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Habitat preferences and distribution of some common bryophytes in a tropical forest at the Luquillo Experimental Forest, Puerto Rico

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Abstract. A fundamental question in bryology is to identify what environmental factors influence bryophyte distribution in an ecosystem and how they respond to disturbances. We investigated the distribution of the moss *Thuidium urceolatum* and species of the liverwort *Plagiochila*, representing distinct life-forms (wefts and fans), in the Luquillo Forest Dynamic Plot, where the environment and disturbance history is well described. We hypothesized that if the presence of *T. urcealutum* and *Plagiochila* spp. are affected by habitat (riparian *versus* upland) and past land use, then there will be differences in the number and size of bryophyte patches within these areas. Using a combination of plot-level and floristic habitat sampling methods, we recorded the size and number of patches of these bryophytes in four mesohabitats, riparian and upland forest in areas of high and low past land use history. We measured canopy openness for each patch, documented the substrate it was growing on and associated vegetation. The number of patches and mean patch size was not significantly different between sites, except in upland forest with high past agricultural land use, that had fewer and smaller patches of *T. urceolatum*. The effects of habitat and past land used were not clear for *Plagiochila* spp. However, the lasting effects of past land use, after more than 80 years of conversion to protected forest, still influence the presence and size of *T. urceolatum* in upland forest but not in riparian zones. Riparian zones might serve as corridors for expansion of the species. Canopy openness preference was different among mesohabitats and species, the presence of *T. urceolatum* and *Plagiochila* spp. could reflect changes in canopy cover associated to recent hurricanes. Other environmental aspects likely influence the presence of these bryophytes, as rocks were the most common substrate and other mosses were the most frequent plants associated with the bryophyte patches. We propose that the observed presence and size of these bryophytes may be responding to the effects of past land use and habitat, combined with recent hurricane events, and are part of changes in plant community composition that can be used to track succession in the forest.

Keywords. Caribbean, disturbance, ecology, hurricane, past land use, *Plagiochila*, *Thuidium*.

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The Luquillo Experimental Forest (hereafter referred to as LEF) is a tropical forest with the highest bryophyte diversity among all the forests in Puerto Rico (Sastre-D. J. & Buck 1993) and a long history of research studies that have contributed valuable information on many aspects of tropical forest ecology, plant community composition and physiology (Brokaw et al. 2012; Hogan et al. 2016; Lodge et al. 2008; Lugo 2013; Zimmerman et al. 2021). An important conclusion from these studies is the understanding that tropical forests in the Caribbean are shaped by disturbances like hurricanes, droughts, and land use changes that occur along environmental gradients. In areas where streams are present, environmental gradients are found in the transitional zone between the aquatic and terrestrial systems, also known as riparian zones. These riparian zones may sustain high

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species diversity and serve as refugia during land use change (Heartsill-Scalley et al. 2009; Heartsill-Scalley & Crowl 2021).

A few studies in the LEF have investigated the diversity of bryophytes or their role in the ecology and nutrient cycles of the forest (Bryant et al. 1973; Frangi & Lugo 1992; Fulford et al. 1971; Sastre-De Jesús 1992). However, less is known about the ecological factors that influence the presence and distribution of bryophytes or the effects of disturbances in their population dynamic and demography (Mercado-Díaz & Merced 2020). Studies of other organisms in the LEF have found that past agricultural land use has a strong influence in species composition (Bachelot et al. 2016; Bergman et al. 2006; Heartsill-Scalley & Crowl 2021; Hogan et al. 2017; Thompson et al. 2002; Zimmerman et al. 2021). However, similar studies have never been done for any bryophyte species or functional group. The moss *Thuidium urceolatum* and several species of the liverwort *Plagiochila* are common in mesic to montane moist forests of Puerto Rico, are abundant in the LEF and constitute two distinct life-forms, thus representing an appropriate model to study habitat distribution and preferences of bryophytes in the context of environmental gradients and disturbances.

Bryophytes grow and experience the environment as colonies and rarely as individuals (Bates 1998). Under this framework, we used the patch as the unit of study, with one species of *Thuidium* representing a distinct life-form than the assemblage of species of *Plagiochila*. *Thuidium urceolatum* is a pleurocarpous moss that grows forming loose mats (wefts) and is frequently found over rocks, soil, decomposing logs, and other substrates on the forest floor as well as trunks of alive and dead trees (Buck 1998; Gradstein et al. 2001). About 30 species of the liverwort *Plagiochila* are reported for the LEF (CBH Portal 2023); of those, 19 species are recognized by Gradstein (1989). Although the genus is easy to recognize, delimitation of species of *Plagiochila* is challenging using morphology (Heinrichs et al. 2005; Renner et al. 2017). *Plagiochila* spp. can be found on tree bark, decomposed wood, moist rocks, or soil (Gradstein et al. 2001; Gradstein 2016). Most species in the genus *Plagiochila* grow as fans where individual stems, usually unbranched or with few branches, stand perpendicular to the substrate; therefore, the colonies formed by different species can be considered as similar life-form units in the landscape.

