

## Tree species distributions in relation to stream distance in a mid-montane wet forest, Puerto Rico

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**ABSTRACT.**—Riparian zones are dynamic areas adjacent to flowing freshwater that connect aquatic and terrestrial environments. We measured individual tree distances relative to two permanent streams in the Luquillo Forest Dynamics Plot, Puerto Rico, to determine if tree species exhibit distinct affinities for riparian zones in a mid-montane tropical forest. In addition, we also calculated stem density, species richness, and diversity indices in 20 x 20 m randomly selected quadrats at different distances from the streams. We found that no single species in the study site was predominantly associated with riparian zones; however, almost all species were represented by a few stems in close proximity to streams. Multivariate (Fuzzy Set Ordination) ordination of plot species composition in relation to distance to streams indicated that there is greater variation in species composition closer to streams, and less variation in species composition farther from streams. This study suggests that in mid-montane wet forest, riparian zones include all tree species found throughout the forest landscape.

**RESUMEN.**—Las zonas ribereñas son áreas de gran dinamismo adyacentes a cuerpos de agua dulce que conectan a los ambientes terrestres con los acuáticos. Para determinar si hay especies de árboles que se encuentran exclusivamente asociadas a la zona ribereña en un bosque húmedo de montaña, medimos la distancia de árboles individuales en relación a dos quebradas permanentes en la Parcela de Dinámica Poblacional del Bosque de Luquillo, Puerto Rico. También calculamos cantidad de tallos, riqueza de especies e índice de diversidad en cuadrantes 20 x 20 m que estaban a diferentes distancias de las quebradas. No encontramos especies que estuvieran exclusivamente en las zonas ribereñas, sin embargo, casi todas las especies estaban representadas cerca de las quebradas. Encontramos una densidad más alta de árboles cerca de las quebradas. Un análisis de ordenación multivariado (Fuzzy Set Ordination) a base de composición de especies y distancia a las quebradas de cuadrantes 20 x 20 m indicó que la composición de especies en cuadrantes cerca de las quebradas era más variada que la composición de especies de los cuadrantes a distancias mayores de 50 metros de las quebradas. Este estudio sugiere que en bosques húmedos de montaña las zonas ribereñas incluyen todas las especies de árboles que se encuentran en el paisaje.

**KEYWORDS.**—Luquillo Forest Dynamic Plot, Puerto Rico, riparian, streams, trees

### INTRODUCTION

Throughout the landscape, freshwater and terrestrial systems connect in dynamic and complex areas called riparian zones (Naiman and Décamps 1990, Malanson 1993, Naiman and Décamps 1997, Tabacchi et al. 1998). In montane streams, storm flows produce periodic accumulations of organic matter and nutrients from upland areas, often altering the stream channel

and making available new areas for colonization (Scatena and Lugo 1995). Species that can quickly colonize or reestablish in these areas are capable of dominating riparian zones. In general, riparian species are those that have a suite of life history and physiological attributes that allow success in the transitional and disturbance-prone environment of montane riparian zones (Tabacchi et al. 1990, Kellman and Tackaberry 1993). In some temperate biomes these

communities are composed of species that are distinct from the surrounding non-riparian landscape (Andersson *et al.* 2000, Hylander *et al.* 2002, Shafroth *et al.* 2002). It is often presumed that riparian zones harbor higher species richness and diversity due to resource availability, however, there are few estimates of how many plant species are found exclusively in riparian zones (Metzger *et al.* 1997, Decocq 2002, Sabo *et al.* 2005). Whether distinct riparian plant communities exist in mid-montane tropical wet forests, such as the Luquillo Experimental Forest, is an open question.

In the context of a wet forest, we ask (1) Is there a distinct group of tree species associated with riparian zones? and (2) Are there gradients in community metrics such as stem density or species richness as a function of distance from streams? We hypothesize that in this wet forest landscape, riparian zones may not provide a sufficiently different abiotic or environmental template to result in exclusively riparian tree species or community characteristics. To answer these questions, we analyzed individual tree species distribution patterns and plot-scale community characteristics in the 16 ha Luquillo Forest Dynamics Plot (LFDP) which has two permanently flowing streams, and where the tree species composition and previous land-use practices have been well described and documented (Thompson *et al.* 2002, Uriarte *et al.* 2004).

## METHODS

### *Study area*

The 16 ha Luquillo Forest Dynamics Plot (LFDP; southwest corner 18° 20' N, 65° 49' W), is situated within the Luquillo Experimental Forest in northeastern Puerto Rico (Fig. 1) which is part of the Luquillo Long Term Ecological Research site and the Center for Tropical Forest Science network of long term plots of the Smithsonian Tropical Research Institute. The LFDP is divided into 400 quadrats each 20 × 20 m in a 500 × 320 m grid. The plot is classified as Subtropical wet forest in the Holdridge life zone system (Ewel and Whitmore 1973), and Tropical montane forest in Walsh's

(1996) tropical climate system. The LFDP ranges in elevation from 333 to 428 m above sea level, and has annual mean precipitation of 3,500 mm almost evenly distributed throughout the year (Heartsill Scalley *et al.* 2007).

