

HIGH-LIGHT DEMANDING AND RARE TREE SPECIES DEFINE TROPICAL RIPARIAN TREE COMMUNITIES

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Abstract

Riparian zones are areas of transition between aquatic and terrestrial ecosystems, and their vegetation provides many important ecosystem services that are becoming of greater importance due to the changing climate. To understand riparian conditions along headwater tropical streams in terms of species composition and structure, we surveyed riparian tree communities and physical conditions in adjacent streams in the Luquillo Experimental Forest. We determined riparian substrate condition visually by estimating ground and vegetation attributes and measuring slope and elevation in a series of riparian plots at three stream sites. We determined riparian forest composition by identifying stem species and recording their height and diameter in plots. Our results demonstrated that elevation and slope were the main differences among sites, while all sites had similar ground and vegetation conditions. Species composition in all sites was characterized by hydrophytic species. However, although the most abundant species were generalists, we also found many species that were only observed once or twice per site. Overall, our results indicate that although recent and major hurricanes influence structure and composition at this site, riparian areas still maintain a large proportion of hydrophytic and rare tree species.

Keywords: hydrophytic, land use intensity, Luquillo Experimental Forest, streams, succession, wetlands.

Resumen

Las zonas ribereñas son áreas de transición entre ecosistemas acuáticos y terrestres, y su vegetación proporciona muchos servicios ecosistémicos claves que adquirieren mayor relevancia ante los cambios climáticos proyectados. Para entender las condiciones ribereñas en un sistema tropical de quebradas estudiamos en el Bosque Experimental de Luquillo las comunidades arbustivas y las condiciones físicas ribereñas adyacentes a quebradas. Determinamos visualmente la condición del sustrato ribereño estimando los atributos físicos y de plantas sobre el suelo, más cuantificamos la pendiente y la elevación en una serie de parcelas ribereñas en cuatro quebradas. Determinamos la composición del bosque ribereño identificando en parcelas todas las especies con tallos, y midiendo su altura y diámetro. La elevación y pendiente fueron las variables que generaron las diferencias principales entre los sitios estudiados, mientras que las condiciones de suelo y vegetación entre los sitios fueron similares. Además, encontramos que la composición de especies entre los sitios se caracterizó por ser predominantemente especies hidrofíticas. Sin embargo, las especies más abundantes fueron generalistas, mientras que también encontramos muchas especies que solo

fueron detectadas una o dos veces por sitio. En general, encontramos que, aunque los huracanes recientes y de gran magnitud influyen en la estructura y composición de este bosque, las áreas ribereñas aún mantienen una proporción considerable de especies de árboles hidrofíticas y raras.

Palabras clave: Bosque Experimental de Luquillo, hidrofíticas, humedales, intensidad en uso de tierra, quebradas, sucesión.

INTRODUCTION

Riparian zones are ecotones, transitional zones between terrestrial and aquatic environments (Malanson 1993). Riparian zones modify and influence inputs from terrestrial environments into aquatic systems by filtering sediment and pollutants, accumulating organic matter, and controlling erosion. Vegetation in riparian zones also contributes to organic matter inputs to aquatic systems (Crowl et al. 2006), carbon sequestration in soils (Liu et al. 2020), and microclimate regulation (Pedraza et al. 2021). Because of their proximity to water and higher moisture availability, riparian zones can act as refugia for upland species during droughts (Naiman and Decamps 1997). This refugia function is particularly relevant because the Caribbean is experiencing increasing temperatures and changes in precipitation patterns with the changing climate (Mote et al. 2017; EPA 2016). Gutierrez et al. (2019) assessed the impacts of droughts on tropical headwater streams, motivated by observations during a major drought in 2015. The present study focuses on describing the vegetation of headwater streams to contribute to a thorough understanding of interactions among stream and riparian ecosystems by quantifying riparian forest structure and composition. Droughts and low rainfall periods have been associated with changes in microclimate factors that affect streams, such as canopy opening (Gutierrez et al. 2019), and also to changes in the quantity and quality of organic matter inputs from riparian zones (Heartsill-Scalley et al. 2012). Therefore, to contribute to understanding

stream responses to extreme events such as droughts, quantification of structure and composition of riparian zone vegetation is needed. Most existing tropical forests and tropical riparian zones are in some stage of recovery from past land use (Nagy et al. 2015). In our study site, this is also compounded by the disturbance and recovery dynamics from hurricanes (Hogan et al. 2018). By providing background information on tree species composition and structure of riparian forests, this study establishes an important baseline to observe responses to future extreme events (i.e., droughts, hurricanes) and for proposed experimental flow manipulations (Gutierrez et al. 2019). In addition, in this study we quantified riparian tree species composition at the recovery phase after hurricanes Irma and María at the study site.

