

Research Article

Structure, diversity and the conservation value of tropical dry forests in highly fragmented landscapes

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Handling Editor: Michael O'Brien

Received: 15 November 2021, **First Decision:** 15 December 2021, **Accepted:** 8 January 2022, **Online Publication:** 9 March 2022

Abstract

Although tropical dry forests are among the most degraded and fragmented biomes in the world, we still have a poor understanding of their basic ecological features and conservation status, particularly in the Neotropics. Here, we assess the diversity, composition, structure and conservation value of tropical dry forests in a highly fragmented landscape in Nicaragua. We established 31 plots and transects in and along river corridors, secondary forests, living fences and pasture-woodlands. We recorded all trees with diameters at breast height ≥ 2.5 cm using Hill numbers (qD , where $q = 0, 1$ or 2) and estimated the richness and diversity of trees in each forest type. We calculated the Importance Value Index (IVI) to species and family levels and, finally, performed a Non-Metric Multidimensional Scaling (NMDS) ordination and an Analysis of Similarities (ANOSIM) using the Bray–Curtis index of similarity. Diversity (1D , 2D) but not species richness (0D) differed between forest types ($P = 0.01$ and 0.66 , respectively). IVI was highest for the legume family Fabaceae, followed by the Moraceae and Malvaceae (27.8, 11.1 and 10.5, respectively). *Vachellia pennatula*, *Guazuma ulmifolia* and *Bursera simaruba* had IVIs $>30\%$, the former two being the most abundant trees in all forest types. An analysis of community similarity revealed that each forest type had a distinct composition ($P < 0.01$, $R^2 = 0.30$), thereby underlining the importance of conserving all these different types of land cover.

Keywords Fabaceae, fragmentation, Hill numbers, matrix composition, Importance Value Index, river corridor, tropical dry forests

破碎化景观格局中热带干旱森林的结构、多样性与保护价值

摘要: 尽管热带干旱森林是世界上退化和破碎化程度最严重的生物群落之一, 但我们对它们的基本生态特征和保护状况仍然知之甚少, 尤其是在新热带地区。在本研究中, 我们对尼加拉瓜破碎化景观格局中的热带干旱森林的多样性、组成、结构和保护价值进行了评估。我们在河流廊道、次生林、绿篱和林间牧地之中和沿线地区建立了31处样地和样带。我们使用希尔数(Hill number)对胸高处直径 ≥ 2.5 cm的所有树木进行了记录, 并对每种森林类型中树木的丰富性和多样性进行了估算, 接着计算

了种级分类和科级分类上的重要值指数(Importance Value Index, IVI), 最后则使用Bray-Curtis相似性指数进行了非度量多维标度(Non-Metric Multidimensional Scaling, NMDS)排序和相似性分析(Analysis of Similarities, ANOSIM)。不同森林类型之间在多样性上存在差异, 但物种丰富度却不存在差异。豆科植物的IVI值最高, 其次是桑科植物和锦葵科植物。*Vachellia pennatula*、*Guazuma ulmifolia*和*Bursera simaruba*的IVI值都>30%, 其中前两种是所有森林类型中最为丰富的树木。对群落的相似性进行分析后可知每种森林类型都有着不同的组成, 从而凸显了对所有这些不同类型的土地覆盖开展保护的重要性。

关键词: 豆科植物, 破碎化, 希尔数(Hill number), 重要值指数, 河流廊道, 热带干旱森林

INTRODUCTION

Despite the extremely rich diversity of organisms and high levels of endemism they harbor, tropical dry forests (TDFs) are among the most threatened and degraded of all biomes on Earth (Banda *et al.* 2016). Moreover, worldwide around 97% of the remaining areas of TDFs are severely endangered due to a variety of anthropogenic pressures (Miles *et al.* 2006). These forest ecosystems are characterized by deciduous plant species that are well adapted to the extremely uneven distribution of the otherwise limited precipitation—typically <1800 mm a year—and to the mean annual temperature of >25 °C (Gentry 1995; Gillespie *et al.* 2000; Murphy and Lugo 1986; Sánchez-Azofeifa *et al.* 2005). About 66.7% of the 1 million km² of TDF estimated still to exist lie within the tropical belt of the American continents (Miles *et al.* 2006). These forests provide many ecosystem services including carbon storage, the conservation of nutrient cycles, and water storage and supply (Portillo-Quintero *et al.* 2015) that are indispensable for human society (Balvanera *et al.* 2011; Becknell *et al.* 2012; Calvo *et al.* 2017; Maass *et al.* 2005; Portillo-Quintero *et al.* 2015). However, only 3.9% of the TDF remnants in the Americas are legally protected (Portillo-Quintero and Sánchez-Azofeifa 2010). Globally, land-use changes have already affected 48.5% of the world's TDFs (Hoekstra *et al.* 2005) and, for instance, 66% and 77% of their original surface area in North and South America, and Nicaragua, respectively, have been permanently converted to agricultural production (Portillo-Quintero and Sánchez-Azofeifa 2010). Stevens *et al.* (2001) report that, as a consequence of human pressure, just <1% of primary TDFs remain in Nicaragua. Likewise, recent reports have estimated that up to 661,307 ha of TDFs were lost during 2001–2013 in Central and North America, including 51,336 ha in Nicaragua,

the second highest rate of deforestation in the Central American region (Portillo-Quintero and Smith 2018).

