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Bryophyte Diversity and Distribution in the Virgin Islands Based on Historical Collections

Jahnyah Brooks[1] and Amelia Merced[2,3,*]

[1]*University of the Virgin Islands, St. Thomas, U.S. Virgin Islands*
[2]*International Institute of Tropical Forestry, USDA Forest Service, San Juan, Puerto Rico*
[3]*Herbarium, Biology Department, University of Puerto Rico Río Piedras, San Juan, Puerto Rico*

**Corresponding author: ameliamerced@gmail.com*

Abstract—In botanical research, vascular plants tend to overshadow their counterparts, the bryophytes. This trend can be observed in the Virgin Islands, with roughly 1,200 tracheophytes identified in the region and no official count of bryophytes on record. In this study, we documented the diversity and distribution of the bryophyte species of the Virgin Islands (British, United States, and Puerto Rico) using historical data from collections available through online herbaria. We also documented which islands had the most species recorded, as well as which species and families were the most abundant. Linear regression tests were used to explore what factors may have a strong influence on the total number of species on a particular island, such as elevation, average annual rainfall, and land area. Lastly, we investigated the possibility of collection biases between the study sites by comparing the number of collections to the number of species recorded for each island. Overall, we found 115 species of bryophytes that belong to 28 families: 83 mosses, 30 liverworts, 2 hornworts. A positive correlation was found between the total number of species and the elevation of the island, but no correlation was found for land area and annual rainfall. With 55% of the collections being recorded there, St. Thomas was the island with the most collections. The results of this study will help broaden what is known about the bryophyte species of this region and can potentially open doors for more modern botanical expeditions.

The Puerto Rican Bank is a region east of the Greater Antilles that includes Puerto Rico (PR) and its smaller islands Vieques and Culebra, the United States Virgin Islands (USVI), and the British Virgin Islands (BVI) (Heatwole 1981). The Virgin Islands (VI), except for St. Croix, are part of the Puerto Rican platform and were connected in past geological times based on studies of changes in sea level (Acevedo-Rodríguez 1996). The Virgin Islands consist of two groups of islands, one group under the American flag and the other under the British flag. The islands that make up the USVI are St. Thomas, St. Croix, St. John, and Water Island, as well as smaller islets in the region. The British Virgin Islands also consists of four main islands: Tortola, Virgin Gorda, Jost Van Dyke, Anegada, as well as smaller islands. Being a cluster of islands in the Caribbean Sea, their subtropical climate, lush green topography, and variable elevations ranging from as low as sea level to the highest point being Mt. Sage in Tortola rising to 521m (Evans 2017) has allowed these islands to develop into potential hotspots for species diversity in both terrestrial and marine ecosystems.

Floristic inventories have documented the diversity of tracheophytes in the West Indies, where 72% of seed plant taxa are endemic to the region (Acevedo-Rodríguez and Strong 2008). Over 1,200 of these plant species have been recorded for the USVI, many of which are shared with Puerto Rico and can be considered a subset of the flora of Puerto Rico (Lindsay et al. 2015; Acevedo-Rodríguez 1996). Similar inventories are scarce for non-flowering plants, in particular for bryophytes. The bryophyte flora of the West Indies is estimated to be about 500 species of mosses and 120 genera of liverworts (Gradstein et al. 2001). The occurrence of most species of bryophytes in the area is hypothesized to be the result of long-distance dispersal, these species are shared with North, Central, and South America and few endemics can be recognized (Crosby 1969; Buck 1990; Delgadillo M. 2000). Specific checklists of bryophytes of the VI do not exist, although they are included in some of the treatments for the bryological flora of Puerto Rico, such as the 'The mosses of Porto Rico and the Virgin Islands' by Crum and Steere (1957) and 'A key to the Hepaticae and Anthocerotae of Puerto Rico and the Virgin Islands' by Gradstein (1989). Historically, some botanical and bryological explorations have

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been conducted to these islands (Britton 1915; D'Arcy 1971; Buck 1998), however, there is no official account of the number of species of bryophytes of the VI nor a list of collections.

In this article, we investigate the diversity and distribution of bryophytes in the Virgin Islands using herbarium collections that are available as online databases. We aim to answer several questions: 1) What is the diversity of bryophytes in the VI, specifically what are the most common species and families? 2) What islands have the most species? 3) Are some islands more heavily collected than others? Based on island biogeography theory, we predict that larger islands will have more species. In addition, we examine what factors might drive bryophyte diversity by testing for correlations between the number of species and some environmental factors on each island. Because this study is based on collections from herbaria, we investigated the relationship between the number of collections and species to detect any sampling biases.

MATERIALS AND METHODS

Study Site

The Virgin Islands are a group of islands and islets located east of Puerto Rico (18°20'N, 64°40'W), between the Greater Antilles and the Lesser Antilles. Although some consider the Virgin Islands to be part of the Lesser Antilles, they are treated here as part of the Puerto Rican Bank following Acevedo-Rodríguez (1996). Data were collected when available from all islands: St. Thomas, St. Croix, St. John, Water Island, Tortola, Virgin Gorda, Jost Van Dyke, Anegada, Culebra, and Vieques.