We hypothesized that if past land use alters the condition of tropical riparian forests, then there will be differences between the sampled riparian-stream reach areas with the highest and lowest past land use intensity. The objectives of this study are 1) to determine riparian (parallel or along stream) variation of tropical riparian forest conditions defined as the amount and type of vegetation, ground cover, and geomorphic attributes in relation to past land use intensity, 2) to quantify species composition, and 3) to quantify the structure of tropical stream riparian tree communities. As most studies on riparian vegetation have focused on lateral (across-stream, upland versus riparian) variation, this study begins to fill the knowledge gap on structure and composition of vegetation along streams in tropical montane forests.

METHODS

Study areas

This study was conducted in the Luquillo Experimental Forest, also called El Yunque National Forest, in the northeast of Puerto Rico. We established plots along Quebrada Prieta (QP) and Quebrada Toronja (QT) within the Luquillo Forest Dynamics Plot (LFDP) and along two upstream tributaries of the Quebrada Prieta that lie outside of the LFDP to describe the condition of stream riparian zones. These tributaries are labeled Quebrada Prieta A (QPA) and Quebrada Prieta B (QPB) and are the location of a stream flow reduction experiment (StreamFRE), with QPA being the reference/control stream and QPB being the experimental manipulation stream (Gutierrez et al. 2019). Along the streams in this forest, riparian influence has been documented to extend up to 50 m (Heartsill-Scalley et al. 2009).

For this study, plots were located a maximum of five meters (m) from the wet channel to ensure strong stream/riparian influence and maintain consistency with previously collected riparian tree data (Pastor Ibáñez 2020). All sites fall within the Tabonuco forest type (Thompson et al. 2002), characterized by the dominant species *Dacryodes excelsa*, which exists between 120 and 600 m elevation (Wadsworth 1951). Annual precipitation is estimated at 3,500 mm per year in the Tabonuco forest, almost evenly distributed throughout the year with no distinct wet or dry seasons (Harris 2012). The disturbance regime includes hurricanes, droughts, floods, landslides, and tree falls (Scatena and Lugo 1995).

The land use history of the El Verde Research Area, where the LFDP is located, has been determined using the percent canopy cover from 1936 aerial photographs when most human land use that modified forest cover ceased (Thompson et al. 2002). Low canopy cover is associated with high past land use, and high canopy cover is associated with low past land use. Inside the LFDP, QT flows through land that had >20% and <80%

canopy cover due to commercial logging and agriculture prior to 1936, while QP had > 80% canopy cover and only experienced selective logging prior to 1936. It has been proposed that QPA and QPB have experienced even lower past land use intensity than QP because of their higher number of endemic and uncommon species and higher elevation within the same forest type (Pastor Ibáñez 2020). Based on the findings of Thompson et al. (2002) and Pastor Ibáñez (2020), we classified our riparian study areas as follows: QT as high past land-use conditions, QP as medium past land use, and QPA and QPB as low past land use.

Experimental design and data collection

Twenty 5-m x 5-m plots were established at a maximum of five meters from the wet channel, with five plots in each identified riparian site (Figure 1). At all twenty plots, we recorded geographic coordinates, which were used to determine elevation in meters from Google Earth© and verified with local GIS data layers. Each plot was photographed from the southwest corner and percent slope measured with the Vertex IV hypsometer (Haglöf) from the highest point to the lowest point of the plot, determined visually, and located on the soil level rather than on substrates such as boulders or logs. We determined slope aspect using a handheld compass. We also measured the horizontal distance to the wet channel in meters from the plot corner closest to the stream using a metal carpenter's tape and a level. We estimated percent ground cover visually for the categories of rocks and boulders, exposed soil, leaf litter, and ground cover defined as all vegetation ≤ 25 cm. Likewise, we estimated visually the relative amount of the categories of trees and woody plants < 130 cm, herbaceous vegetation > 25 cm, and vines as estimated percent of trees with visible vines on them. Each category for both ground and vegetation condition were classified as an index of none (0%), few (1–25%), some (26–50%), or many (> 50%). The same observer estimated the percent