Most TDFs are highly fragmented due, above all, to the agricultural practices and economic activities that can easily sidestep the low protection level these forests enjoy (Miles *et al.* 2006; Portillo-Quintero and Sánchez-Azofeifa 2010). Cattle grazing, invasive species and wildfires caused by humans are among the main drivers of forest degradation (Dimson and Gillespie 2020). Domestic cattle in TDFs in the Neotropics, however, are an efficient agent for the dispersal of many TDF tree species preadapted to endozoochory by large mammals, and fire is known to trigger the germination of physically dormant seeds (Janzen and Martin 1982; Peguero and Espelta 2014). The combination of seed dispersal by cattle and frequent pasture fires is a powerful driver that favors a specialized subset of TDF tree species (Peguero and Espelta 2014). Nevertheless, cattle grazing in early successional patches of TDFs seriously reduces the ability of new seedlings and saplings to become established, thereby further degrading these already fragile ecosystems (Hester *et al.* 2006; Quisheuatl-Medina *et al.* 2020).

Landscape fragmentation modifies alpha and beta diversities since it leads to the establishment of new environmental filters and assemblages, and the more than likely disappearance of other assemblages from the landscape matrix (Halffter and Moreno 2005). Although habitat loss provokes important changes in species richness and community structure (Pardini *et al.* 2010), the composition and configuration of the landscape matrix may also be key in the eventual recovery of many taxa. In a low-quality matrix (e.g. roads, annual crops and built-up areas), the mortality of forest species is very high, whereas in high-quality landscape matrices (e.g., arboreal crops and agroforestry systems), the survival of forest species is high (Arroyo-Rodríguez *et al.* 2020). Matrix

composition in farmland explains 30%–40% of the great variation in biodiversity thresholds of mammals and birds (Ochoa-Quintero *et al.* 2015). Boesing *et al.* (2018) found that once the loss of forest cover reaches a critical threshold of around 20%, the fall in avian taxonomic and phylogenetic diversity is abrupt. Thus, matrix quality and, particularly, forest cover play a major role in determining patterns of species richness not only in plants but also in invertebrates, birds, amphibians and reptiles (Reider *et al.* 2018).

Despite the great fragmentation of most TDFs and the many pressures they have to withstand, we lack any full evaluation of their conservation status and the quality of the landscape matrix at local level (Arroyo-Rodríguez *et al.* 2020; Gillespie *et al.* 2000). In particular, we still have little knowledge of the richness and composition patterns of TDF patches in highly fragmented and degraded landscapes. Filling this gap is crucial if we are to successfully implement plans to restore TDFs at a landscape scale. Efforts should be directed towards enhancing biodiversity conservation and recovering ecosystem functions and services including climate regulation, water supplies, crop pollination and biological agricultural pest control (Arroyo-Rodríguez *et al.* 2020). Here, we address this issue by studying the structure, diversity and conservation value of the main TDF types remaining in Nicaragua. We selected river corridors (RC), secondary forests (SF), living fences (LF) and pasture woodlands (PW) because they are the TDF types most commonly found in highly human-modified landscapes (Arroyo-Rodríguez *et al.* 2020). Specifically, we evaluated which forest types retain structures and diversities that are similar to those of other better-preserved TDFs and so could contribute in the future to the spread and restoration of these valuable but endangered ecosystems.

MATERIALS AND METHODS

Study area and sampling

This study was carried out in the upper part of the water catchment of the river Estelí between the natural reserves of Tomabú (13°01'43" N, 86°17'51" W), Quiabúc Las Brisas (13°07'31" N, 86°26'01" W) and Tisey La Estanzuela (12°59'30" N, 86°22'46" W) in northern Nicaragua at an altitudinal range of 620–1470 m a.s.l. (Fig. 1a). Over the past 10 years, the average temperature and precipitation were 23.1 °C and 892 mm year⁻¹, respectively, and the annual water deficit –385.4 mm year⁻¹ (Gómez *et al.*

2021). The study area has a long history of habitat fragmentation due to the conversion of forests into pasture for livestock. This trend can be traced back to the second half of the twentieth century and the rise of extensive cattle ranching and coffee production in the area, which peaked during the first decade of the twenty-first century (Ravera 2007). A detailed study of land-use change showed that by 2011 only 37.7% of the area was covered by forest fragments, with an additional 26.3% being extremely degraded or consisting only of early successional secondary patches (Ruiz *et al.* 2013). It should be noted, however, that the study by Ruiz *et al.* (2013) was carried out in a protected landscape, so the figures for forest loss and fragmentation are even more alarming in our study sites that lack any kind of management regulation or legal protection. We used Google Earth satellite images (Gorelick *et al.* 2017) to select fragments that were representative of the landscape. Additionally, we used a Landsat-8 satellite image with 30 m resolution taken on 20 August 2020 to assess the different land-cover types in the area. We determined the Normalized Difference Vegetation Index (NDVI) using bands 4 and 5 with ArcGis V.10 software. Of the 53 652 ha of our study area, currently 74.3% are devoted to pasturing and other agricultural purposes (39 871 ha), about 10% (5380 ha) is bare ground including roads and built-up areas, 12.9% (6911 ha) is covered by sparse forest vegetation at different successional stages and only 2.8% (1490 ha) is recognizably covered by dense forest vegetation (Fig. 1b).

