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RESEARCH ARTICLE

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Tropical forest understorey riparian and upland composition, structure, and function in areas with different past land use

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Abstract

Questions: Although past land-use effects on composition and structure are described for many forest types, forested riparian areas have been overlooked. Riparian areas may contain unique species and high species richness, as well as contribute basal leaf-litter resources for aquatic fauna. We asked: (a) does past land use alter composition in riparian vs upland areas in wet tropical forest; (b) which vegetation life forms characterize riparian zones; and (c) what is the composition and quantity of leaf litter in riparian zones compared to uplands?

Location: Riparian and upland locations in tropical wet forest, Luquillo Forest Dynamics Plot (LFDP), Luquillo Experimental Forest, Puerto Rico.

Methods: Stratified random sampling was conducted in riparian and upland areas of LFDP with high and low past land use. Understorey vegetation life form composition and cover were sampled in plots. Leaf-litter species composition and components were estimated with collecting baskets placed throughout riparian zones and uplands.

Results: Ferns and lianas were more abundant in riparian areas than uplands. Ordination of species composition groups was distinct for riparian and upland areas with different past land use when based on leaf litter, but this ordination pattern was not as clear in plot vegetation.

Conclusion: Characterized by greater presence of ferns and lianas, riparian zones had higher species richness values and greater leaf litter biomass. Distinct leaf-litter species composition within riparian and upland areas may result from a combination of different land-use histories, various plant types, and environmental conditions. Although riparian areas are proportionally a small component of the forested landscape, they are significant contributors to ecosystem process, terrestrial and aquatic linkages, and plant community composition.

KEYWORDS

composition, ferns, land use, leaf fall, leaf litter, lianas, riparian, secondary forest, species, stream, tropical, understorey

1 | INTRODUCTION

Worldwide, and particularly in the tropics, secondary forests are significant contributors to carbon sequestration, species conservation, and ecosystem services (Chazdon et al., 2009; Norden et al., 2009; Poorter et al., 2016). Riparian areas of tropical secondary forests can be prominent features in fragmented landscapes, from cloud forests to semi-arid highlands (Schmitt et al., 2019; Hernández-Dávila et al., 2020; Villamarín et al., 2020). However, in montane secondary forests with uniform tree canopy, riparian areas of headwater streams may appear to be hidden in plain sight as these do not stand out from the rest of the forest landscape. Long-term studies on tree communities from montane wet forest have identified associations to past land use, topography, and soils, but not to riparian areas (Thompson et al., 2002; Heartsill-Scalley et al., 2009; Hogan et al., 2016). Organic matter from riparian vegetation is an important energy source and structural component in forest streams, where it is efficiently processed and integrated into aquatic and terrestrial food webs (Wallace et al., 1997; Rosas et al., 2020). Riparian vegetation provides direct and lateral inputs of coarse particulate organic matter via leaf litter that reaches stream ecosystems (Fisher et al., 2004; Mbaka et al., 2015; Molinero, 2019).

Forest types and vegetation associations are known to markedly change along large-scale gradients. In tropical forest systems, there is a clear understanding and focus on those longitudinal gradients which may be found in mountains where, for example, elevation and rainfall increase and different forest types occur (Weaver, 1991; González et al., 2013). However, lateral (topographical or geomorphological) gradients can exist within a forest type, such as those observed in riparian vs upland areas (Scatena & Lugo, 1995; Decocq, 2002). There are documented differences in individual tree species distributions among ridges, slopes, upland, and riparian areas in tropical montane wet forests. However, most studies focus on fine-scale variations in abiotic factors, for example, soil moisture and accumulation of organic materials from litterfall and woody debris, not on the resulting influences on vegetation structure and composition (Weaver, 1991; Basnet, 1992; Scatena & Lugo, 1995; Heartsill-Scalley et al., 2009).

Riparian vegetation composition and diversity are related to a variety of environmental factors including elevation, flooding frequency, and light availability in the transition between terrestrial and aquatic systems (Naiman & Décamps, 1997; Lyon & Sagers, 1998; Tabacchi et al., 1998; Decocq, 2002). In montane streams, surface water flow and storm events move organic matter from upland areas along riparian zones (Gomi et al., 2002; Fisher et al., 2004; Liu et al., 2020). Vegetation life forms that quickly colonize or re-establish under these conditions often dominate riparian zones. Riparian vegetation structure and composition affect aquatic fauna and serve as corridors for fauna movement and plant dispersal (Kinnaird, 1992; Andersson et al., 2000; Honnay et al., 2001; Funch et al., 2002; Iwata et al., 2003; de Souza et al., 2013; Yeung et al., 2017; Calle & Holl, 2019; Schmitt et al., 2019; Hernández-Dávila et al., 2020).