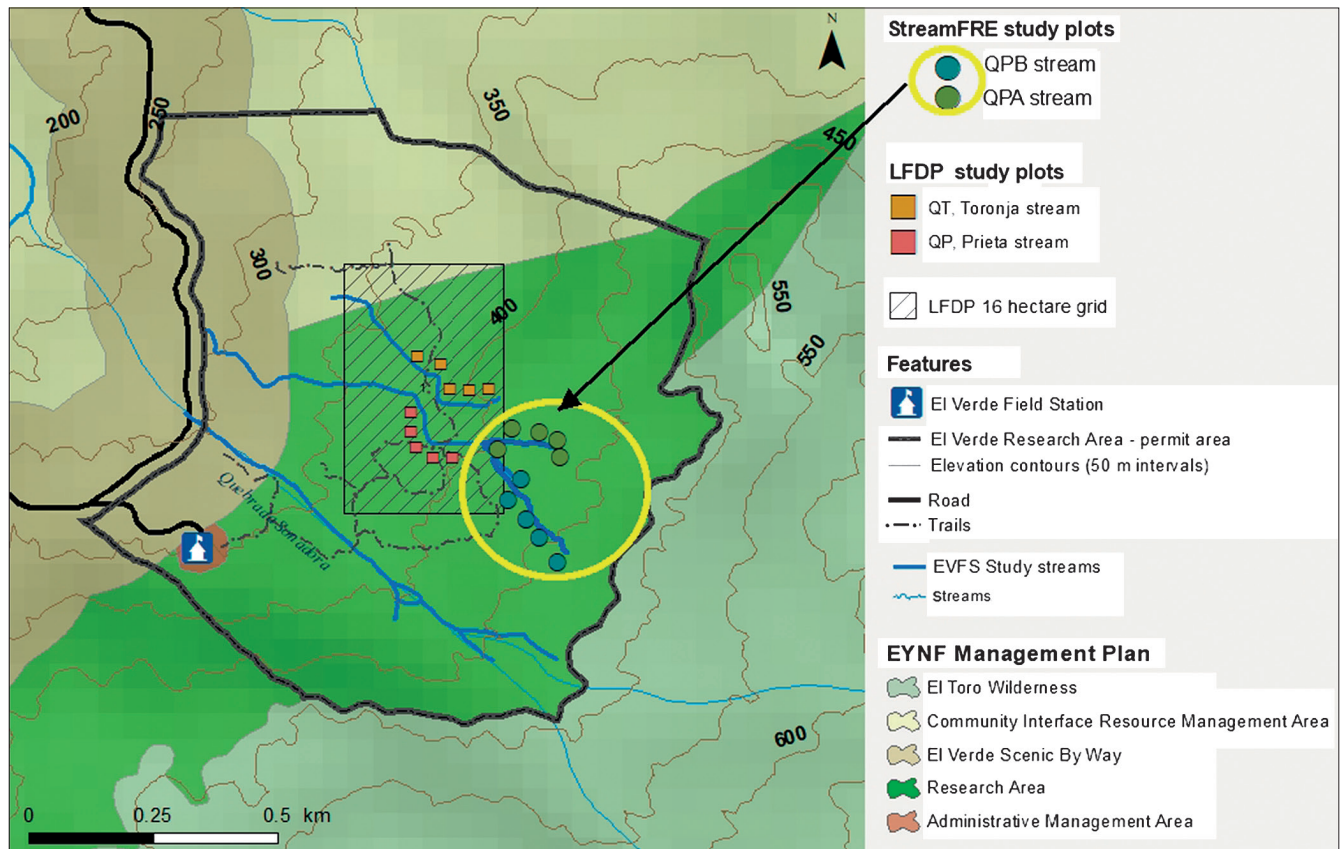


Figure 1. The Luquillo Experimental Forest, Puerto Rico, and location of riparian study plots within El Verde Research Area.

of ground and vegetation categories among plots to minimize differences in estimates attributed to different observers. All data were recorded using ArcGIS Survey123 form.

Within each plot in QPA and QPB, the location of each stem ≥ 1 cm in diameter at 130 cm height was recorded using X and Y coordinates on the scale of the 5-m x 5-m plot. We established a 0,0 coordinate as the southwest corner of each plot. The species of each stem was identified in the field with assistance from the Flora Virtual El Verde website (Flora Virtual) and the Seedlings of El Yunque field guide (Umaña et al. 2014). Species data was obtained for the QP and QT plots from the LFDP 2022 Tree Census (Melissa Salva Sauri, in progress; Zimmerman 2021). The diameter at breast height (DBH) was measured at 130 cm with a DBH tape for stems > 5.0 cm in diameter and calipers

for stems ≤ 5.0 cm in diameter. The height of each stem was measured from base to crown using the Vertex IV vertex hypsometer. Evidence of crown breakage, disease, or other damage was also assessed visually, and each stem was classified as standing ($< 45^\circ$), leaning ($\geq 45^\circ$), or prone (resting on the ground or other object). Each stem was tagged for future measurements. All tree data was recorded using ArcGIS Survey123.

Data analyses

We classified all stem species as obligate wetland, facultative wetland, facultative upland, or obligate upland using the Wetland Indicator Species list (USACE 2020). We used either a one-way analysis of variance (ANOVA) on normally distributed variables (slope, distance to wet channel) or a Kruskal-Wallis (K-W;

H statistic) on ranks for non-normally distributed variables (elevation, ground, and vegetation condition index) to determine variation among stream tributaries and main channels (the four study sites QT, QP, QPA, QPB as sampling groups). Likewise, we used *post-hoc* pairwise multiple comparison procedures based on Holm-Sidak (t) method comparisons following ANOVA or a Tukey test (q) following K-W to determine statistical difference among groups at $p \leq 0.05$. Statistical analyses were performed using SigmaPlot (Version 14). Graphs were constructed using the ground and vegetation condition index data among sites and diameter size-class distribution for QPA and QPB, as well as height and diameter for all stems in both sites using R (Version 4.2.1). We computed Shannon Diversity Index values for each plot in QP, QPA, and QPB and averaged values for each site to compare tree species diversity among sites.