We established sampling plots for pasture woodlands (PW: pasture grasslands with scattered trees, $N = 8$) and secondary forests (SF: closed forest patches at different successional stages, $N = 7$) and transects for living fences (LF: rows of trees used to delimit properties, $N = 8$) and river corridors (RC: the forest fragments that typically line water courses, both permanent and intermittent, $N = 8$). The SF plots, set up following standard procedures for floristic inventories (Gentry 1982, 1988), consisted of 1000 m² divided into ten 2 m × 50 m transects, 2 m apart; the RC plots consisted of two 50 m × 10 m transects (1000 m²), one on either side of the river (Sánchez-Merlos *et al.* 2005); for the LF, we recorded all individuals along a transect of 2 m × 350 m (750 m²), and for PW, 1-ha (10 000 m²) plots were established. We then measured and recorded all trees with diameters at breast height (DBH) ≥2.5 cm in each plot. For

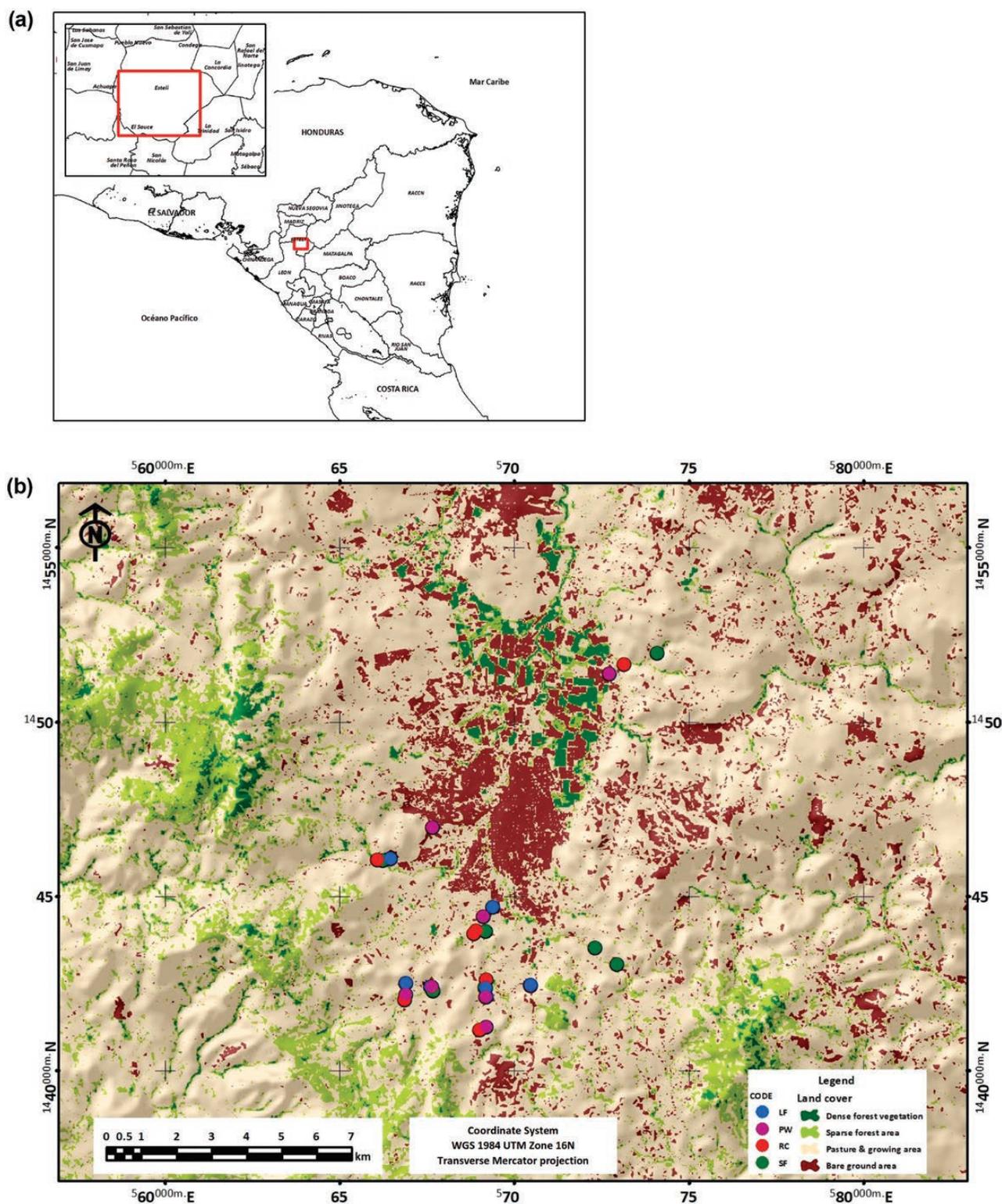


Figure 1: (a) Map with the location of the study area. (b) Map of the land-use cover in the study area. Red, blue, green and purple circles show the location of transects along river corridors (RC) and living fences (LF), and of plots in secondary forests (SF) and pasture woodlands (PW), respectively. Land cover types are as follows: dense forest vegetation (dark green), sparse forest vegetation (light green), pasture and agricultural areas (light brown) and bare ground built-up areas (dark brown).

atypical individuals with buttresses or more than one trunk or on steep slopes, DBH was measured following the recommendations in Aranda *et al.* (2005) and Camacho (2000). All recorded trees were identified to species and family levels using the Flora de Nicaragua database (Stevens *et al.* 2001).