Two perennial streams, Prieta, 2nd order, and Toronja, 1st order, flow through the LFDP from east to west (Fig. 1). Average width of the stream channels is 3 m and average depth is 0.5 m (Heartsill Scalley *et al.* 2001). These are high gradient streams with small floodplain areas. The streams are not incised, and due to the presence of large boulders, stream channel elevations can be near the surrounding bank elevations. Both Prieta and Toronja streams are boulder and bedrock lined, and carry small amounts of silt, clay, and sand. Common disturbances in the Luquillo Mountains and the LFDP include tree falls, landslides, and hurricanes (Scatena and Larsen 1991, Scatena and Lugo 1995, Reagan and Waide 1996). Tree falls create small gaps in the forest canopy, while landslides produce larger disturbed areas with exposed mineral soil. Hurricanes produce large-scale effects on the forest landscape, including decrease in canopy cover, high precipitation and stream flows, and high wind velocity that increases the occurrence of tree falls and landslides. Details on the effects of hurricane Hugo on the LFDP can be found in Brokaw and Grear (1991), Thompson *et al.* (2002) and Uriarte *et al.* 2004.

The forest type in the LFDP is known as "Tabonuco" after the dominant tree, *Dacryodes excelsa*, which occurs below 600 m asl in the Luquillo Mountains (Brown *et al.* 1983). Current species composition in the LFDP is related to past land-use history and soil type, which have resulted in definable species-composition patterns in the forest landscape of the Luquillo Experimental Forest (Zimmerman *et al.* 1995, Thomlinson *et al.* 1996, Reed 1998, Thompson *et al.* 2002). The present species composition pattern includes species brought for restoring forest canopy, those left as remnants from agricultural activities, ruderal species, and non-native species that have invaded the plot (Taylor 1994, Thompson *et al.* 2002). Prior to 1932, land-use activities within the

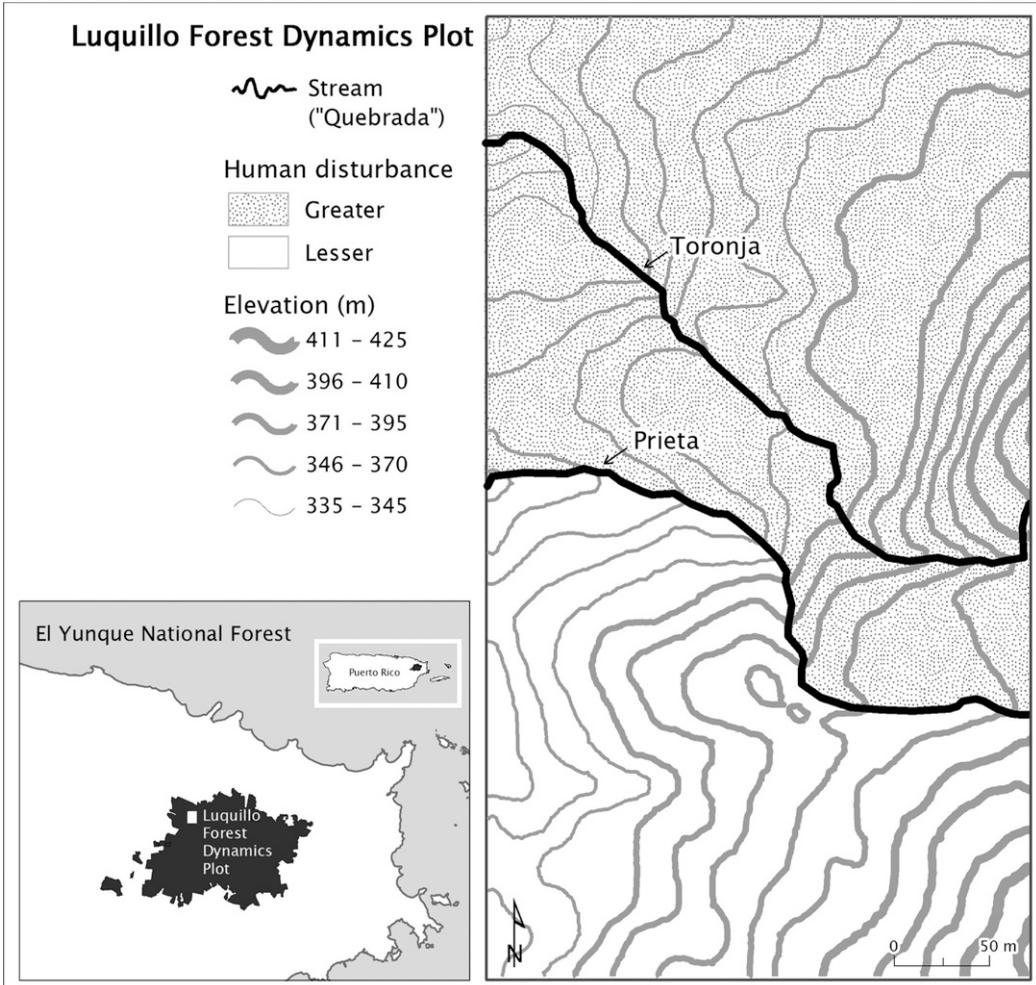


FIG. 1. Luquillo Forest Dynamics Plot (LFDP), with study streams Toronja and Prieta in relation to elevation contours and human disturbance due to previous land uses within the 16 hectare plot, located in the Luquillo Experimental Forest, northeast Puerto Rico.