RESULTS

Ground cover, physical and geomorphic conditions along riparian zones

Average site elevation decreased with increasing distance downstream, with QPB and QPA being the most upstream sites and QP being the farthest downstream. There were differences in mean riparian site elevation among the four study sites ($H = 15.231$, $p = 0.002$; Figure 2), with QPB having the highest elevation compared to QT and ($q = 5.03$, $p = 0.002$) and QP ($q = 4.08$, $p = 0.020$). The mean riparian site slope was different among the four study sites ($F = 5.74$, $p = 0.007$; Figure 2), with significant differences in slope between QP and QPB ($t = 4.13$, $p = 0.005$). In terms of riparian distance to the wet channel, there were differences among the study sites ($F = 3.818$, $p = 0.031$; Figure 2), with QP having the highest values compared to QT ($t = 3.05$, $p = 0.045$).

There were no significant differences among the four sites for any ground or vegetation index of condition

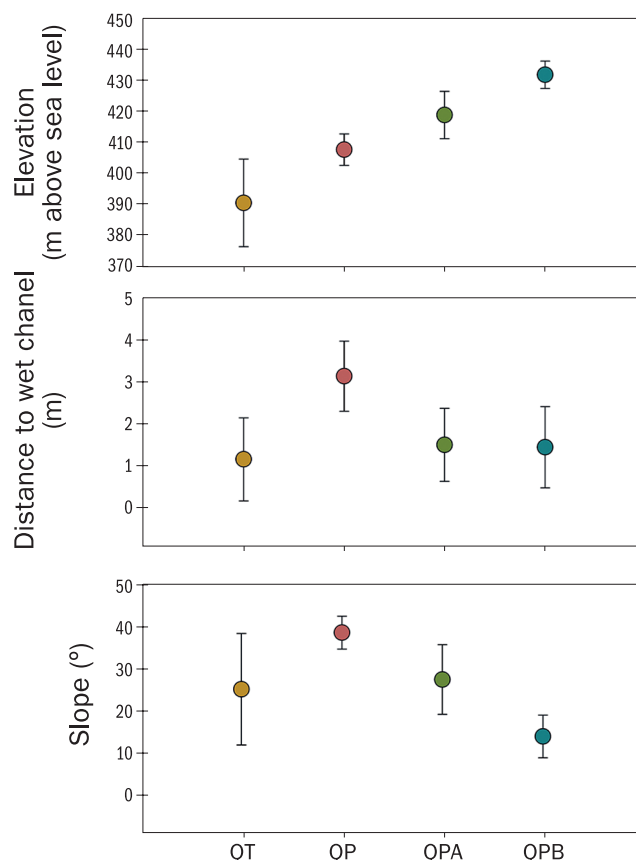


Figure 2. Average elevation in meters above sea level, longitudinal distance to wet channel, and slope angle for sites QT (Quebrada Toronja), QP (Quebrada Prieta), QPA (Quebrada Prieta A), and QPB (Quebrada Prieta B) streams in El Verde Research Area, Luquillo Experimental Forest, Puerto Rico.

variables (Figure 3). The majority of the plots have trees occupying less than 25% of the plot surface area. All plots have between 26% and 50% ground cover, leaf litter, and trees, while exposed soil, rocks and boulders, herbaceous vegetation, vines, and woody plants are not all found in all plots (Figure 3).

Riparian tree community composition

We found that most species (28/41 or 68.3%) in our riparian plots were hydrophytes (Table 1, Figure 4, Appendix). Site QPA had the highest total stems, stems per hectare, species richness, and species diversity, while QPB exhibited the lowest (Table 2). Site QPB had