In this study, we investigated habitat preferences of these common bryophytes to understand their distribution in an area of the LEF and how environmental factors such as proximity to a stream, past land use, and microhabitat diversity, provide the conditions to support them. First, we surveyed the presence, abundance, and size of patches of *Thuidium urceolatum* and *Plagiochila* spp. in the forest. Since the species of *Plagiochila* present in this site have similar life-forms, they were grouped together for the analysis. Then we asked if there were differences in the number and size of patches of *T. urceolatum* and *Plagiochila* spp. throughout the forest landscape. Since bryophyte occurrence is influenced by the presence of microhabitats, we focused on the sets of microhabitats arranged in discrete mesohabitats delimited by the physical features of the landscape (Vitt & Belland 1997). We defined four mesohabitats: riparian and upland areas with high or low past land use. We hypothesize that if the distribution of *T. urceolatum* and *Plagiochila* spp. is affected by past land use (high or low) and habitat (riparian or upland) then we expect to find differences in the number and size of patches within our tropical forest study area. Our second hypothesis is that there will be differences in microhabitat preferences between *T. urceolatum* and species of *Plagiochila*. Wefts (such as *T. urceolatum*) are presumed to grow in intermediate sunlight and humidity, while fans (such as *Plagiochila* spp.) will grow in shaded places with high humidity because of the trade-offs between capturing sunlight and avoiding dehydration of these two distinct life-forms (Bates 1998). This study will help us understand how some bryophytes are distributed in a heterogeneous tropical forest landscape.

Methods

Study site. Data were collected in the Luquillo Forest Dynamic Plot (LFDP) (18°20′N, 65°49′W, elev. 333–428 m above sea level) located in the El Verde Research Area of the LEF in northeast Puerto Rico (**Fig. 1**). Annual mean precipitation in this forest is 3,500 mm and generally it is evenly distributed throughout the year (McDowell et al. 2021). The LFDP was established to better understand forest dynamics and environmental factors, particularly with