Vegetation composition and structure of tropical riparian zones often focus on individual vegetation life forms, such as herbs, ferns, or trees, and is characterized in terms of distance to stream channels (Druker et al., 2008; Heartsill-Scalley et al., 2009; Paixão et al., 2013). Riparian areas are described as having higher rates of productivity and diversity of vegetation life forms than non-riparian areas (Gregory et al., 1991; Naiman & Décamps, 1997; Martin et al., 2004). It is expected that changes in species richness and vegetation structure associated with past land use would also be found in riparian areas. Identifying and understanding riparian vegetation is an important component of forest management, especially in forests that harbor a high density of streams providing permanently flowing water and aquatic resources (Lowe & Likens, 2005; Alexander et al., 2007; Meyer et al., 2007; Bleich et al., 2014).

Tree species associations can be the dominant vegetation life forms in riparian areas in temperate, savanna, and arid systems (Kinnaird, 1992; Kellman & Tackaberry, 1993; Metzger et al., 1997; Pabst & Spies, 1999; Beschta, 2003). In a previous analysis of this forest landscape, however, particular tree species were not found to be uniquely or exclusively associated with riparian areas, at least not in terms of the distribution of trees with stems >10 cm in diameter (Heartsill-Scalley et al., 2009). The suggestion has been made that in tree-dominated riparian landscapes, distribution of tree species is not necessarily related to the distribution of other vegetation forms (Lyon & Sagers, 1998; Scatena, 1990). Studies that integrate riparian vegetation community composition with past land use are needed to understand the legacy effects on riparian vegetation and explore potential ramifications for streams and aquatic resources.

We investigated stream-side riparian vegetation components of wet montane forest to determine if they are different from upland forest areas. Further, we identify forest areas with contrasting past land use to understand their effects on riparian vegetation. The goal of this study was to answer the following questions: (a) does past land use alter composition in riparian vs upland areas in wet tropical forest; (b) which vegetation life forms characterize riparian zones; and (c) what is the species composition and quantity of leaf litter in riparian zones compared to uplands, and does this vary depending upon past land use? We hypothesized that the riparian areas in wet tropical forests would be characterized by non-tree vegetation life forms, and that leaf litter would be higher in riparian areas. Past land use is expected to mask or alter differences between riparian and upland vegetation characteristics. To address these questions, vegetation distribution patterns were analyzed in upland and riparian areas of two permanently flowing streams within a tropical wet forest site where past land use, natural disturbance regime, tree community structure, and species composition are well known (Thompson et al., 2002; Uriarte et al., 2012; Hogan et al., 2016).

2 | METHODS

2.1 | Study area

The study area is within the Luquillo Experimental Forest located in northeastern Puerto Rico (Zimmerman et al., 2021). The 16-ha LFDP

Luquillo Forest Dynamics Plot (Figure 1; LFDP; southwest corner 18°20′ N, 65°49′ W) is part of the Luquillo Long Term Ecological Research program and the Center for Tropical Forest Science, now ForestGeo global network (Anderson-Teixeira et al., 2015). The LFDP is divided into quadrats, marked with coordinates every 5 m in a 500 m × 320 m grid. The forest is classified as subtropical wet forest in the Holdridge life zone system (Ewel & Whitmore, 1973) and tropical montane in Walsh's (1996) tropical climate system. The LFDP ranges in elevation from 333 m to 428 m above sea level, with an annual mean precipitation of 3,500 mm (Harris et al., 2012). Two perennial second-order streams, Quebrada Prieta (QP) and Quebrada Toronja (QT), flow through the LFDP from east to west (Figure 1); average stream channel width is 3 m and average depth is 0.5 m. These are high gradient streams, with incised banks that limit over-bank flooding and large floodplain development. Both streams are lined with boulders and bedrock and carry negligible amounts of silt, clay, and sand (Ahmad et al., 1993). Disturbances in the Luquillo Mountains and the LFDP include tree falls, landslides, droughts, and hurricanes (Scatena et al., 2012; Gutierrez et al., 2020). The forest type in the plot is known as "tabonuco" after the dominant tree, *Dacryodes excelsa*, which occurs below 600 m in the Luquillo Mountains. Taylor (1994) described the dominant life forms of the vascular flowering vegetation (by approximate quantity of species) in the LFDP study area as: 44% woody self-supporting shrubs and trees (172 species), 44% herbaceous plants including large monocots and graminoids (170 species), and 12% vines and lianas (48 species). In addition, 80 species of pteridophytes, ferns and fern-like vegetation, have been identified (Taylor, 1994; Thompson et al., 2002).