Collections of specimen data

To gather collections data we used online herbaria databases through the Consortium of North America Bryophyte Herbaria Portal (2020) which compiles digitalized specimen information from over 100 herbaria around the world. We navigated through the database searching at terms relevant to the study such as location and species. The species search was done using the category of division: Bryophyta (mosses), Marchantiophyta (liverworts), and Anthocerophyta (hornworts). The location search was based on the regions of interest within the PR Bank, namely USVI, BVI, Vieques, and Culebra. To maximize the location search results, we also searched the following sections of the databases: continent, country, state/province, county/municipality, and precise location using the names of each of the main islands. This step was necessary to make sure all available records were included because not all collections recorded from the same area were documented in the same fashion. To eliminate records that were mislabeled and were not from the VI, the localities listed were verified thoroughly, when available. After collecting information from the specimens, it was necessary to cross-reference the samples that came from different herbaria to ensure no collections were added twice to our samples and eliminate the duplicates. Duplicate records with the same collector and number were removed if they were from the same date, species, and locality. We then extracted the information from the herbaria in the form of comma-separated values (CSV) files and organized the data for the descriptive statistics as well as linear regressions. Maps used to illustrate the collections were acquired through the Global Biodiversity Information Facility (2020).

Descriptive Statistics and Linear Regression

Histograms were used to illustrate the relative abundance of bryophyte families and species distribution in the region as well as bryophyte collection efforts. Collection efforts were shown by comparing the number of species recorded on each island to the number of collections per island. A linear regression test was used to understand what factors of each island such as, elevation, area, and annual average precipitation, had the strongest influence on the distribution and number of species of mosses and liverworts. Statistical analyses and graphs were made in Google Sheets (Google LLC).

RESULTS

The bryophytes recorded for the Virgin Islands, consist of a total of 115 species in 58 genera and 28 families (Table 1). The highest number of species was recorded for mosses with 83, followed by 30 species of liverworts and only two hornwort species (Table 1). These numbers are lower compared to those reported from Puerto Rico that have a total of 526 bryophyte species (Table 1) (Sastre-D. J. and Tan 1995). Most bryophyte species were recorded in St. Thomas; with 47 mosses, 16 liverworts, and two hornworts (Fig. 1). The number of species was highly variable between islands, but for all islands, the number of mosses were higher than the other groups. We also found *Fissidens zollingeri* Mont. (Fissidentaceae) to be the most frequently collected species of bryophyte in this region, with 34

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TABLE 1. Diversity of bryophytes of the Virgin Islands (VI) from this study compared to the diversity of bryophytes of Puerto Rico (PR) based on Sastre-D. J. and Tan (1995).

	Family		Genera		Species	
	VI	PR	VI	PR	VI	PR
Mosses	26	40	44	120	83	284
Liverworts	5	36	13	92	30	237
Hornworts	2	3	2	5	2	5
Totals	**28**	**69**	**59**	**217**	**115**	**526**