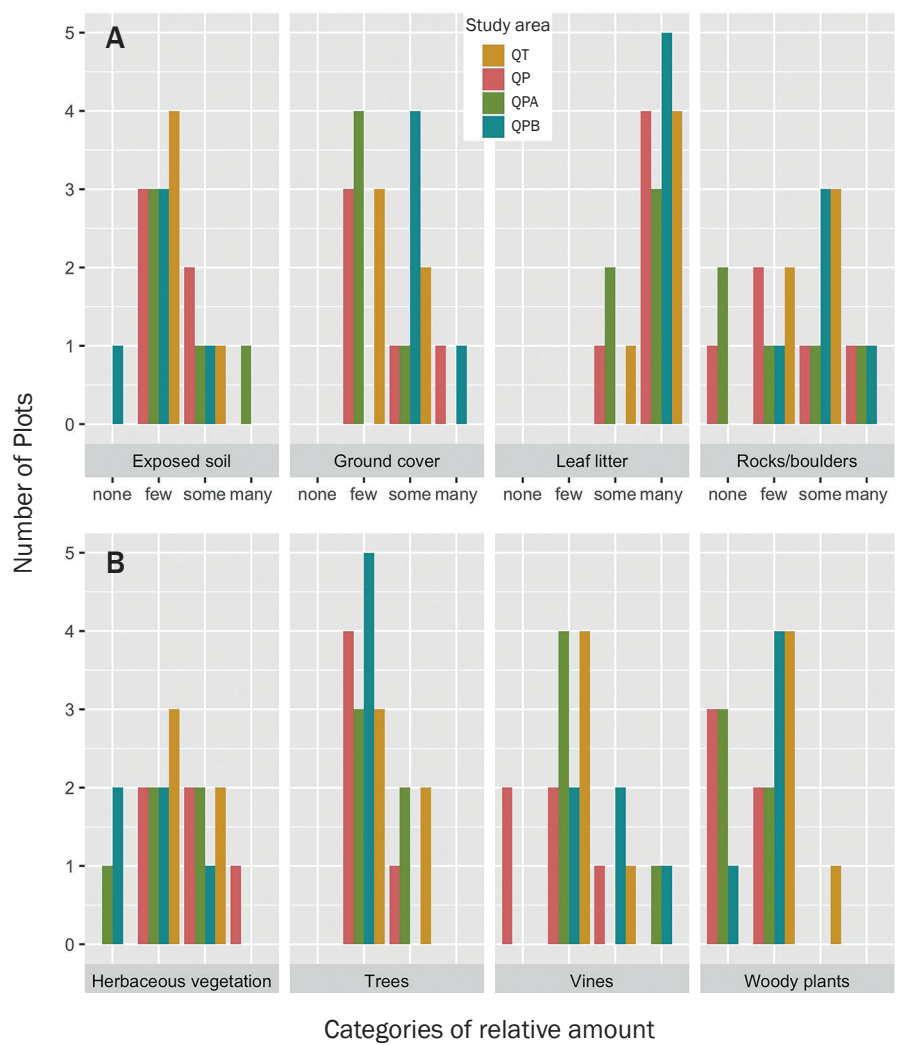


Figure 3. Ground and vegetation condition of plots in QT, QP, QPA, and QPB assessed in amount of area (none: 0%; few: 1–25%; some: 26–50%; many: > 50%) in number of plots per site. Vines were assessed as the percentage of stems with visible vines. See Figure 2 for site codes.

the highest percentage (68.4) of obligate and facultative wetland species (Table 2). The most common species at all three sites are *Psychotria berteriana*, *Prestoea acuminata* var. *montana*, and *Cecropia schreberiana* (Figure 4). Many species only appear once or twice per site, and

many of these species are unique to only one site (Figure 4).

Riparian tree community structure of headwater streams

The mean diameter of stems in QPA is 5.5 cm, and the median diameter measurement is 3.3 cm (Figure 5). Most stems in QPA have a diameter between 1.0 and 3.0 cm, and no stems have a diameter between 17.0 and 24.0 cm. In QPA, the species greater than 24.0 cm are *Manilkara bidentata* (25.6 cm), *Inga laurina* (25.3 cm), *Homalium racemosum* (25.6 cm), and *Dacryodes excelsa* (29.9 cm). The mean diameter of stems in QPB is 8.3 cm, and the median diameter measurement is 3.8 cm (Figure 5). The majority of stems in QPB have a diameter between 1.0 and 3.0 cm, and no stems have a diameter between 25.0 and 41.0 cm (Figure 5). In QPB, the species greater than 41.0 cm are *D. excelsa* (42.5 cm), *I. laurina* (45.5 cm), and

Micropholis garciniifolia (45.9). Stems in QPA tend to be slightly taller, while stems in QPB tend to have slightly larger diameters (Figure 6). The majority of stems in both sites (87%) are 10 m or under in height (Figure 6). Five stems, one from QPA and four from

Table 1. Wetland indicator species codes, status, and designation definitions of the species found in riparian plots along streams QP, QPA, QPB of El Verde Research Area.

Code	Indicator Status	Designation	Species count	Species percent	Comment
OBL	Obligate	Wetland Hydrophyte	4	9.8%	Almost always occur in wetlands.
FACW	Facultative Wetland	Hydrophyte	24	58.5%	Usually occur in wetlands, but may occur in non-wetlands.
FACU	Facultative Upland	Nonhydrophyte	9	22%	Usually occur in non-wetlands, but may occur in wetlands.
UPL	Obligate Upland	Nonhydrophyte	4	9.8%	Almost never occur in wetlands.