Past land use in the area includes subsistence agriculture, cut-over tree removal for plywood production, and selective logging, all of which have been found to affect tree species composition (Thompson et al., 2002; Uriarte et al., 2012; Hogan et al., 2016). The United States Department of Agriculture Forest Service purchased the land that includes the LFDP in 1934; conducting initially selective logging and timber stand improvement activities in the area, but it has remained under forest cover ever since (for details see Thompson et al., 2002, and sources within). The plot's northern sections are comprised of three zones of secondary forest of differing, but high, past land use as all three areas had ≤80% forest cover in 1936 aerial photographs. In this study, the northern plot zones were combined to delineate one area of younger secondary forest identified as past high land-use that had cleared areas and logging prior to 1934 (Figure 1). In contrast, the plot's southern third contains conserved tabonuco forest subjected to minor selective logging and with 80–100% canopy cover. In this study, land-use areas in the LFDP are delimited by the permanently flowing stream QP in the plot's southern end (Figure 1). The riparian and upland areas south of QP had the greatest (>80%) canopy cover, while the upland area north of QT had high past land use and less (<80%) canopy cover in the 1936 aerial photos (Thompson et al., 2002).

The tropical montane wet forest LFDP was divided into four sites based on history of land-use intensity (high or low) and geomorphic setting (riparian or upland). The four sites are: (1) past high land-use north upland (HIGH); (2) riparian area with past high land-use QT; (3) riparian area with past low land-use QP; and (4) past low land-use south upland (LOW). Upland areas (HIGH and LOW) were defined as ≥60 m away from the stream channel edge based on Heartsill-Scalley et al.'s (2009) findings that at distances <50 m from streams there was a riparian or stream-side "edge effect" on species composition of trees >10 cm in diameter, and therefore to avoid any such

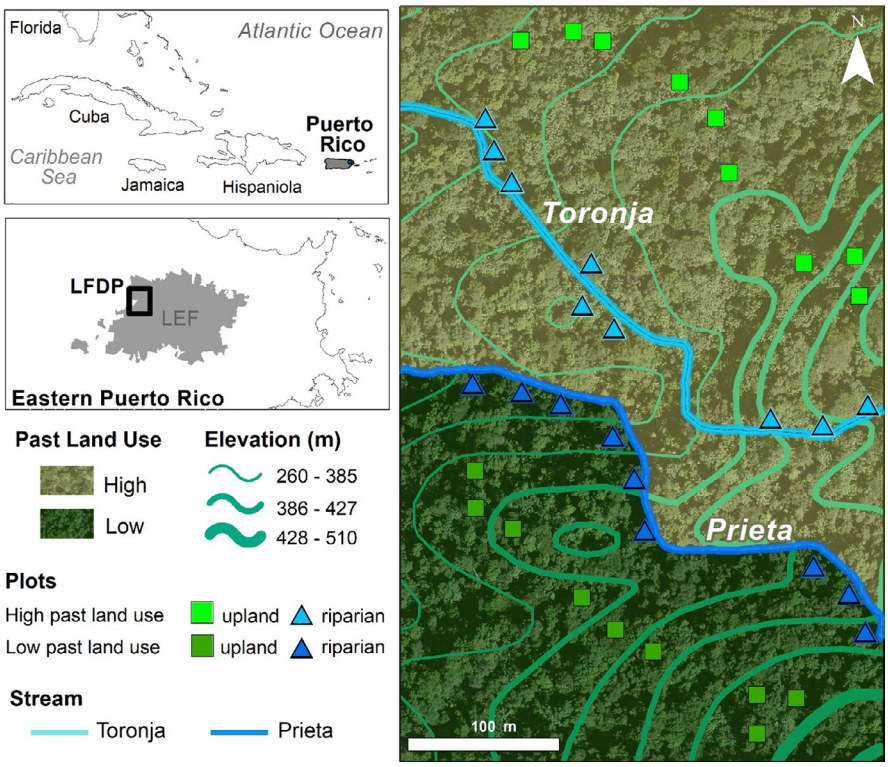

FIGURE 1 The 16-ha Luquillo Forest Dynamics Plot (LFDP), within the Luquillo Experimental Forest (LEF), in northeastern Puerto Rico. Relative locations of sampled vegetation plots are identified for illustrative purposes

effects we extended our definition of upland to 60 m. Riparian areas (QT and QP) were ≤5 m away from the wet stream channel.

2.2 | Vegetation composition

Stratified random vegetation sampling was used in each of the four sampling sites within the LFDP; nine 5 m × 5 m plots (25 m^2), for a total of 36, were randomly selected. Plot location was recorded using the column and row numbers of the existing grid system (Thompson et al., 2002). All vegetation ≥25 cm in height within the plots was counted and identified to species or the lowest taxonomic level possible (nomenclature follows https://plants.sc.egov.usda.gov/ and http://floraelverde.catec.upr.edu/). Species were then classified by life form: grass, herb, fern, liana (the term includes all climbers: vine or liana), shrub, tree, or palm. Field work was conducted in 2004. Voucher samples were taken for vegetation not identified to species in the field and were identified at El Verde Field Station facilities.