Data analysis

We compared the diversity of the different TDF types using Hill numbers (Hill 1973; Jost 2006) and the R library iNEXT (Hsieh *et al.* 2016). We used Hill numbers since they allow us to calculate the effective number of species—or true diversity (qD)—present in a community (Hill 1973) and are considered to be equivalent to diversity indices (Jost 2006). Hill numbers are defined for $q \neq 1$ as

$${}^qD = \left(\sum_{i=1}^S P_i^q \right)^{1/(1-q)} \quad (1)$$

where qD is the effective species richness, S the number of species in the assemblage and the i th species has a relative abundance P_i . The parameter q determines the sensitivity of the measure to the relative abundances (Chao *et al.* 2014). Hill numbers of order 0 (0D) correspond to species richness without considering abundance and so award high values to rare species. Hill numbers of order 1 (1D) take abundance into account and reflect the effective number of common species in the assemblage, whereas Hill numbers of order 2 (2D) give a high value to abundance and thus identify the effective number of dominant species in the assemblage (Chao *et al.* 2014; Hsieh *et al.* 2016).

We performed individual-based rarefaction and extrapolation curves of tree diversity based on Hill numbers ($q = 0, 1, 2$) (Chao *et al.* 2014) to compare gamma diversity: species richness ($q = 0$), effective number of common species ($q = 1$) and effective number of dominant species ($q = 2$). This method allows for the effective species richness to be extrapolated to a certain number of individuals; in this study, the rarefaction/extrapolation curves were estimated as the mean of 100 replicate bootstrapping runs with 95% confidence intervals and were standardized to 800 individuals given that this was the maximum number of trees recorded in any one of the forest types. Whenever the 95% confidence intervals did not overlap, species numbers differed significantly at $P < 0.05$ (Colwell *et al.* 2012). Additionally, we built generalized linear models

(GLM) with the extrapolated values of the Hill numbers ($q = 0, 1, 2$) to identify differences in alpha diversity between forest types. We standardized alpha diversity using an extrapolation-interpolation of the Hill numbers (Chao *et al.* 2014) for each sampling plot or transect. To extrapolate the effective species richness to a specific number of individuals, we used 200 individuals as this was the maximum tree density recorded at plot or transect level. The forest type was included as a fixed effect term, the distribution family was the negative binomial and the link function was a logarithm. The assumption of normality was checked using Shapiro–Wilks' tests and the models were fitted using the diagnostic plots of residuals. Differences between sites were determined using the Fisher LSD *post hoc* tests ($P < 0.05$).

Tree species dominance was assessed by means of

$$D_i = \frac{Ab_i}{E \text{ (ha)}} \quad (2)$$

$$DR_i = \left[\frac{D_i}{\sum_{i=1 \dots n} D_i} \right] \quad (3)$$

where D_i is the absolute cover, DR_i the relative cover of species i with respect to the cover, Ab the basal area of species i , and E the surface (ha).

The relative frequency was evaluated by

$$F_i = \frac{P_i}{NS} \quad (4)$$

$$FR_i = \left[\frac{F_i}{\sum_{i=1}^n F_i} \right] \times 100 \quad (5)$$

where F_i is the absolute frequency, FR_i the relative frequency of species i with respect to the sum of the frequencies, P_i the number of sites where species i is present and NS the total number of sampling sites.

We calculated the relative density, frequency and dominance of each species to determine their contribution to the structure of each forest type and their Importance Value Index at the species and family levels (IVI_{sp} and IVI_r , respectively) (Graciano-Ávila *et al.* 2018; Linares and Fandiño 2009; Nebel *et al.* 2001; Vargas and Hidalgo-Mora 2013). The Importance Value Index (IVI) for family and species was defined as

$$IVI = \frac{AR_i + DR_i + FR_i}{3} \quad (6)$$

The absolute and relative abundance were defined by

$$A_i = \frac{N_i}{E} \quad (7)$$

$$AR_i = \left[\frac{A_i}{\sum_{i=1}^n A_i} \right] \times 100 \quad (8)$$

where A_i is the absolute abundance, AR_i the relative abundance of species i with respect to total abundance, N_i the number of individuals of species i and E the sampling area (ha).