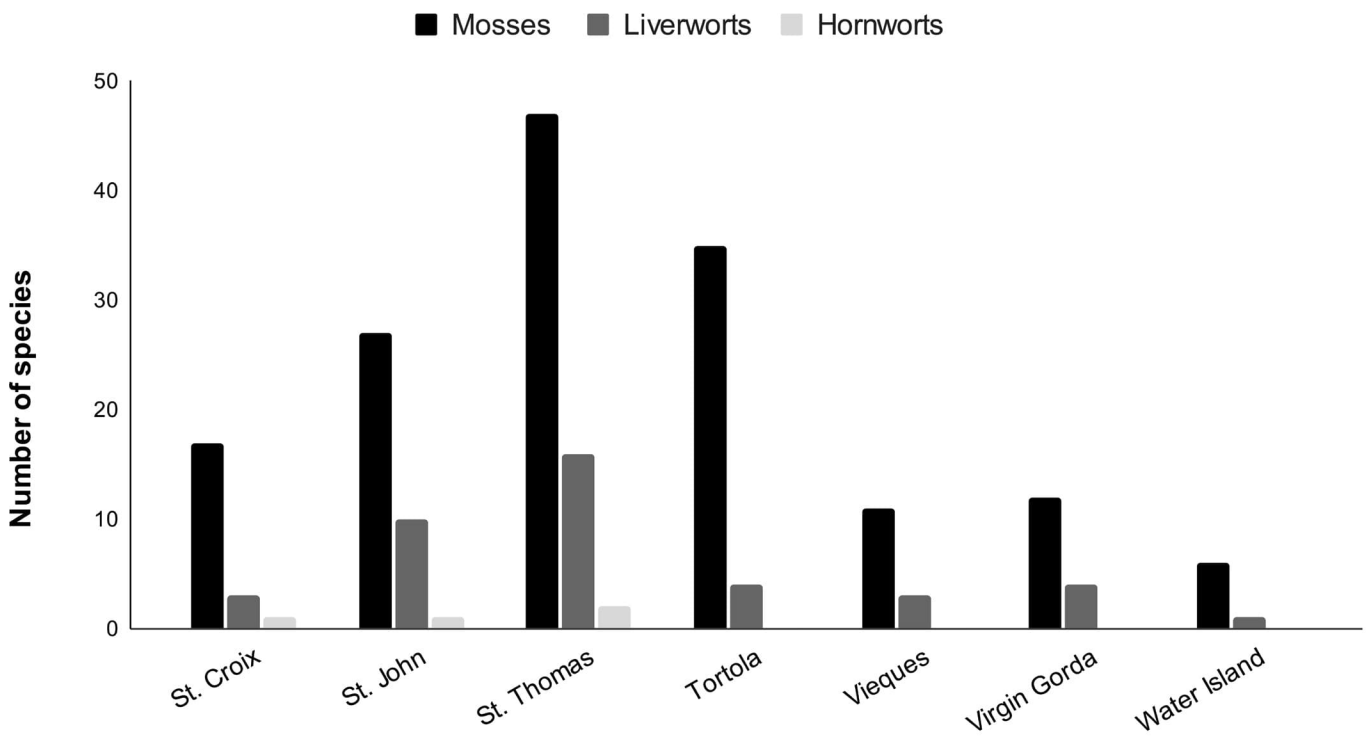

FIG. 1. Number of bryophyte species recorded throughout the main islands of the Virgin Islands.

specimens collected in St. Thomas. The family with the most species (n=21) represented in the VI was the Pottiaceae, accounting for roughly 30% of all mosses recorded in this region (Fig. 2A), and for the liverworts the Lejeuneaceae with 17 species, which accounted for almost 60% of the liverworts recorded in this region (Fig. 2B). *Calymperes palisotii* Schwägr. (Calymperaceae) was found in most of the islands, followed by *Weissia breutelii* Müll.Hal. (Pottiaceae), and *Fissidens zollingeri* (Appendix 1). Only two species of hornworts were recorded in the region: *Notothylas breutelii* Gottsche (Notothyladaceae) and *Anthoceros punctatus* L. (Anthocerotaceae), both of which were located on St. Thomas, and *N. breutelii* also found in St. Croix and St. John (Appendix 1).

To test what factors might be driving the diversity of bryophytes for each island, a linear regression was done to compare the number of species collected to the island's elevation (Fig. 3A), average annual rainfall (Fig. 3B), and total island area (Fig. 3C). The linear regression test showed that elevation had the strongest relationship with the total number of species on an island, with an R^2 value of 0.739, compared to average annual rainfall and the total land area of the islands, with R^2 values of 0.167 and 0.124, respectively.

To investigate if the number of species was a good representation of the diversity of the island, the number of species and collections for each island were displayed as a histogram (Fig. 4). The number of collections is considerably higher for the USVI than for the

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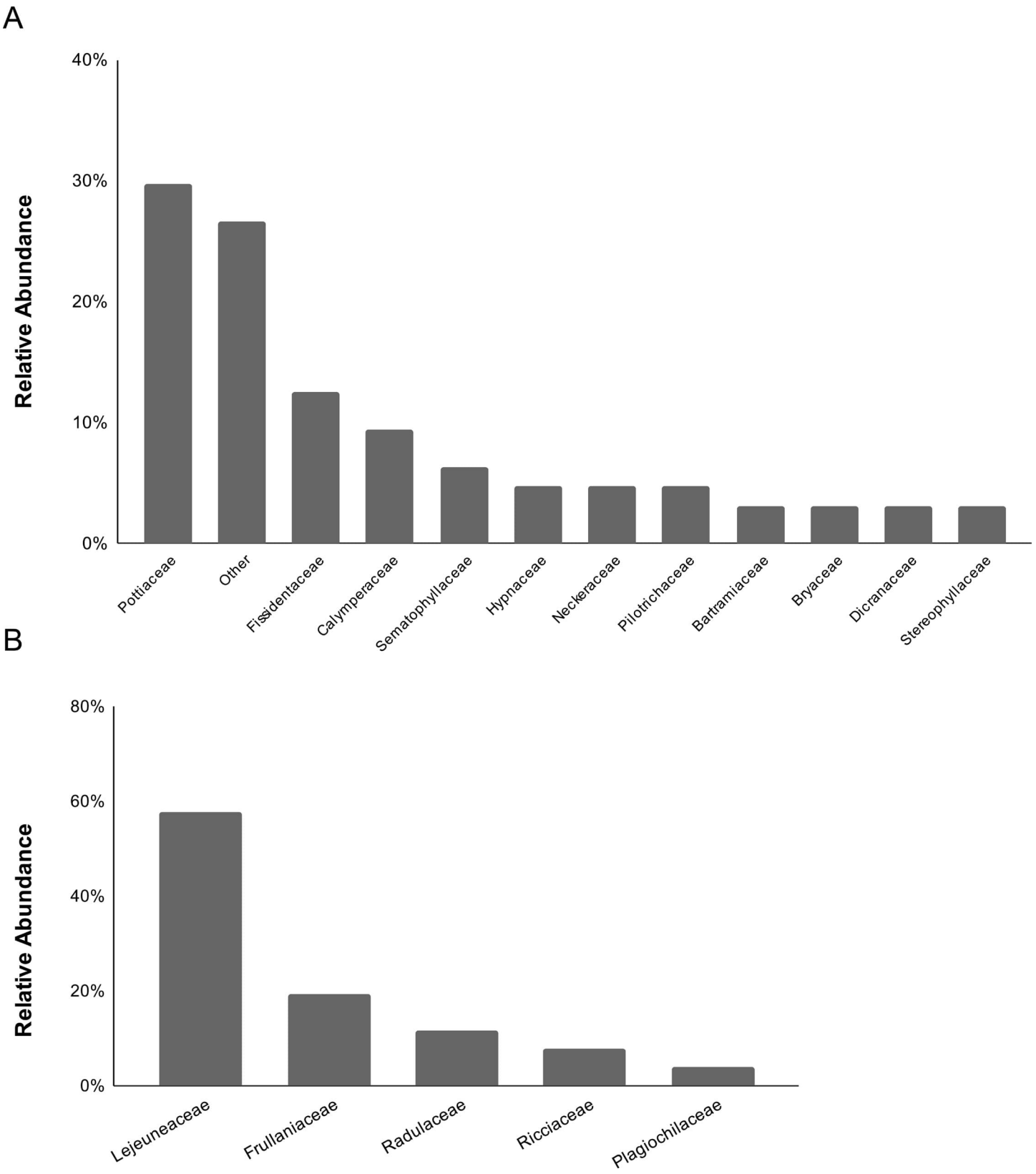