2.3 | Leaf litter components

Leaf-litter biomass was characterized by placing 15 collection baskets in each of the four sites in the LFDP, for a total of 60 collection baskets, following the established protocol described by Zimmerman and et al. (2007). Plastic litter baskets were placed 80–100 cm above the ground, lined with fine (~1 mm) plastic screen mesh. The basket sampling area was 0.25 m^2. All accumulated basket contents were collected every two weeks, from April 2003 to April 2004 (i.e., 25 samplings per basket from each of 60 baskets). Plant parts larger than the sampling basket found lying across the basket at time of collection (e.g., palm or fern fronds, large inflorescences) were cut to represent the area of the basket. Samples from each basket were collected on the same day and taken to the laboratory where they were air-dried using a dehumidifier and constant temperature of ~32°C. Litter samples were sorted by plant parts: leaves, wood (only material <3 cm diameter), reproductive parts (flowers and fruits), and miscellaneous. All leaves in samples were identified to species. Petioles and rachises were weighed as leaves if still attached to leaf blades or separated but clearly identifiable. Miscellaneous material included all vegetative parts too small to identify with certainty. Afterward, all sorted litter was oven-dried at 65°C for a minimum of seven days to constant weight.

2.4 | Statistical analyses and ordinations

Multivariate analysis of variance (MANOVA) was used to compare the density, richness, and diversity values (H') of vegetation life forms among the four sampling sites in the LFDP. Univariate post-hoc tests of mean differences were conducted for each vegetation life form within the MANOVA model to assess which life forms were different among sites. Repeated-measures MANOVA was used for comparing the four sampling sites in the LFDP with the response variables of total litter (sum of all litter components) and per each of the leaf-litter components of leaves, wood, and reproductive parts. Univariate post-hoc tests of mean differences were conducted for each leaf-litter component and for total litter within the MANOVA model to assess differences among sites. To focus on the low past land-use upland and riparian sites the high past land-use upland site was excluded, and analyses repeated on a subset of the data. All statistics were conducted with an alpha of 0.05, and computed in the program SAS (Version 9, SAS Institute, 2004).

Species composition among sites was explored using non-metric multidimensional scaling (NMS) based on a Bray–Curtis distance matrix: one with species abundance per 36 plots and another with leaf mass per species in 100 litter-fall collections (PC-Ord 7.08, Wild Blueberry Media LLC, Corvallis, USA). Both distance matrices were relativized by maximum values of species per plot and final ordination fit stress values were <12, which is well under the value of 20 for acceptable algorithm optimization criteria and interpretation of the resulting ordinations (McCune & Grace, 2002; Dexter et al., 2018). Following McCune and Mefford (2018) correlations between distances in the ordination space and distances in the original data space for each ordination axis are reported as percent (%) proportion variance represented by each axis. Pearson correlations (r) of species to NMS ordination axes with values ≥20 (positive or negative) are reported in the *Results* section. We selected NMS as a method to visually explore community composition as it is robust for heterogeneous community data sets and does not assume linear relationships among variables (McCune & Mefford, 2018).

3 | RESULTS

3.1 | Vegetation structure, community metrics and composition

Relative density of understorey vegetation per life form varied ($F = 3.00$, $p = 0.0008$) among sites; however, all understorey vegetation life forms were observed in each of the four sampling sites (Figure 2). In post-hoc analyses (Figure 2), the highest density of grasses ($F_{3,32} = 5.35$, $p = 0.0042$) and shrubs ($F_{3,32} = 6.77$, $p = 0.0012$) was found in the high land-use upland relative to the low land-use upland and both riparian sites. The highest density of ferns was observed in the low land-use QP riparian area ($F_{3,32} = 3.26$, $p = 0.0342$). When excluding the high land-use upland, there were no overall differences among sites ($F = 1.71$, $p = 0.1167$) in relation to all understorey vegetation life forms. However, post-hoc analysis of means suggests that ferns and lianas were highest in the QP riparian site ($F_{2,24} = 4.60$, $p = 0.0204$; $F_{2,24} = 4.10$, $p = 0.0295$ respectively).

The highest density of individual plants was 160 per 25 m^2 plot in both the high past land-use upland and the low past land-use riparian QP, while the minimum was 17 in the high past land-use riparian QT. The greatest number of species per 25 m^2 plot was 42 in the low past land-use riparian QP, and the lowest, 9, in the high past land-use

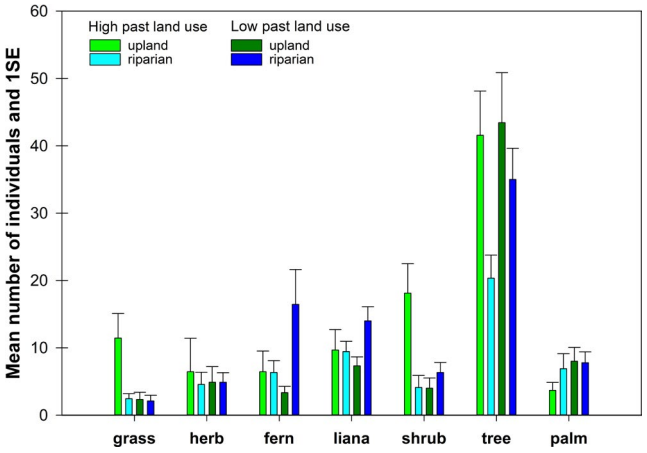

FIGURE 2 Mean abundance and standard error of vegetation life forms in upland and riparian sites of the Luquillo Forest Dynamics Plot, Luquillo Experimental Forest, Puerto Rico. Bars represent means of nine 25-m^2 plots per site