LFDP area included selective logging, and subsistence agriculture. However, the forest surrounding the LFDP has remained protected since 1934 when the United States Department of Agriculture, Forest Service purchased the area. The LFDP was divided into land-cover classes based on the amount of canopy cover recorded in aerial photographs in 1936 (Thompson *et al.* 2002). These photographs reveal that the area south of Prieta stream showed the greatest canopy cover as a result of minimal human disturbance, while the area north of Prieta stream, encompassing the Toronja stream and covering the rest of the LFDP, had greater

human disturbance and less canopy cover (Fig. 1; Thompson *et al.* 2002).

#### *Luquillo forest dynamics plot dataset*

We used data from the 1989 rapid tree damage inventory taken after hurricane Hugo, (<http://luq.lternet.edu/data/lterdb60/metadata/lterdb60.htm>) as well as the plot inventory, started in 1990. During this inventory, all trees >10 cm in diameter at a height of 130 cm from the ground (DBH) were measured, identified to species, and mapped in x,y coordinates within the grid. The dataset is described

in <http://luq.lternet.edu/data/lterdb119/metadata/lterdb119.htm> and Thompson *et al.* (2002). Species identification follows the nomenclature presented in the Liogier volumes (1985-1997) and codes from Taylor (1994). For all the analyses presented, we excluded species that had five or fewer stems in the LFDP (<1%). Thus, our dataset consisted of 12,935 stems representing 60 species (Appendix 1).

#### *Calculation of distance to streams within the LFDP*

We calculated the minimum distance of individual stems to the nearest of the two streams, Prieta and Toronja, described above. This calculation was generated using the freeware program R (R Version 1.6.2 2003) using the *x,y* coordinates of each individual stem and the *x,y* coordinates of the stream channels within the LFDP. To determine the accuracy of these computer-generated distances, we randomly selected 20 individual trees and measured the actual ground distance to the nearest stream with a tape measure. We then correlated the computer-generated distances against the measured distances. The correlation between our calculated and actual measured distances was nearly 1 ( $n = 20$ ,  $r^2 = 0.97$ ). In addition to calculating minimum distances for individual stems, we also calculated the minimum distance to a stream from the southwest corner of 50 randomly chosen 20 x 20 m quadrats. We calculated mean quadrat elevation with the elevation data of the four corners of all 20 x 20 m quadrats.

#### *Community composition from random quadrats*

Fifty, 20 x 20 m quadrats were selected at random within the LFDP. The use of randomly selected quadrats was to avoid or minimize the effects of autocorrelation that occur when doing analyses based on contiguous data points as described in Harms *et al.* (2001). For each quadrat, we calculated mean elevation, number of stems, species richness, and species diversity ( $H'$ ). We used linear regressions to determine the relationship between number of stems, species richness and species diversity for each quadrat by using the minimum distance of the quadrat to the

nearest stream. In addition, we conducted linear regressions between mean elevation per quadrat and number of stems, species richness, and species diversity. We use elevation as a surrogate for soil moisture, as elevation has been shown to be a good representative variable for the abiotic environment of this forest (Thompson *et al.* 2002).

We repeated these analyses using another 50 randomly selected quadrats from the minimally disturbed area south of Prieta stream, in the southern part of the LFDP (Fig. 1) to control for previous land-use effects on analysis of quadrat community characteristics. This was done to assess the potential effect of previous land use in the LFDP (human use of the forest resources as described in the Study area section under Methods) on riparian tree species distribution and composition patterns. Thus, we conduct all analyses twice, once with the complete LFDP data set and then only with the data from the area south of the Prieta stream, with minimal human disturbances from previous land uses (Fig. 1).

All community metrics and regressions were assessed at a statistical level of significance of  $P < 0.05$ , and computed using the program SAS (Version 9, SAS Institute 2004). Using the data on species and abundances per quadrat from both the 50 random quadrats from the whole LFDP and then on those from the minimally disturbed area south of the Prieta stream, we generated similarity matrices (Sorensen's index) of species abundance per quadrat using the program R and its *Labdsv* and *Vegan* packages (R Version 1.6.2, 2003). We performed Fuzzy Set Ordination (FSO) analysis on the similarity matrices. The FSO analysis creates an axis that is relativized (zero to one) using both a vector variable and the similarity matrix (Roberts 1986). In this study, the environmental vector variable was the minimum distance to the nearest stream of the southwest corner of each quadrat. The resulting relativized axis is termed the "apparent distance to stream," based on the similarity matrix of species abundance, and distance to stream of the quadrat. In this way, the environmental vector of "distance to stream" is used to predict the species composition of the quadrats, and their variation in relation

to the environmental variable, in this case, distance to stream (Roberts 1986).

RESULTS

*Individual species distributions in relation to stream distance*

For all species in the study area, the median distance of occurrence was >20 m away from streams. No species was completely distributed in the LFDP with median distance of <20 m away from the streams. For six species, *Clusia rosea*, *Coccoloba diversifolia*, *Margaritaria nobilis*, *Ixora ferrea*, *Trichilia pallida*, and *Guettarda valenzuelana*, median distance to the streams was between 21 and 29 m, however standard deviation values were large (Appendix 1). Of these six species with median distance of <30 m, all except *C. rosea* also had stems at distances greater than 100 m from the streams.