FIG. 2. Relative abundance of bryophyte families recorded throughout the Virgin Islands. A. Mosses families. "Other" represents the moss families that accounted for less than 2% of the families collected. B. Liverwort families.

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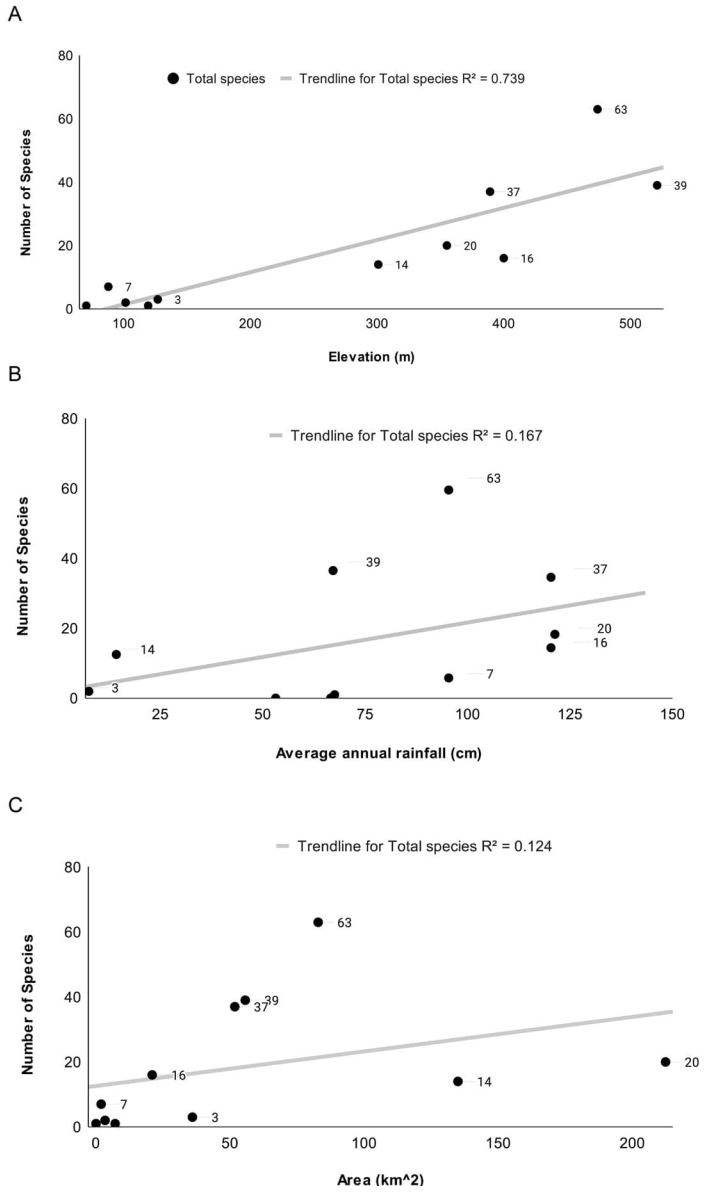

FIG. 3. Correlations between island highest elevation (m), annual rainfall (cm), and land area (km^2) and total number of bryophyte species (only mosses and liverworts). A. Correlation between island elevation (m) and number of species, R^2 value of 0.739. B. Correlation between island annual rainfall (cm) and number of species, R^2 value of 0.124. C. Correlation between island area (km^2) and number of species, R^2 value of 0.124. Number of species by island: St. Croix (n=20), St. John (n=37), St. Thomas (n=63), Tortola (n=39), Vieques (n=14), Virgin Gorda (n=16), Water Island (n=7), Anegada (n=3), Guana Island (n=2), George Dog Island (n=1), Peter Island (n=1).