riparian QT. The highest species diversity (H') was in riparian areas with low past land use; past high land-use upland had the lowest values (Figure 3). Vegetation density ($F_{3,32} = 4.53$, $p = 0.0093$) and species diversity ($F_{3,32} = 3.34$, $p = 0.0313$) were different among sites. However, there was no difference in species richness among sites. In the post-hoc analysis of means, the lowest species diversity and the highest density of vegetation were in the high past land-use upland. The highest species diversity was observed in the QP riparian zone. Excluding the high past land-use upland yielded no differences in density among sites. However, there were significant differences among sites for species richness ($F_{2,24} = 4.60$, $p = 0.0204$) and species diversity ($F_{2,24} = 3.74$, $p = 0.0385$). The analysis of means which excludes the high past land-use upland presents the highest values for species richness and diversity in the low past land-use QP riparian site.

The ordination analysis with plot-based species composition placed all the plots from the past high land-use upland site distant from other sites in the ordination space (Figure 4a). Species composition in high and low past land-use riparian sites overlapped with the low past land-use upland site in the ordination (Figure 4a). Two NMS axes in the ordination represent a cumulative proportion of 50% of the variance (33% in axis 1 and 17% in axis 2). Species correlated with the low past land-use upland and riparian sites included older-growth trees (*Manilkara bidentata*, *Tetragastris balsamifera*, and *Eugenia stahlii*) and various fern and orchid species (Figure 4a). Species correlated to the negative horizontal axis, where the plots from the high past land-use upland site are located, included grasses (*Pharus latifolius*, *Ichnanthus pallens*), various shrubs (*Piper* spp.) and herbs (*Commelina* spp.). The vertical axis had positive correlations to understorey species including grasses (*Olyra latifolia*), lianas (*Rourea surinamensis*, *Heteropterys laurifolia*), shrubs (*Gonzalagunia hirsuta*), and trees (*Casearia arborea*); while the vertical axis had negative correlations to various older-growth tree species (*Sloanea berteriana*, *Dacryodes excelsa*, *Ocotea* spp.).