We also built rank-abundance curves (RAC) to determine the patterns of abundance distribution for each type of forest community (Whittaker 1965). RACs and model fitting were done with R package *vegan* 2.5-6 (Oksanen et al. 2019). We selected the best adjusted rank-abundance model (i.e., Null, Preemption, Lognormal, Zipf or Mandelbrot) based on their Akaike Information Criterion (AIC). Finally, we compared differences in composition between forest types using an analysis of similarity (ANOSIM) and applied non-metric multidimensional scaling (NMDS) to visualize the data. We used standardized values of tree density per area and the Bray–Curtis index of similarity for both procedures. The ANOSIM was conducted with 1000 permutations using non-standardized data, and P values were adjusted using the SidaKSS method (Benjamini and Hochberg 1995) with the library *vegan* (Community Ecology Package) (Oksanen et al. 2013). The NMDS was conducted using a maximum of 50 iterations and a convergence tolerance threshold of 0.00001, which was reached at 10 iterations with the libraries MASS and the isoMDS functions (Venables and Ripley 2002).

All analyses were performed using InfoStat v2019 (Di Rienzo et al. 2019) and Qeco (Di Rienzo et al. 2010) with R v3.5.1 (R Core Team 2019).

RESULTS

We recorded data from 2,489 trees belonging to 84 species and 32 families at 31 sampling sites (Table 1). The commonest RC species were *Inga vera* Kunth., *Ficus insipida* Willd. and *Vachellia collinsii* (Saff.) Seigler & Ebinger; the commonest SF species were *Vachellia pennatula* (Schltdl. & Cham.) Seigler & Ebinger, *Guazuma ulmifolia* Lam. and *Tecoma stans* (L.) Juss. ex Kunth; the commonest LF species were *Bursera simaruba* L., *V. pennatula* and *T. stans*; and, finally, the commonest PW species were *V. pennatula*, *V. collinsii* and *Lysiloma auritum* (Schltdl.) Benth. (Supplementary Fig. S1). Species richness did not differ significantly between forest types (Table 1). The rarefaction curves indicated a complete overlap, thereby indicating that the effective species richness did not differ substantially between forest types (Fig. 2). Despite the lack of difference in the total effective number of species, RC and SF were more diverse (Table 1; Fig. 2). The corresponding linear models confirm that RC and SF were the most diverse forest types, with the diversity of RC being significantly higher than the diversities of both PW and LF (Table 1; Supplementary Table S2 for complete model specifications and outputs).

The legume family (Fabaceae) was represented by 20 species and 851 individuals, 34.3% of all trees in the inventory, and was the most diverse family in all forest types. The legumes were followed by Malvaceae (six species, 288 individuals; 11.6%), Burseraceae (two species, 288 individuals; 11.5%), Moraceae (five species, 132 individuals; 5.3%) and Meliaceae (eight species, 105 individuals; 4.2%; Fig. 3; Supplementary Table S1). The IVI_t consequently indicated that the Fabaceae (27.8%) was the most important family in all forest types, followed by

Table 1: Characteristics of the types of fragments of tropical dry forests in Nicaragua

	River corridor	Secondary forest	Living fence	Pasture woodland	P
Individuals sampled	872	624	531	462	–
Number of species	51	51	46	40	–
Tree density (no./ha)	108 ± 12 b	78 ± 12 ab	66 ± 12 a	58 ± 12 a	0.0278
Species richness (0D)	23.6 ± 3.3 a	18.7 ± 2.9 a	18.7 ± 2.7 a	18.0 ± 2.6 a	0.5262
Shannon diversity (1D)	16.4 ± 1.8 a	12.8 ± 1.7 ab	10.0 ± 1.3 b	9.2 ± 1.2 b	0.0104
Simpson diversity (2D)	12.8 ± 1.3 a	9.9 ± 1.2 ab	6.8 ± 0.9 bc	6.3 ± 0.9 c	0.0010

All values are means ± 1 standard error. Species richness and diversity indices per plot are estimated using Hill numbers. Different letters within a row denote significant ($P < 0.05$) differences between forest types in a Fisher LSD *post hoc* test.

