant substrate in most sites and coincided with higher diversity and richness; however, the substrate group itself did not independently predict richness after accounting for bryophyte cover. This pattern is consistent with between-site differences in substrate availability: site D included two plots without rock, whereas site B had the greatest diversity of substrates and rocks in every plot. Distribution patterns of bryophytes, at a local scale, might depend more on substrate occurrence than dispersal ability (Vitt & Belland 1997).

Rocks are an especially important substrate for bryophytes in streams as they are mostly permanent and can protect bryophytes from flooding and other disturbances that may fragment or destroy communities on other substrates (Stream Bryophyte Group 1999; Lagos *et al.* 2008). One species in our sampling, *Frullania kunzei*, was found in multiple sites only on rocks. This highlights the importance of rocks as a permanent substrate. Other leafy liverworts were also found only on rock, but these were recorded only once or twice in this study. Changes in canopy cover and humidity could affect the persistence of these species on this substrate.

Of the 56 bryophytes we observed under the microscope, 57% of bryophytes (32 species) and over half of the liverworts (20 species) had cyanobacteria. Symbiosis of cyanobacteria with liverworts are rare (Adams & Duggan 2008), but commensalism associations can occur. In tropical cloud forests, the activity of bryophyte-associated cyanobacteria changed when exposed to lowered moisture and higher temperatures, decreasing N_2-fixing activity (Permin *et al.* 2022). Although the presence of cyanobacteria in bryophytes does not necessarily translate to an increase in nitrogen fixation (Jean & Bellenger 2024), bryophytes might provide a stable wet habitat for these organisms. In boreal ecosystems, cyanobacteria growing on mosses provide a large amount of new nitrogen inputs, however the contribution of bryophyte-associated cyanobacteria