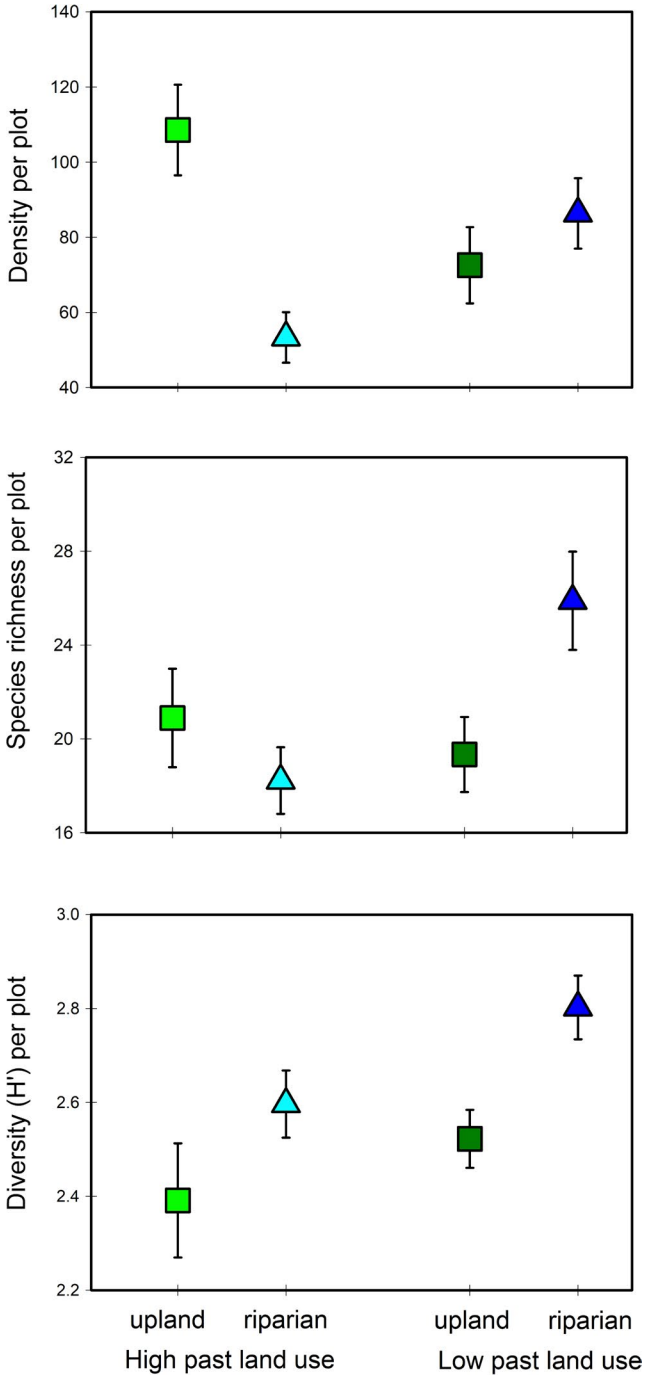

FIGURE 3 Mean values and one standard error bars for density, species and diversity (H'), per nine 25-m^2 plots in each of the four Luquillo Forest Dynamics Plot sites

3.2 | Leaf litter characterization and composition

Total leaf litter (leaves, wood, plant reproductive components) rates were different among sites ($F_{3,1491} = 4.23$, $p = 0.005$), with the highest rates found in high past land-use upland. The leaf-fall component was also greatest in high past land-use upland ($F_{3,1491} = 2.6$, $p = 0.0510$). Plant reproductive components, flowers and fruits, were greater in the QT riparian site. No difference was observed in the amount of

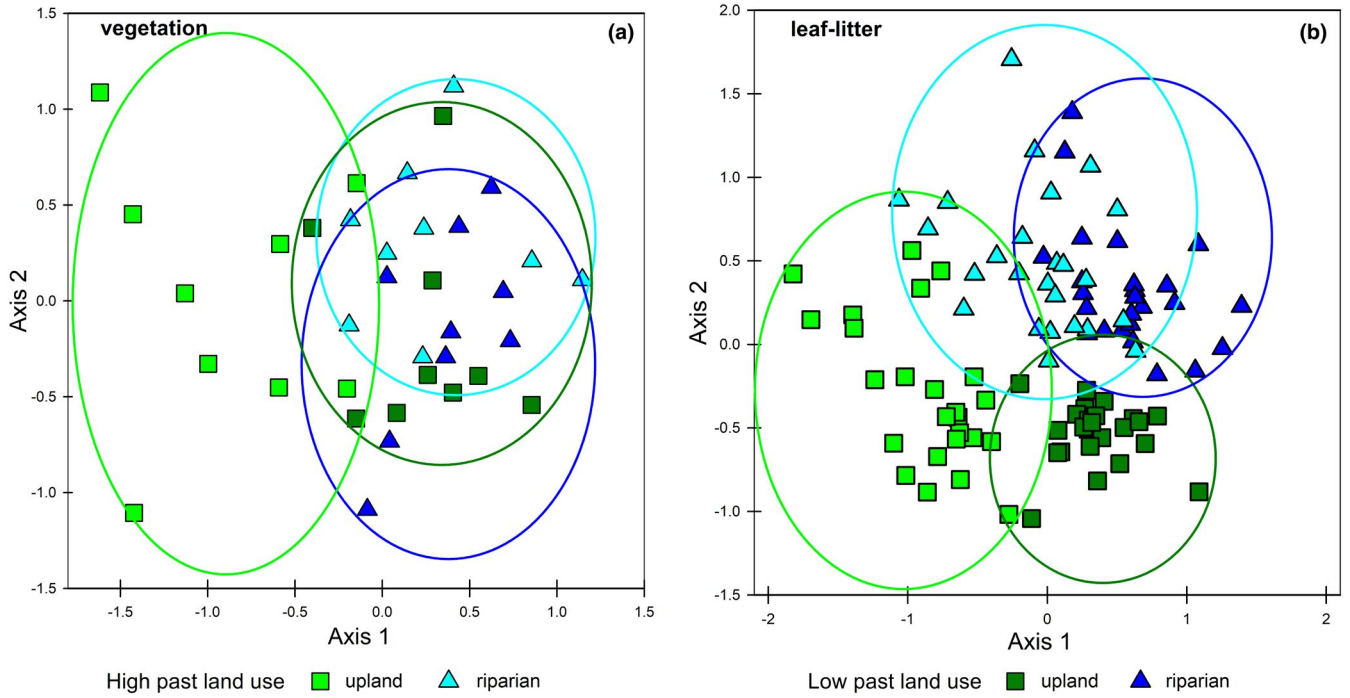

FIGURE 4 Species composition among upland and riparian sites with different past land use in the LFDP, Luquillo Experimental Forest, Puerto Rico. (a) Plot-based understorey species composition ($n = 9$ per site); (b) leaf litter-based species composition ($n = 25$ per site)

wood leaf-litter component among sites. When excluding the high past land-use upland, total leaf litter was higher in QT and QP riparian sites than in low past land-use upland ($F_{2,1118} = 5.25$, $p = 0.005$). Leaf-fall rate was also higher in QT and QP riparian sites compared with the low past land-use upland ($F_{2,1118} = 2.89$, $p = 0.0558$). Plant reproductive components were higher in QT riparian than in QP riparian and the low past land-use upland ($F_{2,1118} = 9.54$, $p = 0.0001$). Total litter, leaves, and reproductive parts were overall higher in both riparian areas when compared to the low past land-use upland.