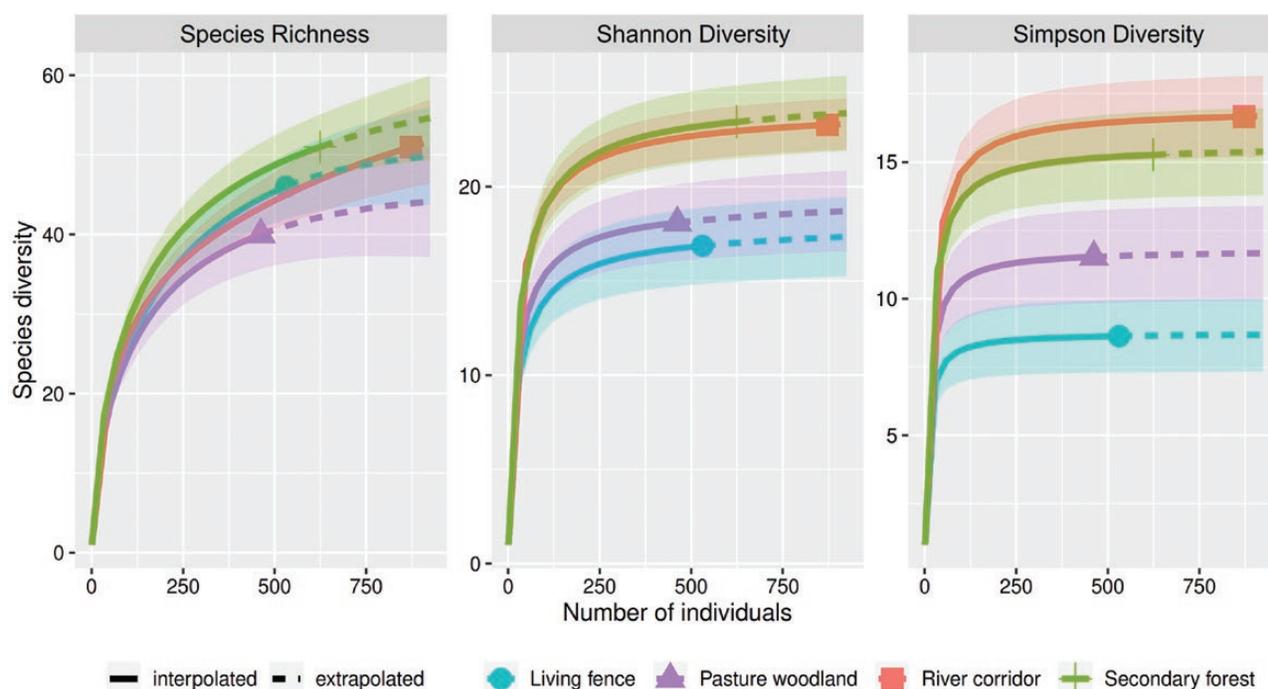


Figure 2: Individual-based rarefaction (solid line) and extrapolation curves (dashed lines) of gamma diversity based on Hill numbers ($q = 0, 1$ or 2) for the four tropical dry forest types in the study area.

Moraceae (11.1%), Malvaceae (10.5%), Burseraceae (9.1%) and Meliaceae (5.9%), with $IVI_T < 5\%$ for the other 27 families (Fig. 4a).

Of the 84 species found in the study area, a group of 15 act as the most significant contributors to the structure of the sampled sites: *V. pennatula* (Fabaceae), *G. ulmifolia* (Malvaceae) and *B. simaruba* (Burseraceae) had $IVI_{sp} > 30\%$, whereas the other 12 species had $IVI_{sp} < 25\%$, which demonstrates the relative dominance of just a few species in these highly modified forests (Fig. 4b). This dominance was particularly clear when assessing species composition using rank-abundance curves, in which *V. pennatula*, *V. collinsii* and *T. stan* were dominant in all forest types (Supplementary Fig. S1).

A preemption model best accounted for the distribution of RC abundance, with *I. vera* and *F. insipida* being the most dominant species. SFs and PWs were better fitted to a Zipf-Mandelbrot model, with *V. pennatula* as the most abundant species in both forest types, whereas LF was best explained by a log-normal function, with *B. simaruba* and *V. pennatula* being the most dominant species. Overall, the most abundant species were *V. pennatula* (307 individuals, 12.38%), *B. simaruba* (259 individuals, 10.45%), *G. ulmifolia* (193 individuals, 7.78%), *V. collinsii* (183 individuals, 7.38%), *T. stans* (172 individuals,

6.94%), *Cordia alliodora* (Ruiz & Pav.) Oken (121 individuals, 4.88%), *I. vera* (110 individuals, 4.47%), *L. auritum* (102 individuals, 4.1%) and *F. insipida* (85 individuals, 3.4%). These 10 species represented 64.82% of all sampled individuals (Supplementary Table S1).

The number of individuals in the DBH classes differed between forest types ($F = 2.32$, $P < 0.01$, Fig. 5). Trees with DBHs of 10–20 cm were the most abundant (1,108 individuals, 44.7%), followed by trees with DBHs < 10 cm (522 individuals, 21.1%) and ≥ 20 cm (508 individuals, 20.5%). These three DBH classes represented 86.3% of all trees. RC had the most trees in all classes, usually followed by SF. The most distinctive and dominant species of each forest type were also the largest (Supplementary Table S1).

Finally, the analysis of similarity showed that the studied TDF differed in terms of species composition. This implies that each land cover type was dominated by a distinct set of species ($P < 0.01$, $R^2 = 0.30$). The *post hoc* tests indicated that RC species diverged significantly from the compositions of SF, LF and PW. The first two axes of the NMDS represented 77% of the compositional variation; NMDS2 also separated the TDF types well (Fig. 6). The RC plots were the most similar