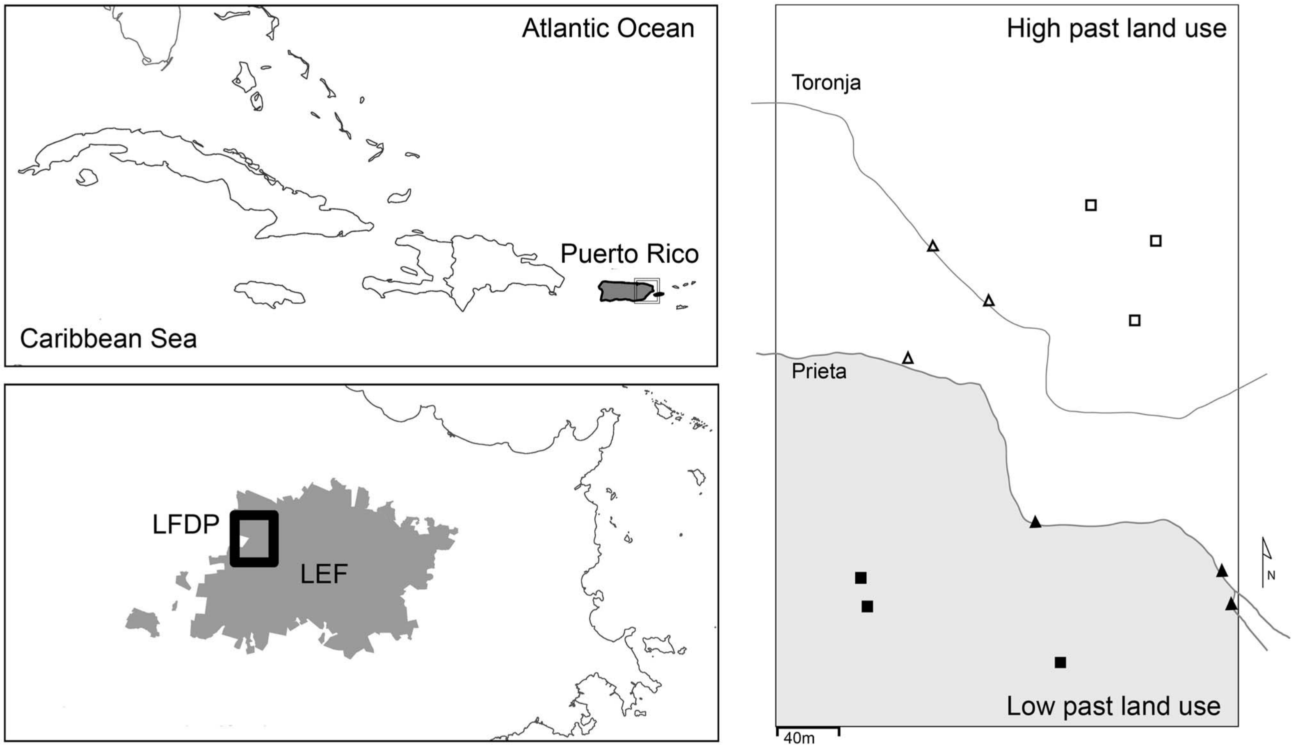

Figure 1. Puerto Rico is easternmost in relation to the Greater Antilles. The Luquillo Experimental Forest (LEF) in the East region of Puerto Rico, with the Luquillo Forest Dynamic Plot (LFDP). The LFDP is a 16 hectares experimental plot that is 480 m North/South and 320 m East/West. Map of 5 × 5 m subplots in the LFDP, squares: upland forest, triangles: riparian zone; white: high past land use intensity (< 80% canopy cover in 1936), gray: low past land use intensity (> 80% canopy cover in 1936).

regards to disturbance recovery from hurricanes and past land use (Thompson et al. 2002; Zimmerman et al. 1994). The LFDP is a 16-hectare forest plot divided into four hundred 20 × 20 m quadrats, each with sixteen 5 × 5 m subquadrats, which we refer to as subplots in the sampling design of this study.

The forest type in the LFDP is known as Tabonuco forest which refers to the dominant tree, *Dacryodes excelsa* in the *Dacryodes-Sloanea* plant association that is present in various Caribbean islands (Beard 1949). There are two perennial streams or quebradas (**Fig. 1**) within the LFDP: Prieta to the south and Toronja to the north, both flowing from east to west (Heartsill-Scalley et al. 2009). The northern two-thirds of LFDP, delimited by Quebrada Prieta, were used for subsistence agriculture and logging until 1934; these areas had 0–80% canopy cover in 1936 according to Thompson et al. 2002 (**Fig. 1**). The remaining third of the area, south of Quebrada Prieta, had 80–100% canopy cover in 1936, did not experience subsistence farming, and encountered little disturbance from selective logging (Thompson et al. 2002). Therefore, for this study we divided the LFDP into four mesohabitats based on the documented history of past land use intensity (high or low) and the habitat (riparian or upland). The four mesohabitats are: high past land use upland, high past land use riparian, low past land use riparian and low past land use upland (**Table 1**, **Fig. 1**).

Species. The bryophytes selected for this study are widespread in tropical forests, common throughout Puerto Rico, and relatively easy to find and identify to the genus level in the field (Gradstein 1989; Gradstein et al. 2001; Sastre-D. J. & Buck 1993). *Thuidium* (Thuidiaceae) is a pleurocarpous moss that forms loose mats or wefts, plants are green to yellowish-green with creeping or arched stems that are double or triple-pinnate. One species, *T. urceolatum* is common in Puerto Rico and can be distinguished from other species and from *Pelekium* by the larger size and papillose leaves only in the back side (Buck 1998). *Plagiochila* (Plagiochilaceae) is a genus of leafy liverwort growing as individual plants, as fans or forming turfs, plants are green to brown with succubous decurrent leaves and lacking underleaves

Table 1. Description of sites sampled for bryophyte patches in the Luquillo Forest Dynamics Plot, Puerto Rico. **High** past land use refers to < 80% canopy cover in 1936, **Low** past land use refers to >80% canopy cover in 1936, **Upland** sites are distances of ≥25 meters from wet stream channel, **Riparian** sites < 25 m away from wet stream channel. Patches observed by mesohabitat (**T** is *Thuidium urceolatum*, **P** is *Plagiochila* spp.).