BVI and Vieques (Fig. 4). For some of the islands, no records were found and could not be included in the analysis, islands with no collection records in these databases were: Culebra and Jost Van Dyke, and most of the other smaller islets in the region. The oldest bryophyte records are the collections of J. C. Breutel from 1841, and the most recent collections are three records from 2017 by B. H. Allen. Excluding those specimens, most recent collections are from the 1980s. Important collections with more than 50 records are those of E. G. and N. L. Britton (1913–1924), W. D. Reese (1981), W. R. Buck (1981), and H. A. Miller (1982–1983). In terms of taxonomic diversity, mosses had the highest number of collections recorded followed by the liverworts, and hornworts had the lowest number of collections. The number of collections for the three bryophyte groups in the VI is lower (Fig. 5A, B, C) than the number of collections of flowering plants in the Virgin Islands and eastern Puerto Rico (Fig. 5D).

DISCUSSION

The bryophyte species richness and diversity were lower for the Virgin Islands than for Puerto Rico, but still more diverse than we expected. This can be explained by the large differences in size between the studied islands and Puerto Rico; since there is a positive relationship between species richness and area, where larger islands have more species of plants including bryophytes (Patiño et al. 2014). Along with Puerto Rico's larger size, it also has more life zones than the islands in this study. There are six life zones in this region; subtropical dry, wet, rain, and moist forests, as well as subtropical lower mountain wet and rain forests, all of which can be found on Puerto Rico, but only subtropical dry and moist forests can be found in the VI and Vieques (Ewel and Whitmore 1973). The limited number of life zones on these smaller islands can account for the lower diversity of bryophyte species found, with fewer forests and habitats to occupy there would be fewer species present. Nevertheless, when compared to natural reserves in Puerto Rico with two life zones where the number of species of mosses ranges from 32–47 (Sastre-D. J. and Buck 1993), the number of mosses in VI is higher (83 total, 47 for St. Thomas). Bryophyte diversity in tropical areas depends, among other factors, on the diversity of habitats available (Frahm et al. 2003) and a higher number of bryophyte species can be found in islands with more life zones (Vitt 1991).

Among islands, the most commonly collected species of bryophytes were found on soil, rocks, or epiphytes in disturbed or secondary forests. Much of the vegetation of the Virgin Islands is secondary forests,

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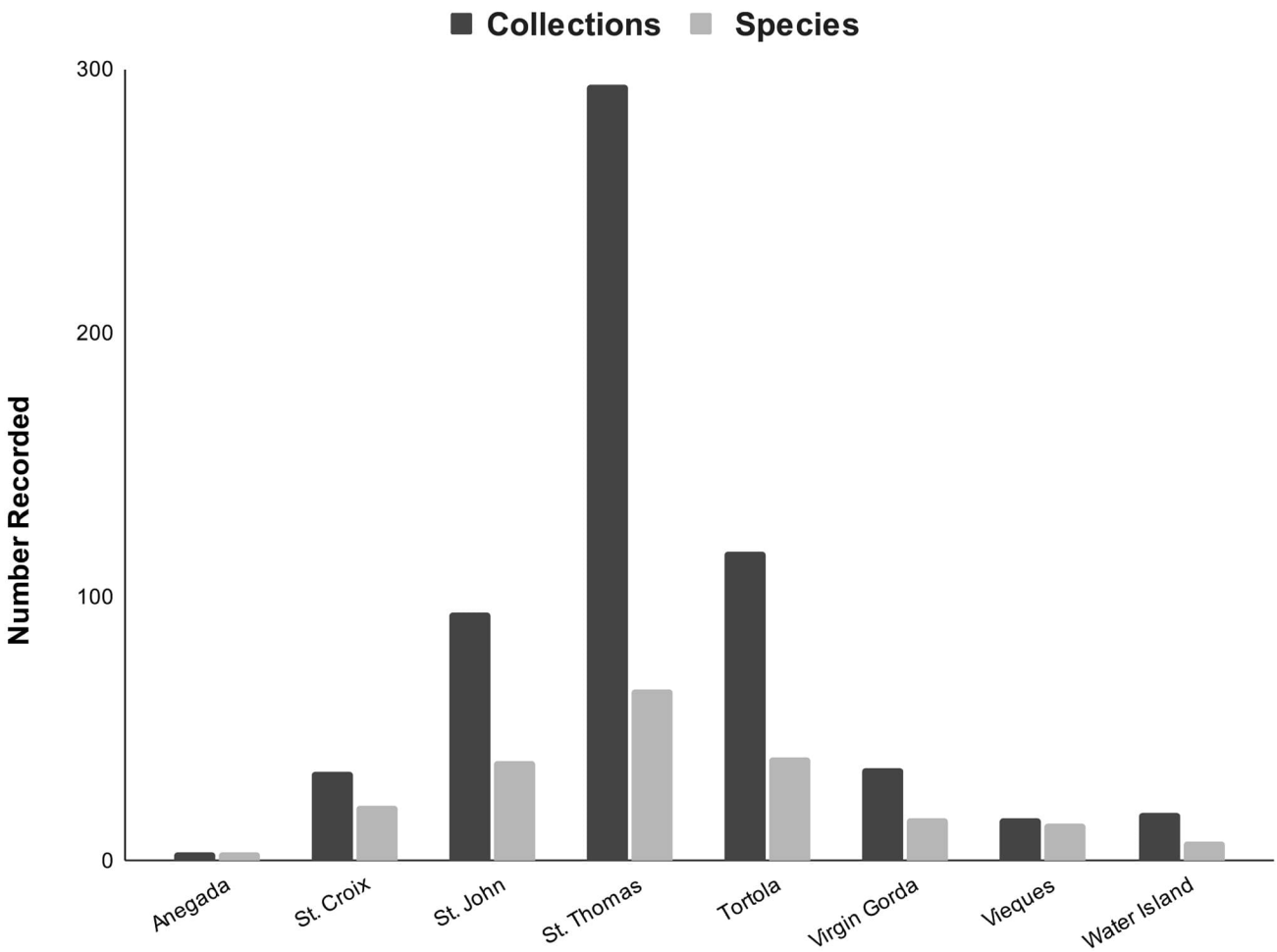