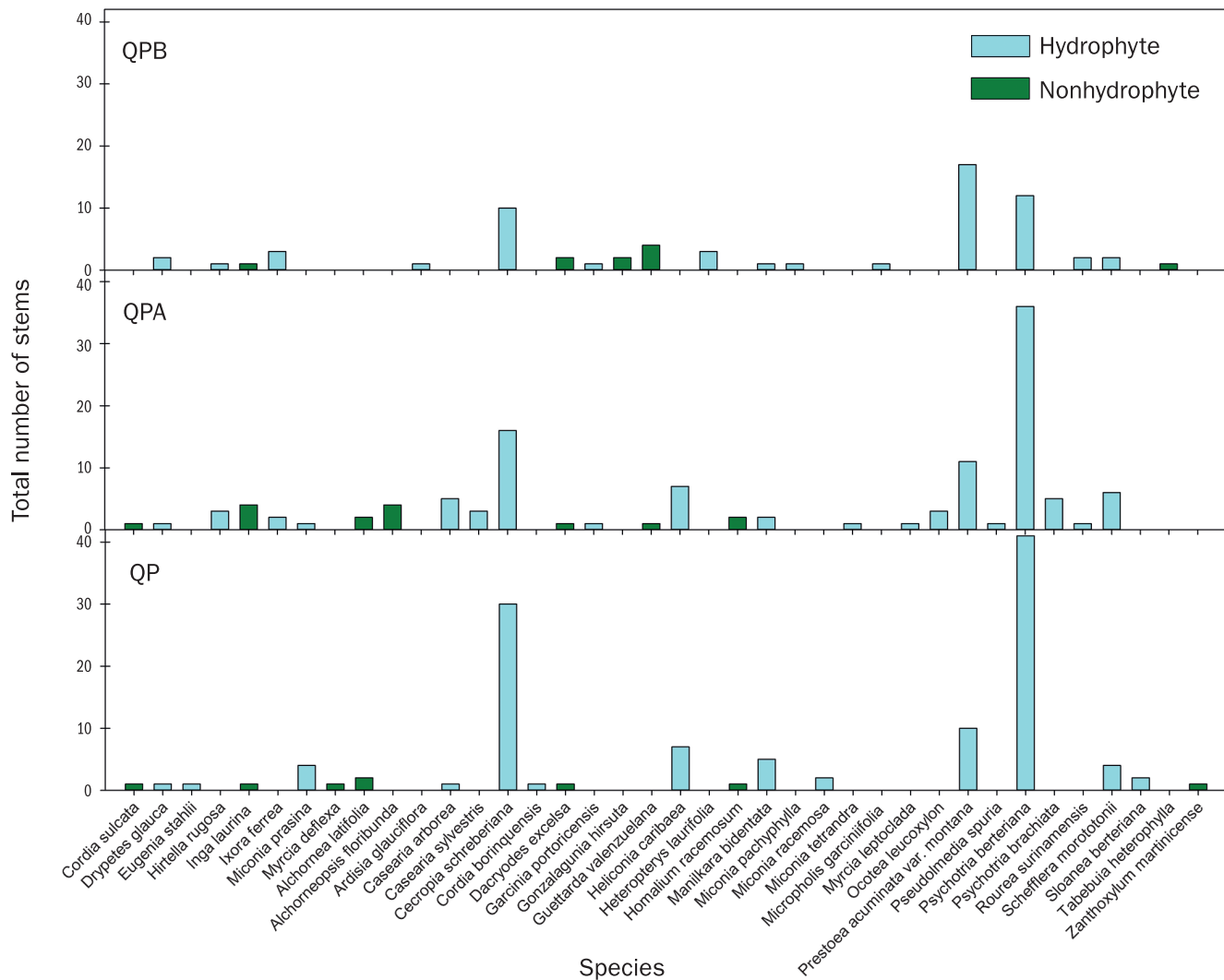


Figure 4. Stem abundance by species in riparian sites of streams QP, QPA, and QPB in El Verde Research Area, Luquillo Experimental Forest, Puerto Rico. See Figure 2 for site codes.

QPB, exceed 20 m in height (Figure 6). In QPA, this tree is a *H. racemosum* (23.4 m). In QPB, the trees are *D. excelsa* (21.3 and 22.1 m), *M. garciniiifolia* (23.9 m), and *I. laurina* (25.4 m).

Table 2. Riparian tree composition of sites QP, QPA, and QPB.

Parameter	QP	QPA	QPB
Total stems	118	125	73
Stems per hectare	9,440	10,000	5,840
Species Richness	20	28	19
% Wetland species	60%	64.3%	68.4%
Shannon Index	1.71	1.90	1.61
Number of plots	5	5	5

DISCUSSION

Variation of riparian sites

We hypothesized that if past land use alters the condition of tropical riparian forests, we would observe differences in conditions between the sampled riparian areas with the highest and lowest past land use intensity. Because QT is located in the north of the LFDP corresponding to the area that experienced the highest levels of human land use prior to 1936 (as defined by Thompson et al. 2002), we expected to find differences