Past land use	Habitat	Mesohabitat	Subplots	Area m^2	Elevation m asl	Patches observed
High	Upland	High upland	3	75	351.0 ± 7.3	11 (T:4, P:7)
High	Riparian	High riparian	3	75	373.6 ± 6.1	28 (T:20, P:8)
Low	Upland	Low upland	3	75	369.8 ± 32.4	37 (T:20, P:17)
Low	Riparian	Low riparian	3	75	400.0 ± 25.3	25 (T:25, P:0)
		Total	12	300	376.3 ± 27.9	101 (T:70, P:31)

(Gradstein 2016). There are about 23 species of *Plagiochila* in Puerto Rico, seven species are present in upland forest south of the LFDP (González-Hernández & Merced, unpublished), and the genus can be recognized by the erect stems with distichous ovate-square leaves with teeth on the margins (Gradstein 1989). Data collection for species of *Plagiochila* was done at the genus level by grouping all the species present in the sample areas and, as noted previously, named as *Plagiochila* spp. Voucher specimens were collected to verify identification at the genus level and deposited at the Herbarium of the University of Puerto Rico Río Piedras Campus (UPRRP).

Data collection. To document the presence and abundance of *Thuidium urceolatum* and species of *Plagiochila* we used a combination of plot sampling and floristic habitat sampling methods (Heinlen & Vitt 2003; Newmaster et al. 2005). Data were collected during the summer and fall of 2019. First, before collecting data, we systematically surveyed the LFDP to identify microhabitats where these bryophytes occurred. Then, three 20 × 20-m quadrats were selected in each of the four mesohabitats (i.e., riparian and upland forest in areas of high and low past land use history), for a total of 12 quadrats that contained those microhabitats (i.e., partial shade, no slopes, and substrates like palms, tree trunks and rocks) in the LFDP (**Table 1**). Riparian zones were defined as those occurring within <25 m of the wet stream channel, uplands were at distances of >25 m from wet stream channel, and past land use is delimited by Quebrada Prieta following Heartsill-Scalley & Crowl (2021) (**Fig. 1**). For each quadrat, a 5 × 5 m subplot was selected that included the variety of microhabitats surveyed in the LFDP.

Each 5 × 5 m subplot was surveyed for 5 min by two persons, to determine the number of patches of *Thuidium urceolatum* and *Plagiochila* spp. present. We considered patches to be distinct from one another if they were separated by 0.5 m unless they were in different substrates. Patches were defined as groups of more than 3 individuals growing together. Measurements of the size of the patch included patch length, plant height (measured as maximum patch height) and patch density. We also collected data about the substrate the bryophytes were growing, associated flora (mosses, liverworts, vines, ferns, seedlings, lichens), canopy openness and GPS coordinates, all of which were recorded for each patch using Survey 123 for ArcGIS (Version 3.13.251, 2021). Canopy openness was measured with a spherical convex densiometer (Model A, Forestry Suppliers) placed over each bryophyte patch, counting the number of empty squares, and calculated to percent canopy openness. Patch density was categorized as very sparse, sparse, medium, and dense; this refers to the relative number of branches or individuals growing together in close proximity forming the patch. Patch length was measured in the longest axis of the patch and plant height was the tallest or thickest area of the patch.

Data analysis. All mean values are presented with associated standard error (mean ± SE). Upon testing for parametric assumptions of normality and equal variance, we conducted either an ANOVA (F statistic) or a Kruskal-Wallis (H statistic) to examine if the four mesohabitats had an effect on the distribution of the number and size (length and height) of patches of *Thuidium urceolatum* and *Plagiochila* spp. combined and separately. To discern any significant differences found among the four mesohabitats we performed *post hoc* Pairwise Multiple Comparison Procedures; Tukey Test (q statistic) for parametric and a Dunn's Method (Q statistic) for non-parametric tests. Because two years before our data collection,