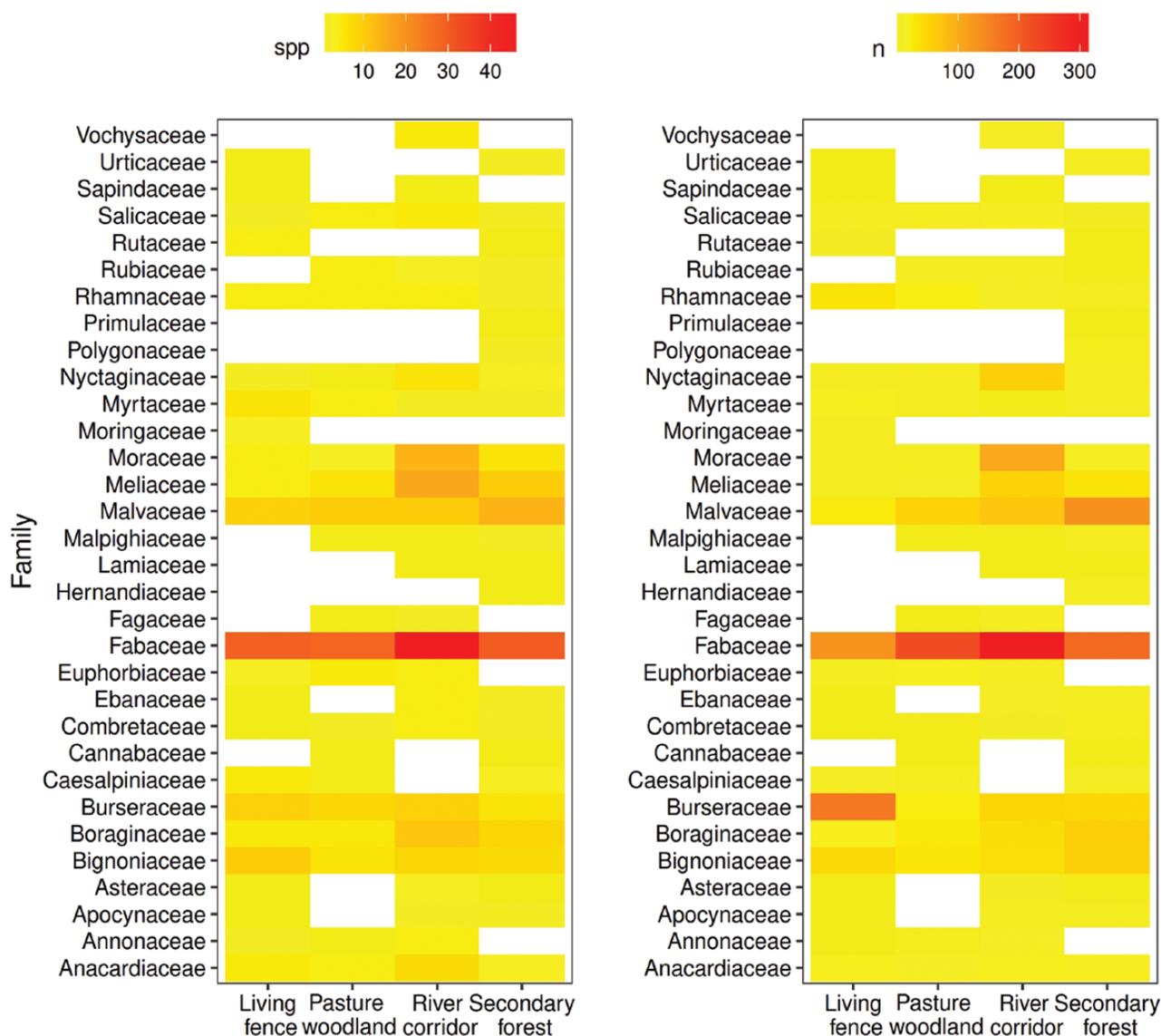


Figure 3: Dominance models based on the number of tree species (spp.) and individuals (n) for each plant family and in each of the four tropical dry forest types in the study area.

to each other, indicating a consistently distinctive tree species composition in this forest type. The distribution of SF and PW plots across the NMDS space notably overlapped, thereby indicating a high level of compositional similarity between these two forest types. The great spread of the points of SF, PW and also of LF across the first axis of the NMDS revealed, however, a high level of between-plot dissimilarity in these forest types.

DISCUSSION

Our comprehensive floristic inventory found that the study area was representative of TDF ecosystems in the Neotropics and that the different types of forest

fragments assessed still conserve a large and valuable degree of diversity (Gentry 1995; Gillespie *et al.* 2000; Tarrasón *et al.* 2010). The number of species per plot was lower than reported in other well-preserved TDFs with some kind of legal protection (e.g. Santa Rosa = 75 and Palo Verde = 65 in Costa Rica; Chacocente = 54 and La Flor = 59 in Nicaragua, Gillespie *et al.* 2000). Our results were, however, consistent with the findings of similar studies carried out in fragmented landscapes at different successional stages with no legal protection like our study area (Hernández-Ramírez and García-Méndez 2015).

The IVI was highest for the legume family, which is a clear reflection of the dominance of this family in many Neotropical dry forests at all conservation