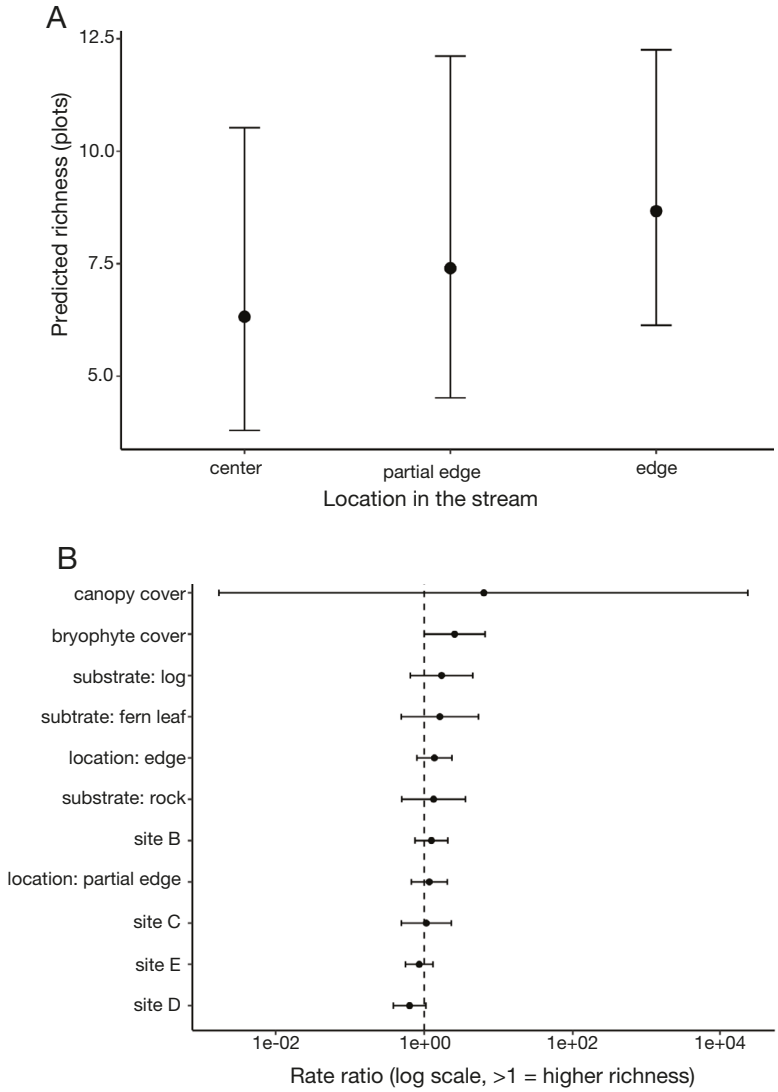

Fig. 3. — Predicted plot-level bryophyte richness by location in the stream from generalized linear models (GLMs). Points are estimated marginal means (EMMs) and bars are 95% CIs: **A**, Five-site Poisson GLM (A-E; log link), adjusting for bryophyte cover, canopy cover, substrate group, and site; predictions are averaged over substrate groups and sites. "**Location**" denotes plot location across the wetted channel (center, partial edge, edge); **B**, effect sizes for predictors of plot-level bryophyte richness from a generalized linear model (Poisson, log link). Points are rate ratios (exp β) and horizontal bars are 95% CIs on a log-scaled axis; the vertical dashed line at 1 indicates no effect. Estimates are multivariable (adjusted for bryophyte cover, canopy cover, location, substrate group, and site). Continuous predictors (cover, canopy) are proportions (0-1). Factor contrasts are relative to the reference levels: "**center**" (location), "soil" (substrate), "site A".

to nitrogen fixation in tropical riparian ecosystems remains undetermined (Permin *et al.* 2022). The association of cyanobacteria with bryophytes increases the ecological importance of riparian bryophytes as this interaction might affect the role of cyanobacteria in this ecosystem.

The Caribbean and the LEF are affected by changes in disturbance regimens such as frequent intense hurricanes, flooding and drought; however, little is known about how bryophytes are affected (Mercado-Díaz & Merced 2021). In 2015, a drought event occurred leaving connected streams to be fragmented pools and resulted in an increase of leaf litter and an opening of the canopy due to the stress on the vegetation present (Zimmerman *et al.* 2021). With a decrease in stream flow and canopy cover, bryophytes on rocks may struggle to persist. One of our sites (site B) is adjacent to The Stream Flow Reduction Experiment, StreamFRE, that diverts 50% of the stream flow to mimic drought conditions (Luquillo LTER 2021). Although bryophyte diversity is high in this site, it had slightly lower humidity compared to the other sites. Some bryophyte species may have a delayed reaction to change (Hernández-Hernández *et al.* 2019) and since this experiment started only two years before data collection, we were not expecting immediate changes to the bryophyte community due to the experimental flow reduction. The large number of bryophyte species in this site could be explained by the high number of different substrates present in site B.

High intensity hurricanes have an immediate effect of opening the canopy and temporarily changing the humidity and temperature of the area (Gutiérrez-Fonseca *et al.* 2020; Leitold *et al.* 2022). These disturbances in turn alter stream

food webs in this forest, for example shrimps use algae and biofilm (including cyanobacteria) as their main food source after a hurricane, instead of leaves (Gutiérrez-Fonseca *et al.* 2024). Bryophytes can act as refuge for cyanobacteria and other microorganisms during periods of drought and other disturbances.

The results of this study expand our understanding of bryophyte diversity and the factors that influence bryophyte community composition in tropical riparian areas. This second-order stream harbors similar bryophyte communities with an overall high number of species and diversity. The now described bryophyte community in this part of the stream in the LEF will serve future research to evaluate how bryophytes respond to drought conditions and assess if there are changes in the communities.

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APPENDICES

Appendix 1. — List of voucher specimens for some of the species recorded at Quebrada Prieta in the Luquillo Experimental Forest, Puerto Rico.

Herbarium barcode	Accession number	Collector	Collection number	Date	Family	Species
UPRRP32217	63555	Merced A. & Sahnow C.	573	12.VI.2023	Lejeuneaceae	*Cheilolejeunea rigidula* (Nees ex Mont.) R.M.Schust.
UPRRP32218	63556	Merced A. & Sahnow C.	574	12.VI.2023	Frullaniaceae	*Frullania kunzei* (Lehm. & Lindenb.) Mont.
UPRRP32219	63557	Merced A. & Sahnow C.	575	12.VI.2023	Orthotrichaceae	*Groutiella apiculata* (Hook.) H.A.Crum & Steere
UPRRP32220	63558	Merced A. & Sahnow C.	576	12.VI.2023	Lejeuneaceae	*Drepanolejeunea crucianella* (Taylor) A.Evans
UPRRP32221	63559	Merced A. & Sahnow C.	577	12.VI.2023	Lejeuneaceae	*Cyclolejeunea convexistipa* (Lehm. & Lindenb.) A.Evans
UPRRP32222	63560	Merced A. & Sahnow C.	578	12.VI.2023	Lejeuneaceae	*Stictolejeunea squamata* (Willd. ex F.Weber) Schiffn.
UPRRP32223	63561	Merced A. & Sahnow C.	579	12.VI.2023	Lejeuneaceae	*Ceratolejeunea cornuta* (Lindenb.) Steph.
UPRRP32224	63562	Merced A. & Sahnow C.	580	12.VI.2023	Lepidoziaceae	*Arachniopsis diacantha* (Mont.) M.Howe

Appendix 2. — Environmental variables in each site.