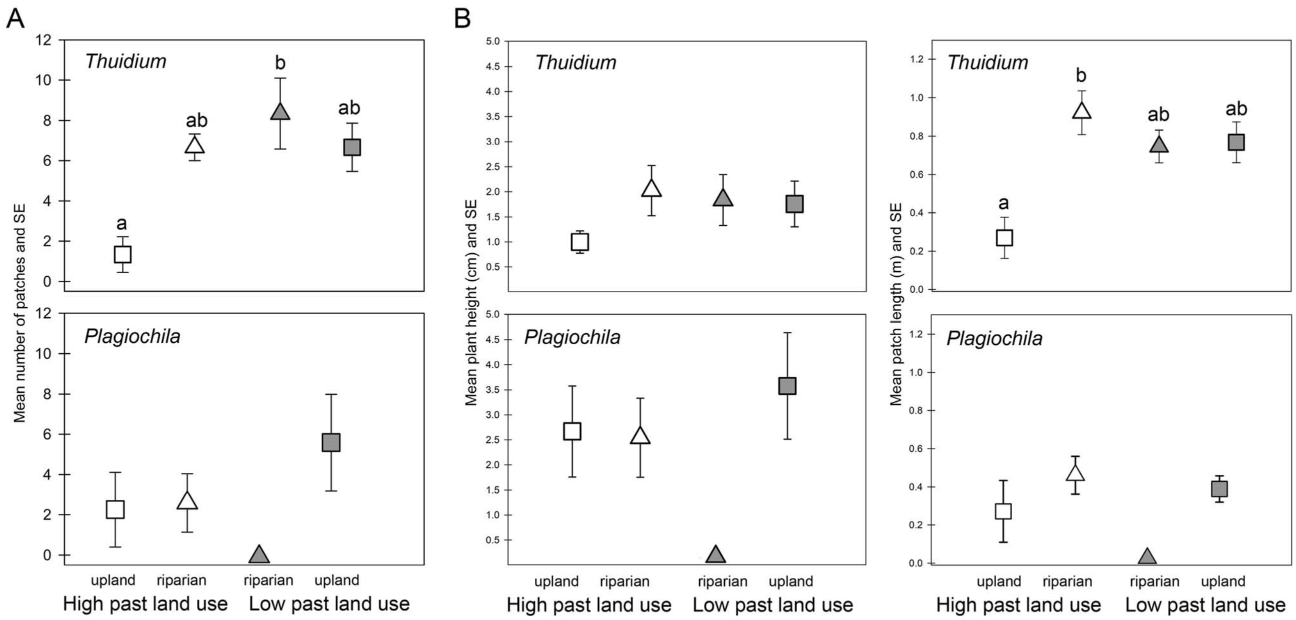

Figure 2. A. Mean number of patches and standard error (SE) by habitat (upland: squares, riparian: triangles) and past land use (high: open symbols, low: closed symbols with gray color), for *Thuidium urceolatum* and *Plagiochila* spp. **B.** Mean plant height (cm) and patch length (m) with standard error (SE) for *T. urceolatum* and *Plagiochila* spp. patches. Different letters as labels indicate statistically significant difference ($p < 0.05$) in *post hoc* test.

Hurricane María landed in Puerto Rico (September 2017) and removed most of the canopy cover in the forest, we investigated if canopy openness between the areas where the bryophytes were present was different. Mean percent of canopy openness was calculated for patches of *T. urceolatum* or *Plagiochila* spp. in each of the four mesohabitats and analyzed with F and H statistics. Pearson correlations were performed to see if canopy openness had an influence on patch length and bryophyte size. Statistics were conducted using RStudio version 1.4.1106 (RStudio Team 2020) and SigmaPlot (Systat Software version 14.0.3.192).

Results

Distribution and size of patches of Thuidium urceolatum and Plagiochila spp. in the LFDP. From the 12 subplots surveyed we found and collected data for 101 patches (**Table 1**), and all the subplots had one or both species. In total, we measured 70 patches of *Thuidium urceolatum* and 31 patches of mixed species of *Plagiochila*. No significant differences were found in the total number of patches between habitat (riparian/upland), past land use (low/high) or the interaction of these factors ($F_{1,8} = 0.14$, $p = 0.72$; $F_{1,8} = 2.88$, $P = 0.13$; $F_{1,8} = 4.57$, $p = 0.07$). Therefore, we proceeded to analyze patch data by mesohabitat. There was no significant difference in mean number of patches between mesohabitats when *T. urceolatum* and *Plagiochila* spp. were combined ($F_{3,8} = 2.5$, $p = 0.13$), but when analyzed separately, there was a significant difference in the quantity of *T. urceolatum* patches ($F_{3,8} = 6.43$, $p = 0.016$). The quantity of *T. urceolatum* patches was significantly different between high past land use upland and low past land use riparian forest (Tukey $q = 5.824$, $p = 0.014$). Overall, fewer patches were observed in upland forest with high past land use, compared to those observed in low past land use riparian forest. There was no statistically significant difference between all other mesohabitat comparisons. No significant difference in mean number of patches of *Plagiochila* spp. ($F_{3,8} = 1.91$, $p = 0.207$) were found among the four mesohabitats. Although no *Plagiochila* spp. patches were observed in the low past land use riparian sites, there was high variation in the total number of patches in the low past land use upland sites (**Fig. 2A**).