The analysis with leaf-fall species composition separated upland sites from riparian sites in the NMS ordination (Figure 4b). Upland sites with different past land use had less overlap in species composition, while there was more overlap between riparian sites. The first two NMS axes in the ordination represent a cumulative proportion of 69.1% of the variance (41.62% axis 1 and 27.5% axis 2). The area occupied mainly by low past land-use upland and riparian sites in the positive side horizontal axis was correlated to the trees *Dacryodes excelsa*, *Hirtella rugosa*, *Matayba domingensis*, *Cyrilla racemiflora*, *Ixora ferrea*, *Guettarda valenzuelana*, and liana species *Rourea surinamensis*. The area occupied by past high land-use upland and riparian sites in the negative side of the horizontal axis was correlated to the tree species *Inga vera*, *Cecropia schreberiana*, *Ormosia krugii*, and *Buchenavia tetraphylla*. The positive vertical axis area where most riparian plots were located was correlated to the palm *Prestoea acuminata* var. *montana*; to tree species *Miconia tetrandra*, *Inga laurina*, *Casearia arborea*, and *Homalium racemosum*; the lianas *Rourea surinamensis*, *Marcgravia rectiflora*, *Hippocratea volubilis*, and the often epiphytic tree *Clusia clusioides*; and various ferns species. The negative vertical axis area where most upland plots are distributed is correlated with the trees *Croton poecilanthus*, *Guarea guidonia*, *Oxandra laurifolia*, and *Alchorneopsis floribunda*.

4 | DISCUSSION

4.1 | Past land use and riparian versus upland vegetation

In this study, distribution patterns of some vegetation life forms were associated with natural upland and riparian features and previous land-use practices in the forest landscape. The high past land-use upland site had the lowest overall species diversity and highest density of grasses and shrubs in the forest. Trees ≥10 cm diameter had lower stem density and species diversity in high past land-use upland when compared to areas with minimal past land use (Thompson et al., 2002). Our findings in high past land-use upland may be associated to the lower tree density that allows more light to reach the forest understorey and favors grasses and shrubs.

In riparian areas, higher density of ferns and lianas and higher values of overall species diversity were observed compared to upland areas. Ferns are common in closed-canopy forests and riparian zones, but are also present in open-canopy forests and thrive in disturbed areas, thus contributing to a high proportion species richness in tropical forests (Gentry, 1990; Russell-Smith & Lee, 1992; Heartsill-Scalley & Aide, 2003; Mehltreter et al., 2010, Royo et al., 2011). Various fern species are probably more abundant in riparian zones due to the higher light and moisture found in these areas, combined with their ability to establish and grow in eroded

soils (Lugo & Scatena 1995). Niklas (1994) suggested that ferns and lianas have analogous growth habits, ferns support horizontal sections with rhizomatous shoots, while lianas support vertical sections of shoot growth. However, lianas may be more susceptible to water stress than other vegetation life forms due to narrow stems in relation to their height. In seasonal Amazonian rainforest, Restom and Nepstead (2004) observed that lianas tend to avoid water stress by deeply rooting in soils. Even though our study area does not currently have a prolonged dry season, lianas were more abundant along riparian areas. Lianas have an affinity for greater light availability at forest edges, to areas with high water availability and soil fertility (DeWalt et al., 2006), and also to particular tree species and larger trees which may characterize the forest areas with relatively low disturbance (Rice et al., 2004). In this study, fern density was also positively associated with riparian areas, and due to their rhizomatous growth habit, ferns may not be negatively affected by the high quantities of leaf litter fall in these areas (Chinea, 1999; Drucker, et al., 2008; Nilsson et al., 1999; Paixão et al., 2013). Riparian zones in this study are prone to surface water flow with litter often accumulating toward the stream channel during storm events. Ferns and lianas are present in areas with an accumulation of litter-fall in the soil substrate and may sustain growth after storm flow events more effectively than other understorey vegetation life forms.

In riparian zones of wet forest landscapes, different vegetation layers do not necessarily have similar responses to environmental conditions and abiotic factors. Interaction among vegetation layers may affect density and composition of riparian vegetation. Lower density and differences in species composition of tree seedlings were found when comparing a fern-dominated understorey to an understorey with experimentally removed ferns (George & Bazzaz, 1999). The presence of an understorey with high fern density could affect recruitment dynamics in riparian areas, as there was greater species richness in the riparian zone.