Site	Elevation (m)	Stream width (m)	Wet channel width (m)	Average temperature (°C)	Average RH (%)	Number of substrates
A	390	5	2	24.41	92.85	4
B	410-420	11	6.5	24.36	91.77	7
C	380-390	6.1	3.7	24.47	91.79	6
D	360-373	6	3.2	N/A	N/A	5
E	350-360	3.2	2.4	24.44	93.26	2

Appendix 3. — Estimated bryophyte cover, canopy cover, location of each plot, and the species and substrates found in each plot.

Plots	Bryophyte cover	Canopy cover	Location	Species	Substrates
A1	45%	98.96%	Edge	*Thuidium urceolatum, Plagiochila* spp., *Taxithelium planum, Microlejeunea acutifolia, Plagiochila* spp., *Crossomitrium epiphyllum, Callicostella belangeriana, Fissidens* spp., *Ceratolejeunea cornuta, Lejeunea minutiloba, Crossomitrium patrisiae, Leucomium strumosum*	Rock, decomposing log
A2	80%	99.22%	Partial edge	*Lejeunea deplanata, Crossomitrium epiphyllum, Thuidium urceolatum, Callicostella rivularis, Leucomium strumosum, Taxithelium planum, Cyclolejeunea convexistipa, Stictolejeunea squamata, Lejeunea minutiloba, Schiffneriolejeunea polycarpa, Ceratolejeunea cornuta, Fissidens* spp.	Root, soil, rock
A3	5%	98.18%	Center	*Cyclolejeunea convexistipa, Drepanolejeunea evansii, Leptolejeunea exocellata, Microlejeunea acutifolia*	Rock
A4	30%	97.14%	Edge	*Thuidium urceolatum, Drepanolejeunea evansii, Crossomitrium epiphyllum, Vesicularia vesicularis, Leptolejeunea elliptica, Metzgeria lechleri, Taxithelium planum, Vesicularia vesicularis, Ceratolejeunea cornuta, Radula pallens, Callicostella belangeriana, Riccardia schwaneckei, Lejeunea deplanata*	Rock, decomposing log
A5	60%	98.96%	Partial edge	*Brittonodoxa subpinnatum, Drepanolejeunea evansii, Thuidium urceolatum, Microlejeunea acutifolia, Frullania kunzei, Taxithelium planum, Lejeunea deplanata, Eulacophyllum cultelliforme, Lejeunea minutiloba, Ceratolejeunea cornuta, Calymperes palisotti, Crossomitrium epiphyllum, Lejeunea glaucescens*	Rock, root
B1	5%	99.22%	Edge	*Taxithelium planum, Cyclolejeunea convexistipa, Arachniopsis diacantha, Lophocolea bidentata, Leucobryum martianum, Fissidens* spp., *Leucomium strumosum, Leucoloma serrulatum, Ceratolejeunea cornuta, Stictolejeunea squamata, Taxithelium planum, Brittonodoxa subpinnatum*	Soil, root, fern leaf, rock