Bryophyte patch size was measured as length of the patch, plant height, and density of patches. *Thuidium urceolatum* mean patch length was 0.73 m (± 0.44) and mean plant height was 1.03 cm (± 0.46). *Plagiochila* spp. mean patch length was 0.38 m (± 0.31) and mean plant height of 1.84 cm (± 1.11). Analyses of species and mesohabitats found significant differences in patch length among the four mesohabitats ($H_3 =$

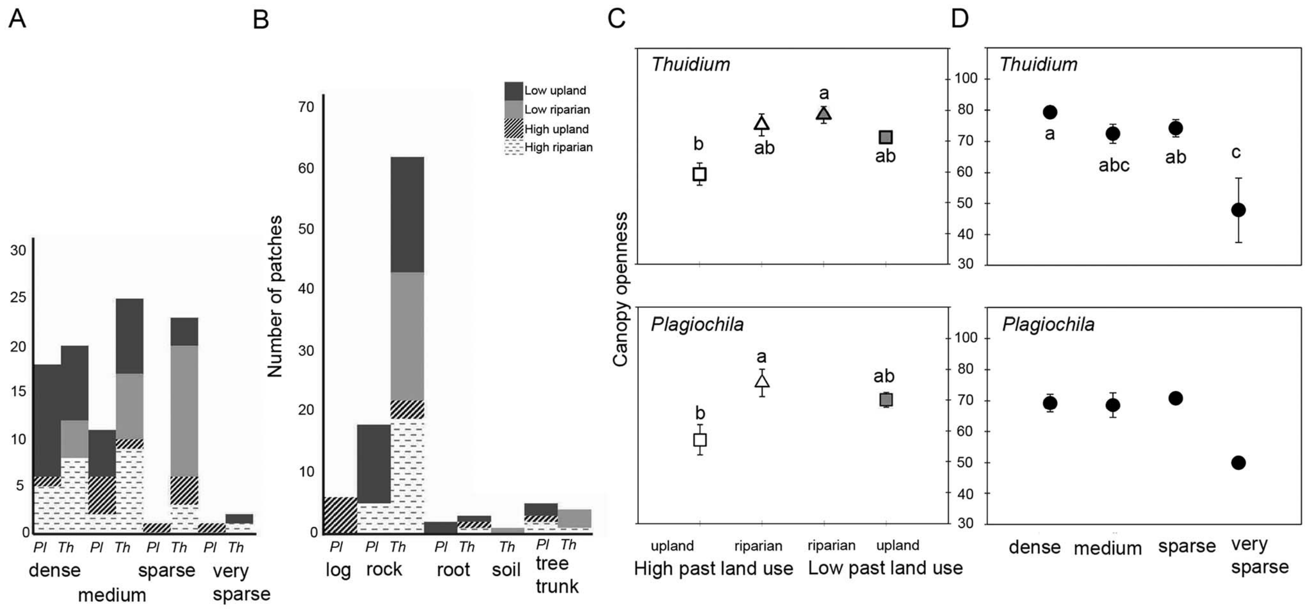

Figure 3. A. Number of patches in each density category by habitat/land use for *Plagiochila* spp. (Pl) and *Thuidium urceolatum* (Th). **B.** Substrate where bryophytes were growing by habitat/land use. **C.** Canopy openness (%) where bryophyte patches grew across land use (high: open symbols, low: closed symbols with gray color) and habitat (upland: squares, riparian: triangles). **D.** Canopy openness (%) and density of patches by species. Different letters as labels indicate statistically significant difference ($p < 0.05$) in *post hoc* test.

16.53, $p \leq 0.001$), but no differences in plant height ($H_3 = 3.66$, $p = 0.30$). Mean patch length of *T. urceolatum* was different among mesohabitats ($H_3 = 8.49$, $p \leq 0.037$). There was a significant difference between high upland (0.27 ± 0.09 m) and high riparian (0.86 ± 0.10 m) mean patch length of *T. urceolatum* ($Q = 2.906$, $p = 0.022$). The mean *T. urceolatum* patch length was shorter in high past land use upland than in high past land use riparian mesohabitat (**Fig. 2B**). For patches of *Plagiochila* spp. no differences in mean patch length ($H_2 = 4.63$, $p = 0.09$) or mean plant height ($F_{2,28} = 0.68$, $p = 0.52$) were found.

The general architecture and life-form of these bryophytes are different; *Thuidium urceolatum* grows as larger patches that are short, while species of *Plagiochila* grow as smaller patches that are taller. Most *T. urceolatum* patches were dense to sparse, and *Plagiochila* spp. patches were dense to medium, with denser patches of *Plagiochila* spp. more frequent in upland areas, and denser patches of *T. urceolatum* frequent in all areas except in upland locations with high past land use (**Fig. 3A**).