FIG. 4. Islands with more bryophyte species also had more herbaria collections records. (Collections, Species): Anegada (3, 3), St. Croix (34, 21), St. John (94, 38), St. Thomas (294, 65), Tortola (117, 39), Virgin Gorda (35, 16), Vieques (16, 14), and Water Island (18, 7).

where St. John has the greatest forest cover of the USVI (Acevedo-Rodríguez 1996; Kennaway et al. 2008), but does not have the highest number of species or collections of bryophytes. Changes in land use could be limiting the diversity of bryophytes found. Our results showed that the total number of species was positively correlated with elevation, while land area and average annual rainfall showed little to no relationship with the total number of species present. From these results, the idea that island topography may be a better indicator than the size of the island for bryophyte species richness can be supported in this region. Topography is known to have a great influence on species richness as well as the overall biodiversity of ecosystems, some studies show that in the case of bryophytes, their species richness tends to increase as the altitude increases (Vitt 1990; Bruun et al. 2006; Sastre-D. J. et al. 2010). For islands with higher elevations, there might be more diverse habitats available for bryophytes to occupy and climatic conditions favorable for the establishment of different species (Frahm et al. 2003).

Bryophytes disperse by spores and asexual propagules that can reach long distances, and it is generally accepted that the bryophyte flora of the Caribbean was influence by dispersal with vicariance playing a smaller role (Buck 1990). In this study, we showed that island area does not correlate to species richness, but elevation does. It is possible that the establishment of bryophyte is limited by habitat more than the arrival of propagules from bryophyte species in the area. A similar pattern was described for orchids of the West Indies, larger islands had more species, but elevation and diversity of habitat was a stronger predictor of orchid species richness (Ackerman et al. 2007). In smaller islands, the area was not correlated to the maximum elevation.

We found St. Thomas to be the island with most collections and species of bryophytes, which may indicate that the island may be a more suitable environment

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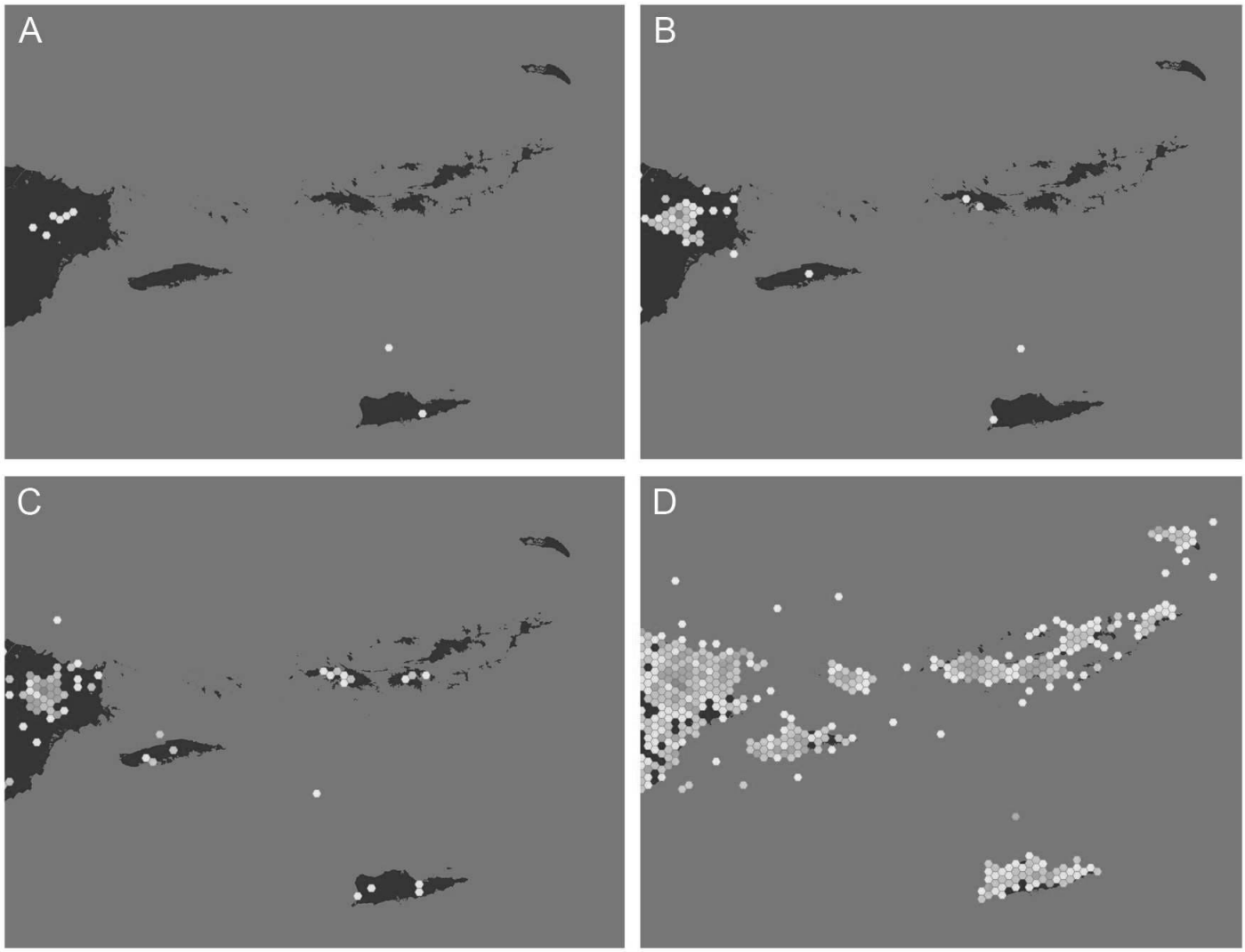