Plots	Bryophyte cover	Canopy cover	Location	Species	Substrates
B2	10%	94.80%	Center	*Plagiochila* spp., *Taxithelium planum, Brittonodoxa subpinnatum, Ceratolejeunea cornuta, Microlejeunea acutifolia, Harpalejeunea tridents, Cyclolejeunea convexistipa*	Rock
B3	20%	97.40%	Center	*Taxithelium planum, Brittonodoxa subpinnatum, Microlejeunea acutifolia, Frullania kunzei, Ceratolejeunea cornuta, Harpalejeunea uncinata, Mnioloma crenulatum*	Rock
B4	60%	93.50%	Partial edge	*Ectropothecium leptochaeton, Callicostella pallida, Calymperes erosum, Lejeunea glaucescens, Cyclolejeunea accedens, Thuidium urceolatum, Groutiella apiculata, Calymperes palisotti, Leucoloma serrulatum, Taxithelium planum, Plagiochila dichotoma, Symbiezidium transversale, Taxilejeunea obtusangula, Ceratolejeunea cornuta*	Decomposing log, fallen branches, vine, rock, root
B5	15%	96.36%	Edge	*Thuidium urceolatum, Taxithelium planum, Riccardia schwaneckei, Octoblepharum pulvinatum albidum, Calymperes palisotti, Lejeunea glaucescens, Microlejeunea acutifolia, Trichosteleum sentosum, Ceratolejeunea cornuta, Leucomium strumosum, Brittonodoxa subpinnatum, Actinodontium pygmaeum, Lejeunea glaucescens, Symbiezidium* sp.	Soil, decomposing log, rock
C1	60%	90.12%	Edge	*Brittonodoxa subpinnatum, Leucoloma serrulatum, Groutiella apiculata, Calymperes palisotti, Cheilolejeunea rigidula, Taxithelium planum, Plagiochila* spp., *Cololejeunea cardiocarpa, Thuidium urceolatum, Frullania kunzei, Microlejeunea acutifolia*	Rock
C2	20%	90.38%	Partial edge	*Taxithelium planum, Brittonodoxa subpinnatum, Microlejeunea acutifolia*	Rock
C3	15%	85.70%	Center	*Brittonodoxa subpinnatum, Cyclolejeunea convexistipa, Microlejeunea acutifolia, Taxithelium planum, Riccardia schwaneckei, Cheilolejeunea rigidula, Drepanolejeunea crucianella, Lejeunea glaucescens*	Rock, log
C4	65%	97.66%	Edge	*Taxithelium planum, Brittonodoxa subpinnatum, Cyrtolejeunea holostipa, Radula pallens, Cyclolejeunea convexistipa, Leucoloma serrulatum, Thuidium urceolatum, Frullania kunzei, Microlejeunea acutifolia, Plagiochila* spp., *Plagiochila* spp., *Cyrtolejeunea holostipa*	Rock, branch
C5	15%	96.10%	Edge	*Neckeropsis undulata, Leucoloma serrulatum, Leucolejeunea xanthocarpa, Calymperes palisotti, Plagiochila* spp., *Taxithelium planum, Ceratolejeunea cornuta, Stictolejeunea squamata, Ceratolejeunea sp., Cyclolejeunea convexistipa, Microlejeunea acutifolia, Thuidium urceolatum*	Vine, decomposing log, trunk, rock
D1	10%	94.28%	Edge	*Fissidens* spp., *Thuidium urceolatum, Leptolejeunea elliptica, Brittonodoxa subpinnatum, Taxithelium planum*	Rock
D2	45%	99.48%	Edge	*Dumortiera hirsuta, Thuidium urceolatum, Fissidens* spp., *Calymperes palisotti, Plagiochila* spp., *Riccardia schwaneckei, Taxithelium planum, Lejeunea minutiloba, Cyclolejeunea accedens, Lejeunea glaucescens, Callicostella pallida*	Soil, decomposing log, root
D3	1%	97.92%	Center	*Stictolejeunea squamata*	Rock
D4	25%	99.22%	Edge	*Thuidium urceolatum, Taxithelium planum, Taxilejeunea obtusangula, Ceratolejeunea cornuta, Radula pallens, Lejeunea glaucescens, Brittonodoxa subpinnatum*	Log, soil, decomposing log, root
D5	15%	98.96%	Center	*Brittonodoxa subpinnatum, Cyclolejeunea convexistipa, Ceratolejeunea cornuta*	Rock
E1	60%	99.74%	Edge	*Thuidium urceolatum, Fissidens* spp., *Calymperes palisotti, Plagiochila* spp., *Taxithelium planum, Lejeunea minutiloba, Callicostella belangeriana, Riccardia schwaneckei, Brittonodoxa subpinnatum, Lejeunea minutiloba, Cyclolejeunea accedens*	Rock, decomposing log
E2	45%	98.96%	Partial edge	*Thuidium urceolatum, Fissidens* spp., *Plagiochila* spp., *Lejeunea glaucescens, Cyclolejeunea convexistipa, Brittonodoxa subpinnatum, Stictolejeunea squamata, Ceratolejeunea cornuta, Syrrhopodon incompletus var. incompletus*	Rock
E3	45%	98.96%	Partial edge	*Thuidium urceolatum, Fissidens* spp., *Dumortiera hirsuta, Radula pallens, Lejeunea minutiloba, Lejeunea glaucescens, Taxithelium planum, Crossomitrium epiphyllum*	Rock, root
E4	15%	99.22%	Center	*Fissidens* spp., *Microlejeunea acutifolia, Stictolejeunea squamata, Drepanolejeunea crucianella, Cyclolejeunea convexistipa*	Rock
E5	15%	99.22%	Center	*Radula pallens, Thuidium urceolatum, Brittonodoxa subpinnatum, Lejeunea minutiloba, Crossomitrium epiphyllum, Stictolejeunea squamata, Cololejeunea cardiocarpa*.	Rock