Although no species occurred at a median distance of 20 m or less from streams, 56 of the 60 species had at least one stem within 20 m of a stream (Fig. 2, Appendix 1). Two species, *M. nobilis* and *C. diversifolia*, are

more predominant within 30 to 40 m of streams. The four species that did not have stems in the first 20 m away from the streams were *Calophyllum antillanum* (previously known as *calaba*), *Eugenia domingensis*, *Myrcia leptoclada*, and *Pterocarpus officinalis*.

In terms of percentiles of the total distribution of stems, no species were observed to have 75 percent of their stems at a distance of 20 m away from the streams. However, we observed that 75 percent of the stems of *M. nobilis* and *C. diversifolia* occurred between 30 and 40 m from the streams. Seventy five percent of the stems of *C. rosea*, *Guatteria caribaea*, *G. valenzuelana*, *Byrsonima wadsworthii*, and *Eugenia stahlII* occurred at distances between 40 and 50 m away from the streams (Appendix 1).

*Community metrics and composition based on quadrats*

The community metrics of 50 quadrats within the whole LFDP, revealed a significant relationship between stem density and distance to streams; the overall number of stems increased with proximity to the

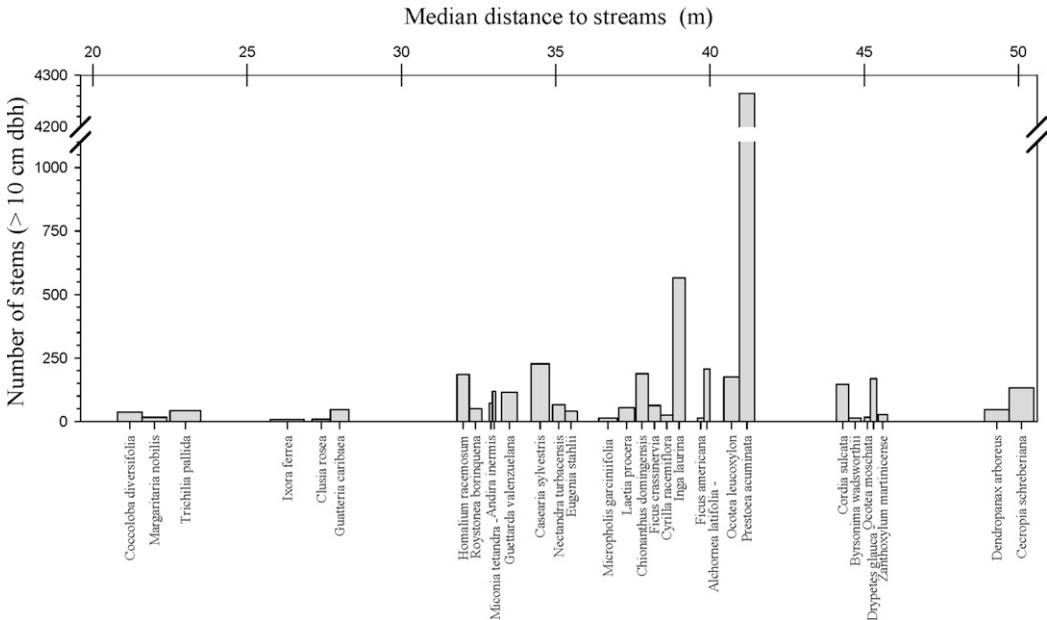


FIG. 2. Median distance to streams and number of stems per tree species in the 16 ha Luquillo Forest Dynamics Plot (LFDP), Puerto Rico. Data presented for species with median distance to streams of ≤ 50 meters only. See Appendix 1 for median distances of all species.

TABLE 1. Linear regressions of distance to stream with plant community characteristics of randomly selected 20 x 20 m quadrats in the LFDP ( $n = 50$ ) and south of Prieta stream ( $n = 50$ ). Asterisks\* represent significant differences.

|                 | Whole LFDP |       |         | South of QP |       |         |
|-----------------|------------|-------|---------|-------------|-------|---------|
|                 | $r^2$      | $F$   | $P$     | $r^2$       | $F$   | $P$     |
| Number of stems | 0.3510     | 26.51 | <.0001* | 0.1849      | 10.89 | 0.0018* |
| Richness        | 0.0399     | 2.04  | 0.1597  | 0.2150      | 13.15 | 0.0007* |
| Diversity (H')  | 0.0027     | 0.14  | 0.7148  | 0.2265      | 14.06 | 0.0005* |

streams (Table 1). There was no relationship between species richness and distance to streams, or diversity and distance to streams. Although there was a significant positive relationship between mean elevation of quadrat and distance to stream ( $r^2 = 0.390$ ,  $F_{1,48} = 30.73$ ,  $P < 0.001$ ), there was no relationship between mean quadrat elevation and number of stems, species richness, or diversity (all values  $r^2 < 0.02$ ,  $F < 1.02$ ,  $P > 0.32$ ). There was no relationship between stem diameter and quadrat distance to stream. When we regressed species richness and stem density against elevation, we again found no significant relationship. Two percent of variation in species richness was explained by elevation ( $F = 1.03$ ,  $P = 0.315$ ), while only 0.3 percent was explained for stem density ( $F = 0.18$ ,  $P = 0.672$ ).