Similar to our findings where non-tree vegetation was more abundant and had different species composition in riparian areas, analyses of trees, shrubs, and herbs conducted in a range of different riparian to upland landscapes concluded that each vegetation life forms responds differently to environmental conditions of riparian areas (Decocq, 2002; Lyon & Sagers, 1998; Druker et al., 2008; Paixão et al., 2013). Those studies highlight what Van Coller et al. (2000) describe as complex environmental gradients that exist away from and along streams. In a mostly forested landscape with low intensity forestry land use (Decocq, 2002) and in a forest reserve (Lyon & Sagers, 1998) studies also found few similarities between species composition of herbs, shrubs, and trees of riparian areas to those of uplands. Distinct riparian understorey fern.

composition and greater species richness were observed in a fragmented forest landscape (Paixião et al., 2013), while unique herb species were found in a narrow buffer a few meters from streams in a forest reserve (Druker et al., 2008), and these studies identified patterns dependent on the size of the stream valley and distance from streams.

4.2 | Riparian and upland leaf-litter species based on past land use

Riparian forests in general have been observed to have higher rates of productivity than upland forests, suggesting that riparian forests may not be limited by factors related to water or nutrient availability (Hanson et al., 1994; Lugo et al., 1990; Naiman & Décamps, 1997). Leaf-litter productivity was highest in the upland area with previous land use, and lowest in the minimally disturbed upland area. However, when excluding the high past land-use upland, riparian areas had higher productivity rates as compared to minimally disturbed upland. Lianas are known to contribute large quantities of leaf biomass to litter-fall, more than trees per unit of basal area (Hegarty, 1991; Phillips et al., 2005). The greater number of lianas observed in riparian areas may be important contributors to the higher leaf-litter production found in these areas, as well as the presence of species such as the palm *Prestoea acuminata*, and the trees *Inga* spp., *Manilkara bidentata*, and *Cecropia schreberiana* which produce relatively large fruits (Lugo & Frangi, 1993; Wunderle, 1999).

Based on observed patterns of higher leaf litter and total litter in riparian areas, these riparian areas contain factors contributing to high productivity: frequent small-scale disturbances due to higher tree turnover rates (Scatena & Lugo, 1995), accumulated materials due to downslope transfer and storm flows (Cox et al., 2002; Scatena & Lugo, 1995), and likely higher light availability due to the partially open canopy above stream channels (MacDougall & Kellman, 1992). In a review on controls of primary productivity in the montane landscape of the Luquillo Mountains, Waide et al. (1998) suggest a combination of nutrient availability, disturbance, and competition for light are the major factors controlling primary productivity. Riparian areas may harbor greater soil humidity and, in times of decreased rainfall, non-tree vegetation, such as lianas, may capitalize on this resource contributing to carbon sequestration and forest productivity (Schnitzer & Bongers, 2002; DeWalt et al., 2006). Riparian areas provide an environmental template that is conducive to higher litter fall, which is a basal energy resource for headwater streams under the canopy of these forests (Wallace et al., 1997; Rosas et al., 2020). In areas dominated by secondary forests, riparian areas provide many essential resources and services despite their low proportion in the forest landscape (Calle & Holl, 2019; Dybala et al., 2019).

4.3 | Concluding remarks

Although there is clear evidence that some vegetation patterns result from anthropogenic effects and the intensity of previous land-use practices (García-Montiel & Scatena, 1994; Heartsill-Scalley & Aide, 2003; Hogan et al., 2016), when excluding the high past land-use upland site, differences in vegetation structure, composition, and function were evident between the geomorphic settings of upland and riparian areas. The effect of past land use on riparian areas directly affected species richness and composition but did not eliminate riparian vs upland differences. The vegetation in riparian areas indicates a different range of

environmental conditions than those found in other geomorphic settings within the tropical wet forest landscape.

Riparian areas in tropical, warm, wet climates are known to harbor significantly more carbon than upland areas and contain a distinct species composition and vegetation structure (Dybala et al., 2019; Liu et al., 2020). In addition, riparian areas are critical for other taxonomic groups and therefore important for comprehensive landscape management beyond river and riparian conservation (Sabo et al., 2005; Dufour et al., 2019). Therefore, managers of riparian areas need to consider the characteristics that make them unique, including non-tree vegetation and the presence of higher leaf-litter inputs, compared to the upland wet forest landscape. The structural heterogeneity and high productivity found in riparian areas may be associated to the higher presence of ferns and lianas in these sites. Tropical headwater riparian zones within secondary forest are natural landscape features that may effectively conserve a variety of vegetation life forms and ecosystem processes.

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AUTHOR CONTRIBUTIONS

Both authors designed the study; TH-S collected and analyzed data and wrote the first draft of the manuscript. TAC collaborated in data analyses and reviewed manuscript drafts. Both authors wrote and approved the final manuscript.

DATA AVAILABILITY STATEMENT

The datasets collected and prepared as a part of this study are available from the EDI Data Portal under https://doi.org/10.6073/pasta/8fb57bba77e8c9a4bdfa55299bde9d83 (Accessed 2021–07–16).

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