FIG. 5. Number of collections of bryophytes and flowering plants in the Virgin Islands and compared to eastern Puerto Rico. A. Hornworts; B. Liverworts; C. Mosses; D. Flowering plants.

for bryophytes in this region compared to the other sites in this study. However, the high number of collections could also indicate geographic collection bias and raises the question of whether the number of species reflects the bryophyte diversity of the island or if it means that there are more recorded species because the island had more botanical expeditions compared to the other islands. St. Thomas is home to the capital of the USVI, Charlotte Amalie, so most activities ranging from tourism to research occur there. It is also the largest island in the USVI if the combination of both the elevation and the land area are accounted for. The least number of collections was from Water Island and Virgin Gorda. Virgin Gorda and Water Island are both relatively small islands and are mostly used for tourism. Although for some islands we found none or few collections, for the rest of the islands, especially the USVI, there were many collections that indicate that the collection efforts for bryophytes in this region are not lacking. However, none of the recorded collections were made by local collectors, and our efforts to find other sources of specimens besides online herbaria were unsuccessful.

This study is the first to describe the bryophyte flora of the VI and adds to the knowledge of bryophytes in this region. In particular, the finding that bryophyte diversity is relatively high and is related to the topography of the island and how land is used demonstrates the importance of including bryophytes in management practices and conservation projects. A thorough survey of the bryophytes of the VI is necessary to assess the present status of the species. Most of the collections date to the beginning of the 20th century and the 1980s, since then, the islands have gone through many changes from anthropogenic and non-anthropogenic disturbances that might drive bryophyte species to disappear. We intend to keep adding to the data and the narrative as

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we continue to uncover more collections of bryophytes.

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APPENDIX 1. List of bryophyte species by island based on herbarium records.

Species	St. Croix	St. John	St. Thomas	Tortola	Virgin Gorda	George Dog Island	Guana Island	Peter Island	Water Island	Anegada	Vieques
Antocerotophyta											
Anthocerotaceae											
Anthoceros punctatus L.			x								
Notothyladaceae											
Notothylas breutelii Gottsche	x	x	x								
Marchantiophyta											
Frullaniaceae											
Frullania brasiliensis Raddi		x									
Frullania ericoides (Nees ex Mart.) Mont.			x								
Frullania kunzei Lehm. & Lindenb.		x									
Frullania Raddi					x						
Frullania squarrosa (Reinw., Blume & Nees) Dumort.		x	x								
Lejeuneaceae											
Archilejeunea (Spruce) Steph.					x						
Ceratolejeunea (Spruce) Schiffner				x							
Cheilolejeunea (Spruce) Schiffner				x	x						
Cheilolejeunea rigidula (Mont.) R.M. Schust.		x	x								
Cheilolejeunea trifaria (Reinw., Blume & Nees) Mizut.			x								x
Cololejeunea (Spruce) Schiffner				x	x						
Cololejeunea cardiocarpa (Mont.) Steph.			x								
Myriocoleopsis minutissima subsp. *Myriocarpa* (Nees & Mont.) R.L. Zhu, Y. Yu & Pócs	x										
Frullanoides corticalis (Lehm. & Lindenb.) van Slageren			x								
Frullanoides liebmaniana (Lindenb. & Gottsche) van Slageren											x
Lejeunea glaucescens Gottsche			x								
Lejeunea laetevirens Nees & Mont.			x								
Lejeunea minutiloba A.Evans	x		x								