In the analysis of community composition using FSO (Fig. 3), we found a significant relationship between species abundance and composition as a function of stream distance. The FSO indicated that there was a relationship between species composition of quadrats and distance to streams ( $r^2 = 0.439$ ,  $F_{1,48} = 11.48$ ,  $P = 0.001$ ; Fig 3a). At distances of less than 50 m away from the nearest stream, we observed greater differences among quadrats in species composition. At distances greater than 50 m from the streams, however, composition was much more similar among quadrats. The ordination analysis indicates that there is greater variation in species composition closer to streams at the quadrat level, and less variation in species composition farther from streams. When analyzing community metrics in the minimally disturbed area, south of Prieta stream, there was a significant relationship between increased stem density, species richness, and

diversity as distance to stream decreased (Table 1). In the FSO analysis using random quadrats from the minimally disturbed area (Fig 3b), environmental factors related to distance from the Prieta stream also seemed to exert an influence on species composition ( $r^2 = 0.533$ ,  $F_{1,48} = 19.49$ ,  $P < 0.0001$ ). The decreased scatter of quadrats at distances greater than 50 m south of Prieta stream suggests that species composition and abundance may be more limited at distances greater than 50 m from the stream (Fig. 3b). Within 50 m of the stream a greater range of species associations are possible, whereas more than 50 m away from the stream there is a limited number of possible species compositions in each quadrat.

## DISCUSSION

### *Individual species distributions in relation to stream distance*

Most tree species throughout the LFDP seem to be spatially distributed independent of stream locations. Reed (1998) found that none of the four most common species found in riparian areas of the LFDP had more than 30 percent of their total plot population in the riparian area. Species such as *Guarea guidonia* and *Prestoea acuminata* (previously known as *montana*) that have been observed to be associated with valley bottoms in the Luquillo Mountains (Basnet 1992), were no more or less common at any distance from these streams. Riparian areas in montane regions lack well-defined valleys and floodplains, and the boundary defining the stream edge is abrupt (Malanson 1993). In headwater streams of montane regions, there can be an overlap of vegetation found in the adjacent forest, slopes, and upland areas because the smaller valleys and

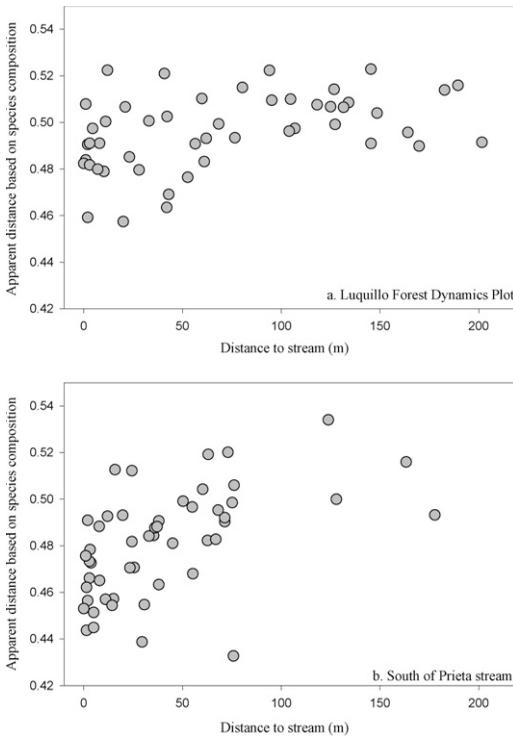


FIG. 3. Plot of ordination analysis (Fuzzy Set Ordination; FSO) based on species abundance and distance to stream for 50 randomly chosen quadrats from (a) the whole LFDP and (b) the minimally disturbed south of Prieta stream.

floodplains reduce the development of a riparian zone (Pinay *et al.* 1990, Wissmar and Swanson 1990).

The distribution of species not found close to the streams, *C. antillanum*, *E. dominicensis*, *M. leptoclada*, and *P. officinalis* could be a result of a combination of total low numbers of stems and/or previous land-use practices such as enrichment planting and harvesting. In the 1940s *C. antillanum*, a native, was planted to recover the canopy in a small area in the northeastern part of the LFDP. This area corresponds to the area of lowest observed canopy cover in the 1936 aerial photographs, north of the Toronja stream (Thompson *et al.* 2002). The distribution of *E. dominicensis* and *P. officinalis* may be the result of harvesting prior to 1932; *E. dominicensis* was used for posts and fuel, while *P. officinalis*, known to have riparian distributions in the Luquillo Mountains, was locally used for fishnet floats and gold

panning (Little and Wadsworth 1995). The only non-native tree species in our LFDP data set, *Syzygium jambos*, another tree previously used for fuel, was not observed close to the streams. However, *S. jambos* is a common non-native tree found along other riparian areas in Puerto Rico (Heartsill-Scalley and Aide 2003, Brown *et al.* 2006). Our dataset only included stems >10 cm DBH, therefore the many small stems of *S. jambos* which are present along parts of the streams in the LFDP could eventually become common along the riparian areas (Heartsill Scalley pers. obs.).