Microhabitat preferences: substrate, associated vegetation, and canopy openness. *Thuidium urceolatum* and *Plagiochila* spp. were found growing on diverse substrates such as rocks, roots, fallen branches/decaying wood (classified as log/humus), soil, the trunk of palms and trees. Rock was the most common substrate for these bryophyte species (**Fig. 3B**), followed by roots and tree trunks for *T. urceolatum*. *Plagiochila* spp. grew often on tree trunks, on logs only in upland forest with high past land use, and on roots only in upland forest with low past land use (**Fig. 3B**). Other mosses, liverworts, lichens, ferns, vines, and seedlings were observed to be growing next to the bryophyte patches on the same substrates. In 85% of the patches, other mosses were growing near *T. urceolatum* and *Plagiochila* spp., while 28% had other liverworts and 21% ferns. Lichens were only observed in 17% of patches, 15% of patches had vines, and only 11% of patches were observed to have seedlings.

We found significant differences in canopy openness among the four mesohabitats ($H_3 = 18.99$, $p < 0.001$). Canopy openness was significantly different above patches of *Thuidium urceolatum* ($H_3 = 9.47$, $p = 0.024$) and *Plagiochila* spp. ($F_{2,28} = 5.32$, $p = 0.011$) (**Fig. 3C**). For *Thuidium urceolatum* patches, there was a significant difference between canopy openness in low riparian ($77.0\% \pm 2.2$) and high upland ($59.3\% \pm 3.5$) ($Q = 2.66$, $p = 0.047$). For patches of *Plagiochila* spp., mean percent canopy openness in high past land use riparian zones (75.1% ± 4.5) was greater than in high past land use upland (57.1% ± 5.0) (q = 4.42, p = 0.011). Canopy openness was also different above patches of *Plagiochila* spp. in low past land use upland (70.1% ± 2.4) and high past land use upland forest (57.1% ± 5.0; q = 3.69, p = 0.04).

Although canopy openness was similar for the various densities of patches of *Plagiochila* spp. (F = 2.21, p = 0.15), there were differences for *Thuidium urceolatum* (F = 3.88, p = 0.01, **Fig. 3D**). Canopy openness above *T. urceolatum* patches was greater for dense (79.36% ± 2.0) versus very sparse (47.9% ± 10.4) patches (q = 4.59, p = 0.01), and for sparse (74.3% ± 2.8) patches than very sparse (47.9% ± 10.4) patches (q = 3.871, p = 0.04). Canopy openness had no significant effect on patch length (F = 1.21, p = 0.27) or height (F = 2.88, p = 0.09) of the bryophytes; and there was no correlation between patch length (r = 0.11, p = 0.27) or plant height and canopy openness (r = –0.17, p = 0.09).

Discussion

Bryophytes generally occupy habitats characterized by low concentration of nutrients, frequent high humidity, enough sunlight, and limited competition with vascular plants (Glime 2017). In this tropical forest, we predicted that the distribution and habitat preference of *Thuidium urceolatum* and *Plagiochila* spp. would be affected by the combination of habitat (riparian or upland) and past land use (high or low) defined as mesohabitat, and observed as differences in bryophyte patch quantity, size, and density. Additionally, we predicted that microhabitat factors like canopy cover and substrate will influence the presence of these bryophytes. We found that habitat and past land use affected the number and size of patches of *T. urceolatum*, but there were no significant differences for *Plagiochila* spp. This could be the result of grouping several species together or because the sampling method failed to document enough patches. The number of patches of *Plagiochila* were fewer (31) than those of *T. urceolatum* (70). Adding more sites could provide more information about the preferences of the various species of *Plagiochila*, and combined with an identification survey, determine if some species are substrate specific and/or prefer a particular habitat.

We found fewer and smaller patches of *Thuidium urceolatum* in upland areas with high past land use, which is associated to the lingering effects of documented past land use. The areas of high past land use were subjected to logging and subsistence agriculture over 80 years ago, and that has resulted in differences in species composition, structure and reproductive success that lasts to this day (Bachelot et al. 2016; Bergman et al. 2006; Heartsill-Scalley & Crowl 2021; Hogan et al. 2017; McAuliffe et al. 2019; Presley & Willig 2023; Zimmerman et al. 2021). Land use change in tropical forests affects the diversity of bryophytes, driven by factors such as canopy cover, microclimate, and substrate characteristics (Gradstein & Sporn 2010). The secondary vegetation in the upland areas with high past land use, characterized by many small trees, shrubs, and grasses (Heartsill Scalley & Crowl 2021; Hogan et al. 2016), could interfere with the establishment of bryophytes. Nevertheless, rock was the most common substrate occupied by *T. urceolatum* in all mesohabitats, and by *Plagiochila* spp. in riparian zones and upland forest with low past land use. Differences among mesohabitat could reflect the absence or scarcity of substrates available for colonization (Heinlen & Vitt 2003). For example, *Plagiochila* spp. were found on logs (including fallen branches or decay wood) only in upland forest with high past land use, but species of *Plagiochila* are not typical of log communities in the LEF (Sastre-De Jesús 1992). Since we did not measure the percentage of substrates available and occupied, it is relevant to bear in mind that our findings can be biased by the fact that substrates like logs might be absent in some mesohabitats. It would be interesting to study how occupation of different substrates may change over time along with successional processes in each mesohabitat.