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	St. Croix	St. John	St. Thomas	Tortola	Virgin Gorda	George Dog Island	Guana Island	Peter Island	Water Island	Anegada	Vieques
Thysananthus auriculatus (Wilson & Hook.) Sukkharak & Gradst.		x	x								
Lejeunea phyllobola Nees & Mont.		x	x								
Lejeunea trinitensis Lindenb.											
Lejeunea obtusangula Spruce	x	x	x								
Plagiochilaceae											
Plagiochila bunburii T.Taylor			x								
Plagiochila montagnei Nees		x	x								x
Radulaceae											
Radula Dumort.				x							
Radula amazonica Spruce			x								
Radula longifolia Steph.			x								
Radula tectiloba Steph.		x									
Ricciaceae											
Riccia breutelii Hampe ex Steph.		x									
Riccia elliottii Steph.									x		
Bryophyta											
Bartramiaceae											
Philonotis sphaericarpa (Hedw.) Brid.			x	x							
Philonotis uncinata (Schwägr.) Brid.		x	x	x							
Brachytheciaceae											
Lepyrodontopsis trichophylla (Sw. ex Hedw.) Broth.				x							
Bryaceae											
Bryum apiculatum Schwägr.			x		x						x
Bryum coronatum Schwägr.			x								
Bryum microdecurrens E.Britton										x	
Calymperaceae											
Calymperes afzelii Sw.		x	x	x	x						
Calymperes breutelii Besch.			x								
Calymperes erosum Müll.Hal.			x								
Calymperes lonchophyllum Schwägr.		x		x							
Calymperes palisotii Schwägr.		x	x	x	x	x	x		x		x
Calymperes richardii Müll.Hal.			x								
Syrrhopodon incompletus Schwägr.		x		x	x						
Syrrhopodon prolifer Schwägr.				x							
Syrrhopodon prolifer var. *papillosus* (Müll.Hal.) W.D.Reese		x		x							

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	St. Croix	St. John	St. Thomas	Tortola	Virgin Gorda	George Dog Island	Guana Island	Peter Island	Water Island	Anegada	Vieques
Dicranaceae											
Dicranella hilariana (Mont.) Mitt.			x								
Dicranella longirostris (Schwägr.) Mitt.		x									
Leucoloma cruegerianum (Müll.Hal.) A.Jaeger				x							
Leucoloma schwaneckeanum (Hampe) Broth.				x							
Erpodiaceae											
Erpodium domingense (Spreng.) Brid.			x								
Fissidentaceae											
Fissidens Hedw.			x								
Fissidens dissitifolius Sull.	x										
Fissidens elegans Brid.				x							x
Fissidens guianensis Mont.			x								
Fissidens hornschuchii Mont.		x	x		x				x		
Fissidens neglectus H.A. Crum				x							
Fissidens pallidinervis Mitt.	x	x	x								x
Fissidens perfalcatus Broth.			x								
Fissidens radicans Mont.					x						
Fissidens zollingeri Mont.	x	x	x	x	x						x
Fontinalaceae											
Dichelyma capillaceum (With.) Myrin			x								
Fontinalis antipyretica var. *gigantea* (Sull.) Sull.			x								
Funariaceae											
Funaria calvescens Schwägr.										x	
Hypnaceae											
Chryso-hypnum diminutivum (Hampe) W.R.Buck		x	x								
Isopterygium subbrevisetum (Hampe) Broth.				x							
Isopterygium tenerum (Sw.) Mitt.		x	x								
Vesicularia vesicularis (Schwägr.) Broth.	x										
Leskeaceae											
Haplocladium microphyllum (Hedw.) Broth.			x								

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	St. Croix	St. John	St. Thomas	Tortola	Virgin Gorda	George Dog Island	Guana Island	Peter Island	Water Island	Anegada	Vieques
Leucobryaceae											
Leucobryum polakowskyi (Müll.Hal. ex Besch.) Cardot				x							
Meteoriaceae											
Lepyrodontopsis trichophylla (Sw. ex Hedw.) Broth.				x							
Meteorium deppei (Hornsch. ex Müll. Hal.) Mitt.	x										
Neckeraceae											
Neckeropsis disticha (Hedw.) Kindb.			x	x							x
Neckeropsis undulata (Hedw.) Reichardt		x	x	x							x
Porothamnium ramosissimum(Hampe) M. Fleisch.	x										
Octoblepharaceae											
Octoblepharum albidum Hedw.	x		x	x	x						
Pilotrichaceae											
Callicostella belangeriana (Besch.) A.Jaeger			x	x							
Callicostella depressa (Hedw.) A. Jaeger			x								
Callicostella pallida (Hornsch.) Ångstr.		x		x							
Pottiaceae											
Barbula arcuata Griff.			x								
Barbula indica (Hook.) Spreng.		x									
Barbula domestica Brid.		x									
Chenia leptophylla (Müll.Hal.) R.H.Zander			x								
Hymenostomum breutelii (Müll.Hal.) Kindb.				x							
Hymenostomum micaceum (Schltdl.) Hampe	x										
Hyophila involuta (Hook.) A.Jaeger	x	x	x	x							
Hyophiladelphus agrarius (Hedw.) R.H.Zander	x	x	x				x		x		
Plaubelia sprengelii (Schwägr.) R.H.Zander	x		x								
Splachnobryum obtusum (Brid.) Müll.Hal.			x								
Trichostomum brachydontium Bruch	x	x	x		x				x		
Trichostomum brittonianum R.H.Zander		x									
Trichostomum involutum Sull.	x			x							
Trichostomum perviride Broth.			x								

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