#### Community metrics and distance from streams

Both in the entire LFDP and in the minimally disturbed southern area, stem density was highest with proximity to streams (Table 1). Although randomly sampled quadrats showed no clear relationship with stream distance in terms of richness and diversity in the LFDP as a whole, in the minimally disturbed area, richness and diversity values were higher closer to the streams. The combination of these results is best described in the pattern observed in the FSO, where there is a relationship between distance to stream and community composition, indicating greater variation in species composition closer to streams, and less variation in species composition farther away from streams. Environmental factors related to distance from streams, such as light from the open canopy above streams and humidity from the continuously flowing water, may be contributing to affect species distribution. There appears to be a signature of the riparian environment independent of the known land-use history effects on species composition in the LFDP as the plots selected from the minimally disturbed area and the plots selected from the whole LFDP gave similar results related to distance from streams in the FSO analysis.

Species composition in plots (Fig. 3) seems to suggest that at a distance of less than 50 m from streams there could be riparian or stream-side "edge effect". In this forest, maximum tree height is an average of 20 m (Brokaw and Grear 1991), so the observed riparian edge effect can be

thought of as approximately two canopy tree heights. This riparian effect may be indicative of greater environmental heterogeneity and/or enhanced resources near the streams (Gascon *et al.* 2000, Ries and Sisk 2004). For example, the differences in species composition of plots closer to the streams could be due to greater heterogeneity in microclimate (light and moisture) conditions compared to the rest of the forest further away from stream and the riparian edge effect. In this case, qualities of the environment, such as microclimate, are enhanced or concentrated in the riparian areas compared to the areas further away from the streams. This could result in a positive or complementary response (*sensu* Ries and Sisk 2004) in terms of the number of stems and species composition in the first 50 m from the streams.

Several studies in large tropical forest plots have analyzed species distributions in relation to topographic and edaphic conditions and, in general, have observed very few explicit species associations with environmental variables (Harms *et al.* 2001, Gunatilleke *et al.* 2004, Valencia *et al.* 2004). In the 25 ha wet forest plot in Sinharaja, Sri Lanka, where there is no distinct dry season, the lowest elevation in the plot corresponds to two perennial low-order streams and an increase in elevation occurs with increasing distance from the streams (Gunatilleke *et al.* 2004). Although not directly assessing species associations in riparian areas, Gunatilleke *et al.* (2004) found a pattern of species richness in Sinharaja similar to that found in our study, in that there is greater richness close to the streams. In contrast to our results, they found higher tree density occurring at greater distance from the stream, which in Sinharaja, corresponds to > 100 m increase in elevation from valley bottom to ridge top. Preliminary analyses of the 50 ha wet forest plot in Yasuní, eastern Ecuador, which has a distinct dry season, indicated that only a quarter of the species in the plot had abundance differences that could be attributed to topographic positions defined as valley or ridge top (Valencia *et al.* 2004). A "valley" in this location, relates to areas close to several low order perennial streams and a small swamp that occurs in the Yasuní plot. Although they found

less similarity between plots in ridges compared to plots in valleys, half of the species had only slight differences in abundance between valley and ridges. Valencia *et al.* (2004) conclude that only 8 percent of the species in the plot were associated to valleys, and that most species could be considered generalists. In a Panamanian tropical moist forest with non-perennial streams, Harms *et al.* (2001) found that there were differences in the physical environment of the plot, including intermittent streams and a seasonal swamp. Yet very few tree species were distinctly associated with these habitats. In our 16 ha plot, historical and environmental circumstances may have contributed to the species composition differences in relation to distance from streams. Historically it is possible that proximity to stream channels may have afforded some protection to primary native forest tree species.

#### *Connecting previous land-use history and natural landscape features*

Previous land-use decisions and management practices were based on the perception of the features of the natural landscape. Features such as mountain passes, ridges, and valleys are generally considered as connections, while streams, rivers, and steep slopes are generally perceived as barriers (Turner 1989, Forman 1995). These landscape features also contributed to outlining land-use decisions relating to accessibility and transportation of cultivable (such as coffee, bananas) and harvestable resources (such as timber, fire wood, charcoal). With the information provided by long-term data, we now have a better understanding of the effects of previous land-uses on forest structure, composition, and regeneration (Thompson *et al.* 2002, Grau *et al.* 2003, Lugo 2004, Uriarte *et al.* 2004). Even though there is a very clear pattern of species composition resulting from previous land-use practices in the LFDP, these practices occurred within the context of the present natural landscape features such as stream channels, and the combination of these have a cumulative effect on forest structure and composition.

Riparian areas are natural refuge and buffer zones within forested landscapes.

Vegetation in riparian areas can reduce the extent of events such as fires (Kellman and Tackaberry 1993), serve as a spatial refuge during drought and other climate changes (Aide and Rivera 1998), and maintain species richness in areas with anthropogenic disturbance (Heartsill Scalley and Aide 2003). Riparian areas not only link aquatic and terrestrial ecosystems, but also contribute to the maintenance of species diversity in forested landscapes (Lyon and Sagers 1998). Therefore, maintenance and conservation of riparian areas will contribute to the diversity of the entire forest landscape (Sabo *et al.* 2005). This study suggests that in mid-montane wet forests, riparian areas include all species present within the forest landscape at higher densities.