Previous studies have found that species composition was different in riparian and uplands areas and in areas with contrasting past land use. The riparian areas in LFDP have higher species diversity of vascular plants than upland areas, and there is also higher density of vines and ferns which could be associated to high humidity and light in riparian areas (Heartsill-Scalley & Crowl 2021). In low past land use riparian zones, more and larger patches of *Thuidium urceolatum* were found, although *Plagiochila* spp. were absent. Riparian zones in areas with high past land use had patches of *T. urceolatum* and *Plagiochila* spp., suggesting that these areas are more accessible to recolonization or provide the necessary elements for the bryophyte to establish and grow (Dynesius et al. 2009). Differences in the width of the stream channels, humidity and temperature, or other aspects of the stream to riparian environment need to be studied to identify which factors contribute to the presence of bryophyte patches at those sites.

We observed differences in canopy openness with bryophytes in riparian zones having potentially more access to sunlight than the other areas of the forest we sampled. This supports our hypothesis that there would be a difference in canopy openness between mesohabitats occupied by *Thuidium urceolatum* and *Plagiochila* spp. In addition, *Plagiochila* spp. were found in more shaded areas compared to *T. urceolatum*. Higher growth rates have been found in *Thuidium* when under full and intermediate sun compared to when they were in total shade (Benavides-Duque 2007). In upland areas with high past land use, *T. urceolatum* and *Plagiochila* spp. were growing under more shade conditions. This finding could be a strategy for colonizing this type of mesohabitat. Measurements of canopy openness may reflect differences of the microhabitats where *T. urceolatum* and *Plagiochila* spp. were present. Changes in canopy openness are expected to continue as time increases since the passing of Hurricane Irma and María in 2017, which had the initial and immediate effect of completely eliminating canopy cover throughout LFDP (Leitold et al. 2022). *Plagiochila* spp. were often found growing on the Sierra Palm *Prestoea acuminata* var. *montana*, a palm species with high abundance, high recruitment, and low mortality after hurricanes (Zhang et al. 2022). At the time of our field work (2019), only two years had passed since the hurricanes, and we expect that the relationship between canopy openness and presence of bryophytes could become more pronounced with greater successional development.

Differences in habitat preferences between these bryophytes can also be explained by their growth form and the life-form of the patch. *Thuidium urceolatum* is a pleurocarp that forms wefts with continuous growth that can form large mats. In contrast, species of *Plagiochila* grow as individual stems, usually near each other and forming fans. The life-forms of these bryophytes allow them to avoid dehydration and capture water vapor while maximizing photosynthesis (Bates 1988) and might represent different strategies to occupy similar habitats. *Thuidium urceolatum* usually grows short and in larger patches compared to *Plagiochila* spp. that had taller plants growing within smaller patches. The most frequent plants associated with patches of *T. urceolatum* and *Plagiochila* spp. where other mosses, liverworts, and ferns, suggesting that competition with some vascular plants drive the bryophytes away (Rydin 2009). The co-occurrence of bryophytes and vascular plants with specific growth forms or life stages, in particular small ferns, seems to be driving some of the interactions of these communities. In many cases bryophyte patches are dynamic sites that can provide the necessary conditions for the establishment of other plants (García-Cancel et al. 2013).

Bryophyte diversity in the LEF is supported, at the landscape level, by environmental conditions of the forest such as precipitation and life zone category (Sastre-D. J. & Buck 1993). At a finer level, we found that the presence of species of bryophytes is influenced in different ways by forest structure along with past land use, habitat, and the diversity of microhabitats and substrates. Knowledge about the distribution and habitat preferences of *Thuidium urceolatum* and *Plagiochila* spp. provides awareness for plant conservation and can be the basis to develop understanding about how bryophytes respond to disturbances. As forest succession from hurricane disturbance continues and the canopy closes, this initial study of these bryophytes serves as an indicator that tracks forest condition and recovery. The documented effects of past land use, habitat, and canopy cover provide insights into the assembly mechanisms and structure of bryophyte communities in this forest.

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