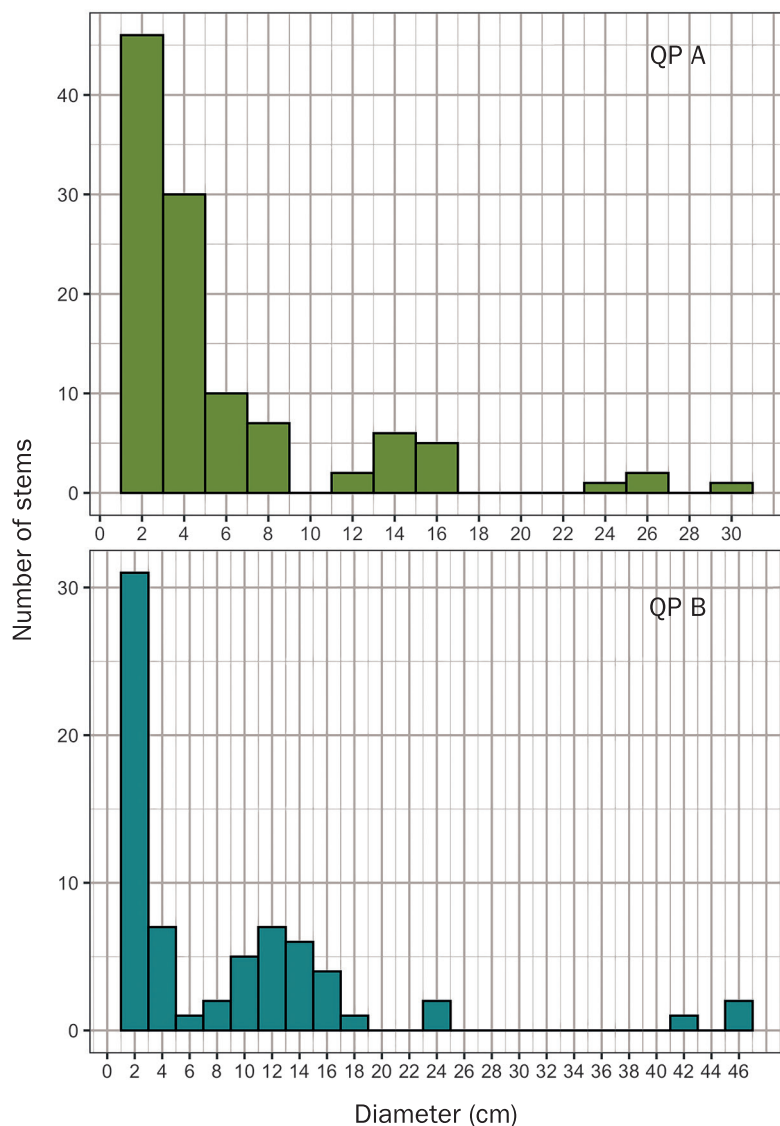


Figure 5. Distribution of diameters for sites QPA (X-axis max: 32; Y-axis max: 50) and QPB (X-axis max: 48; Y-axis max: 30) in El Verde Research Area, Luquillo Experimental Forest, Puerto Rico. See Figure 2 for site codes.

between QT and the southernmost sites QPA and QPB which have no records of past human land use. However, as there was no statistical difference in either the index of vegetation condition or index of ground condition among sites, we rejected our initial hypothesis. There were statistically significant differences between elevation and slope among sites, which can likely be explained by the topography of the mountain on which the sites are located (Figure 2). In another study of

riparian vegetation in headwater streams of the central mountains of Puerto Rico, Heartsill-Scalley and Aide (2003) found in sites which also experienced high anthropogenic land use in the past, ground cover patterns were similar among sites with similar land use histories. We propose that it is likely that there were once ground cover and/or vegetation cover differences between our study sites with high (QT) and low (QPA and QPB) past land use intensities, and that these could be currently masked by the overriding effects from early succession after the recent hurricane disturbance.

While we did not find differences in site (ground cover and vegetation index) conditions, past land use may still be evident in species composition. Previous studies have found differences in distribution between *Casearia arborea* and *Dacryodes excelsa* in areas of different levels of past land use intensity in the Luquillo Experimental Forest (Thompson et al. 2002). Areas of high past land use intensity have higher abundance of *C. arborea*, a secondary species often associated with human disturbance, while areas of lower past land use intensity have higher abundance of *D. excelsa*, which is a mature forest species (Thompson et al.

2002). In tropical riparian forests in the southern Amazon, Nagy et al. (2015) also found differences in species composition based on past land use. Their study reported little overlap of tree species, based on importance value index, between riparian forests adjacent to cleared pasture and intact riparian forests. For further study, comparing species and their size distribution in QT, QP, QPA, and QPB would be helpful to investigate whether or not the influence of past land use is evident in ground cover of riparian areas.