*Acknowledgements.*—We recognize the work of all the people involved in the establishment and inventory of the LFDP. We thank the founders of the LFDP, Robert B. Waide, D. Jean Lodge, Charlotte M. Taylor, and Edwin M. Everham III, the many members of the field teams who inventoried the plot, and John Thomlinson who assisted with the tree maps. Eda Meléndez-Colóm, the Information Manager of the Luquillo LTER site, assisted with data sets. Funds for the LFDP have been contributed by National Science Foundation (NSF) SGER grant BSR-9015961, and NSF Long Term Ecological Research grants BSR-9911902 and BSR-8811764 to the Institute for Tropical Ecosystem Studies, University of Puerto Rico (UPR) and the International Institute for Tropical Forestry. Funds were also provided through grants (RII-880291 and HRD-935349 from NSF to UPR Center for research Excellence in Science and technology. F. N. Scatena, Steven A. Sloan, P. L. Weaver, and Karen Wolfe reviewed previous drafts of this manuscript. Dave W. Roberts, Montana State University, contributed to data analysis while T. del M. López, University of Puerto Rico, contributed with the site figure. The Ecology Center and the College of Natural Resources, Utah State University, provided financial support for Tamara Heartsill Scalley. The International Institute for Tropical Forestry, USDA FS in Rio

Piedras, Puerto Rico provided logistical support.

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APPENDIX 1. Median distance to stream of all species in the LFDP. Stems = total stems, Median = median distance to streams in meters, SD = standard deviation, 75% = distance from streams at which 75% of stems occur, Min = minimum distance, and Max = maximum distance.

| Species  | Stems | Median | SD   | 75%   | Min  | Max   |
|--|-------|--------|------|-------|------|-------|
| <i>Coccoloba diversifolia</i>                          | 37    | 21.2   | 28.4 | 36.8  | 1.1  | 123.1 |
| <i>Margaritaria nobilis</i>                            | 16    | 22     | 33.9 | 38.6  | 4.4  | 148.6 |
| <i>Trichilia pallida</i>                               | 42    | 23     | 45.8 | 58    | 0.7  | 203   |
| <i>Ixora ferrea</i>                                    | 7     | 26.3   | 57   | 110.8 | 13.6 | 158   |
| <i>Clusia rosea</i>                                    | 8     | 27.4   | 18.2 | 48.9  | 12.2 | 59.2  |
| <i>Guatteria caribaea</i>                              | 47    | 28     | 44.3 | 48.9  | 10.4 | 164.6 |
| <i>Homalium racemosum</i>                              | 185   | 32     | 46.6 | 57    | 0.07 | 254.3 |
| <i>Roystonea borinquena</i>                            | 50    | 32.4   | 52.2 | 60.4  | 2.4  | 201.9 |
| <i>Andira inermis</i>                                  | 72    | 32.9   | 48.3 | 75.4  | 1.4  | 195.7 |
| <i>Miconia tetrandra</i>                               | 118   | 33     | 50.7 | 66.2  | 0.83 | 202   |
| <i>Guettarda valenzuelana</i>                          | 115   | 33.5   | 28.1 | 45.5  | 0.66 | 218   |
| <i>Casearia sylvestris</i>                             | 227   | 34.5   | 51.2 | 65.9  | 0.84 | 234.1 |
| <i>Nectandra turbacensis</i>                           | 66    | 35.1   | 55.6 | 80.7  | 2.2  | 194.3 |
| <i>Eugenia stahlia</i>                                 | 40    | 35.5   | 48.4 | 43.6  | 1.2  | 180.6 |
| <i>Micropholis garciniifolia</i>                       | 13    | 36.7   | 30.5 | 76.4  | 9.4  | 112   |
| <i>Laetia procera</i>                                  | 54    | 37.3   | 52   | 72.3  | 3.8  | 203.2 |
| <i>Chionanthus domingensis</i>                         | 188   | 37.8   | 36.3 | 61    | 1.3  | 183   |
| <i>Ficus crassinervia</i>                              | 63    | 38.2   | 31.8 | 53.9  | 0.9  | 233.4 |
| <i>Cyrilla racemiflora</i>                             | 24    | 38.6   | 21.1 | 51.5  | 1.7  | 75.5  |
| <i>Inga laurina</i>                                    | 566   | 39     | 56   | 96.5  | 0.83 | 249.6 |
| <i>Ficus americana</i>                                 | 13    | 39.7   | 63.4 | 101.6 | 6.3  | 130.1 |
| <i>Alchornea latifolia</i>                             | 207   | 39.9   | 53.4 | 100.5 | 1.2  | 250.1 |
| <i>Ocotea leucoxydon</i>                               | 175   | 40.7   | 49.4 | 77    | 2.3  | 241.3 |
| <i>Prestoea acuminata</i> (previously <i>montana</i> ) | 4265  | 41.2   | 54.6 | 95.1  | 0.1  | 255.6 |
| <i>Cordia sulcata</i>                                  | 146   | 44.3   | 56.6 | 92.3  | 1.2  | 240.9 |
| <i>Byrsonima wadsworthii</i>                           | 13    | 44.7   | 20.9 | 50.1  | 12   | 102.1 |
| <i>Ocotea moschata</i>                                 | 16    | 45.1   | 63.7 | 88.9  | 0.7  | 213.2 |
| <i>Drypetes glauca</i>                                 | 168   | 45.3   | 48.8 | 85.9  | 0.8  | 227.3 |
| <i>Zanthoxylum martinicense</i>                        | 27    | 45.6   | 61.5 | 94.3  | 4.3  | 247.5 |
| <i>Dendropanax arboreus</i>                            | 47    | 49.3   | 43.3 | 87.4  | 1.2  | 142.4 |
| <i>Cecropia schreberiana</i>                           | 132   | 50.1   | 51.4 | 106.5 | 1    | 176.3 |
| <i>Syzygium jambos</i>                                 | 21    | 50.8   | 31.8 | 55.8  | 10.6 | 114.4 |
| <i>Matayba domingensis</i>                             | 267   | 51.9   | 49   | 76.6  | 0.6  | 216   |
| <i>Tabebuia heterophylla</i>                           | 337   | 54.4   | 55.8 | 92.9  | 1.1  | 212.7 |
| <i>Buchenavia tetraphylla</i>                          | 189   | 56     | 55.8 | 101.8 | 1.4  | 235.1 |
| <i>Sapium laurocerasus</i>                             | 158   | 56.2   | 60.4 | 128.7 | 0.7  | 229.4 |
| <i>Cordia borinquensis</i>                             | 10    | 57.1   | 49.4 | 120.8 | 10.6 | 130.3 |
| <i>Ormosia krugii</i>                                  | 121   | 59.4   | 43.5 | 80.9  | 3.4  | 221.2 |
| <i>Casearia arborea</i>                                | 1106  | 59.4   | 53.8 | 110.3 | 1.7  | 222.5 |
| <i>Dacryodes excelsa</i>                               | 1037  | 61.1   | 49.3 | 100.3 | 2.2  | 220.9 |
| <i>Myrcia leptoclada</i>                               | 10    | 62.5   | 45.6 | 107.5 | 31   | 177.3 |
| <i>Tetragastris balsamifera</i>                        | 125   | 64     | 59.8 | 148.7 | 7.3  | 206.8 |
| <i>Myrcia splendens</i>                                | 86    | 65.2   | 75.5 | 165   | 1.3  | 255.3 |
| <i>Hirtella rugosa</i>                                 | 13    | 65.5   | 50.6 | 79.9  | 11.9 | 195.8 |
| <i>Pseudolmedia spuria</i>                             | 12    | 68.3   | 40.2 | 118.4 | 6.6  | 123.5 |