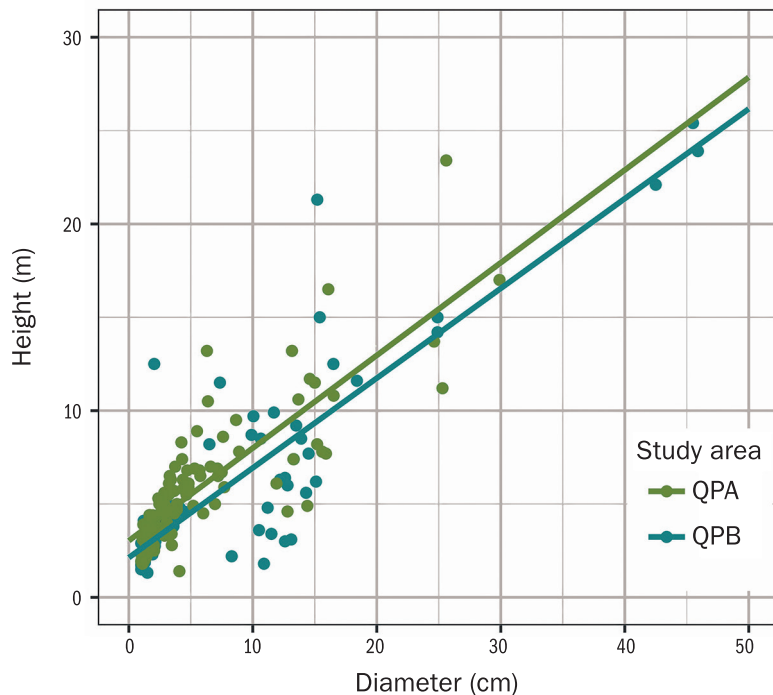


Figure 6. Diameter and height relationship for all sampled trees in riparian sites along streams QPA and QPB in El Verde Research Area, Luquillo Experimental Forest, Puerto Rico. See Figure 2 for site codes.

Riparian tree community composition along headwater streams

Study areas QP, QPA, and QPB share the same three most abundant species: *C. schreberiana*, *P. montana*, and *P. berteriana* (Figure 4). Both *C. schreberiana* and *P. berteriana* are pioneer, early successional species that thrive after hurricanes (Zhang et al. 2021; Heartsill-Scalley 2017). The high abundance of these two species is related to the high light conditions and open canopy structure from the recent disturbance of Hurricane María in 2017. The high abundance of these two species indicates that forest is still in an early succession state after Hurricane María. As succession after the hurricane continues and the canopy forms and closes, resulting in reduced light conditions, these species may not remain the most abundant, and differences or similarities of the riparian tree communities between sites may become more evident. At the time of this study, the main differences between the species composition

of the three sites is due to the large number of tree species that only occurred once or twice per site. For example, *Cordia borinquensis*, which was only documented in QP, *Miconia tetrandia*, which was only documented in QPA, and *Ardisia glauciflora* which was only documented in QPB (Figure 4). Species richness is higher than species evenness in all three sites. A similar pattern was observed in a study of headwater stream riparian zones in the La Plata river system, where the most abundant tree species were pioneer or generalist species, and most species had a single observed specimen per site (Heartsill-Scalley and Aide 2003). Most of the single specimens observed in the La Plata study were among the largest stems in their sites, suggesting they were remnants of past forest conditions, while in our current study, the single species stems were observed in a range of sizes. In our study, the lack of many species with higher abundances suggests that this low species evenness could be in response to disturbances, but this needs further study. We propose that perhaps not enough time has passed since Hurricane María for processes that involve competition and establishment of dominance to take place, and then lead to the later stages of succession associated to canopy dominance.

Riparian tree community structure along headwater streams

The riparian zone sites of stream reach QPA and QPB were similar to each other based on physical substrate, ground cover, and geomorphological conditions. Further, these sites were also similar in height and diameter distribution of their trees. These observations could indicate current environment and resource similarities. If there are underlying differences that we could not observe between the sites, they may be masked by the effects associated to Hurricane

María. Therefore, additional monitoring will be necessary to thoroughly quantify riparian vegetation succession processes as time since the hurricane increases. Both QPA and QPB sites have a high percentage of the same hydrophytic species (Figure 4, Appendix). Despite having higher percentages of hydrophytic species than QP, the individual trees represented by the higher values of both height and diameter of QPA and QPB were predominantly but not exclusively either facultative or obligate upland species. The tallest and biggest tree stems of *D. excelsa* and *I. laurina* were found in QPA and QPB, and these are both obligate upland species and *H. racemosum*, found in QPA, is a facultative upland species (Appendix). However, *M. garciniiifolia*, found in QPB, is an obligate wetland species (Appendix). This range of species represented by the tallest and biggest trees found in our riparian plots suggests that flooding may not be a common occurrence at these headwater sites, and if it does occur, it may not be prolonged flooding.

In a watershed with the same tabonuco forest type, *D. excelsa* and *I. laurina* have been strongly associated with ridge and slope environments, and *D. excelsa* is known to prefer well-drained soils (Basnet 1992; Lugo and Wadsworth 1990). It is possible that the relatively high percent slope of headwater riparian environments promotes drainage and assists in the survival of upland species. Within the Luquillo Experimental Forest, *M. garciniiifolia* also prefers sloped environments but is often associated with wetlands and anaerobic soil conditions like those of frequently saturated soils (Crow and Grigal 1980). On the contrary, *D. excelsa* and *I. laurina* are upland species, and they likely cannot survive in frequently saturated soil conditions that would impede root, cambium, and leaf growth, seed germination, and internode elongation mostly due to lack of sufficient O₂ (Kozlowski 1984). We propose that the riparian environments of tropical montane headwater streams contain a variety of environmental conditions that can successfully recruit, support, and maintain a thriving range dominant canopy species.

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