## APPENDIX 1. Continued.

| Species   | Stems | Median | SD   | 75%   | Min   | Max   |
|---|-------|--------|------|-------|-------|-------|
| <i>Inga vera</i>  | 64    | 69     | 58.3 | 113.6 | 1     | 255.5 |
| <i>Schefflera morototoni</i>                              | 202   | 69.5   | 54.9 | 113.3 | 0.9   | 247.6 |
| <i>Manilkara bidentata</i>                                | 692   | 70.2   | 58.2 | 126   | 0.75  | 224   |
| <i>Myrcia deflexa</i>                                     | 12    | 74.3   | 65.5 | 137.2 | 2.6   | 195   |
| <i>Guarea guidonia</i>                                    | 308   | 75     | 63   | 135.4 | 1.1   | 248.8 |
| <i>Alchorneopsis floribunda</i>                           | 91    | 79.2   | 52.8 | 120.5 | 0.04  | 198   |
| <i>Croton poecilanthus</i>                                | 131   | 80     | 49.5 | 122.5 | 3.5   | 212   |
| <i>Calycogonium squamulosum</i>                           | 9     | 80.5   | 46.8 | 121.7 | 17.9  | 171.6 |
| <i>Eugenia domingensis</i>                                | 7     | 82     | 24.3 | 100   | 49.6  | 117.1 |
| <i>Sloanea berteriana</i>                                 | 531   | 88.2   | 51   | 126   | 0.8   | 246.7 |
| <i>Guarea glabra</i>                                      | 8     | 138.6  | 69.9 | 178   | 7.3   | 204.6 |
| <i>Byrsonima spicata</i>                                  | 156   | 142.2  | 49.8 | 167.2 | 3     | 219.6 |
| <i>Meliosma herbertii</i>                                 | 6     | 147.8  | 94.7 | 223   | 11    | 224   |
| <i>Calophyllum antillanum</i> (previously <i>calaba</i> ) | 61    | 150.8  | 22.2 | 159.5 | 101.8 | 182   |
| <i>Pterocarpus officinalis</i>                            | 6     | 254.6  | 2.5  | 257.8 | 252.3 | 258   |

Please cite this article as:

Heartsill Scalley, T.; Cowl, T.A.; Thompson, J. 2009. Tree species distributions in relation to stream distance in a mid-montane wet forest, Puerto Rico. *Caribbean Journal of Science*. 45(1):52-63.