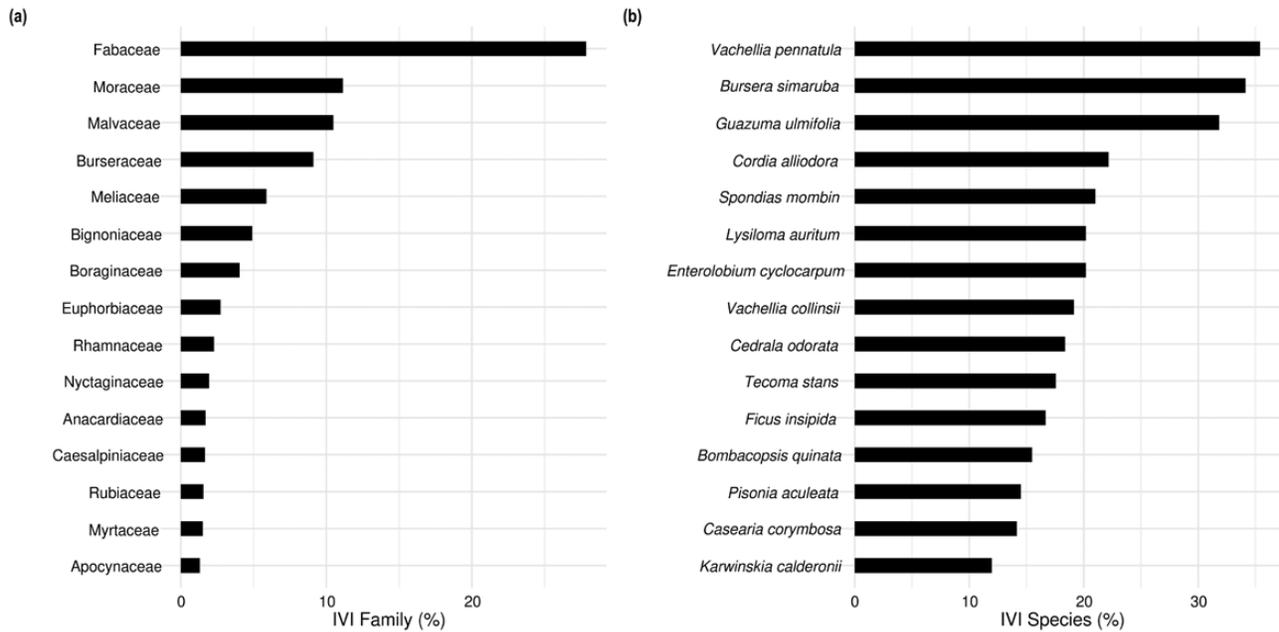


Figure 4: Importance Value Index (IVI) at family (a) and species (b) levels for the four tropical dry forest types in the study area.

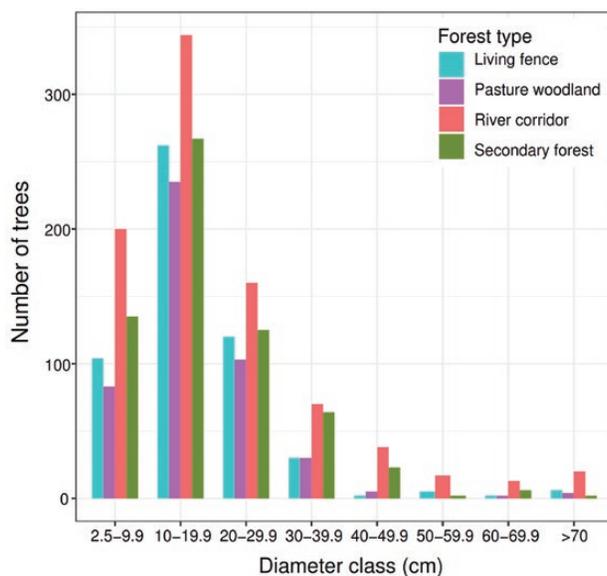


Figure 5: Distribution of tree abundances by diameter at breast height (cm) for the four tropical dry forest types in the study area.

levels (Ballesteros-Correa *et al.* 2019; Gillespie *et al.* 2000; Herazo Vitola *et al.* 2017; Hernández-Ramírez and García-Méndez 2015; Mendoza 1999; Vargas and Hidalgo-Mora 2013). Legumes are also the most dominant tree species (15%–21% of all individuals) in TDFs during early and intermediate successional stages (Hilje *et al.* 2015). The success of this plant family is based on several ecophysiological adaptations such as the usual symbiotic N fixation, their conservative

use of water thanks to their typically bipinnate leaves and the presence of defensive structures (Ceroni Stuva 2003; Gei *et al.* 2018). Other important plant families in our study including the Moraceae, Malvaceae, Burseraceae, Meliaceae, Euphorbiaceae and Anacardiaceae in similar areas throughout the Mesoamerican and Caribbean regions also have high reported IVI values (Ballesteros-Correa *et al.* 2019; Gillespie *et al.* 2000; Hernández-Ramírez and García-Méndez 2015; Hilje *et al.* 2015; Linares and Fandiño 2009).

The 15 species with the highest IVI values at species level in our study area are also among the commonest tree species in Neotropical TDFs (Gillespie *et al.* 2000; Hernández-Ramírez and García-Méndez 2015; Sabogal 1992; Sánchez-Merlos *et al.* 2005; Vargas and Hidalgo-Mora 2013). However, the dominance of three species (*V. pennatula*, *B. simaruba* and *G. ulmifolia*), which represent nearly 30% of all individuals, indicates that the habitats in our study area are greatly altered, and that recurrent disturbances maintain these TDF remnants in early successional stages (Ballesteros-Correa *et al.* 2019; Hilje *et al.* 2015; Sabogal 1992; Sánchez-Merlos *et al.* 2005; Stevens *et al.* 2001; Vargas and Hidalgo-Mora 2013).

Secondary forests (SF) and, particularly, river corridors (RC) had the highest diversity and species richness, with 51 species in each and both within the range of species richness previously reported for these types of TDF remnants (Sánchez-Merlos *et al.*

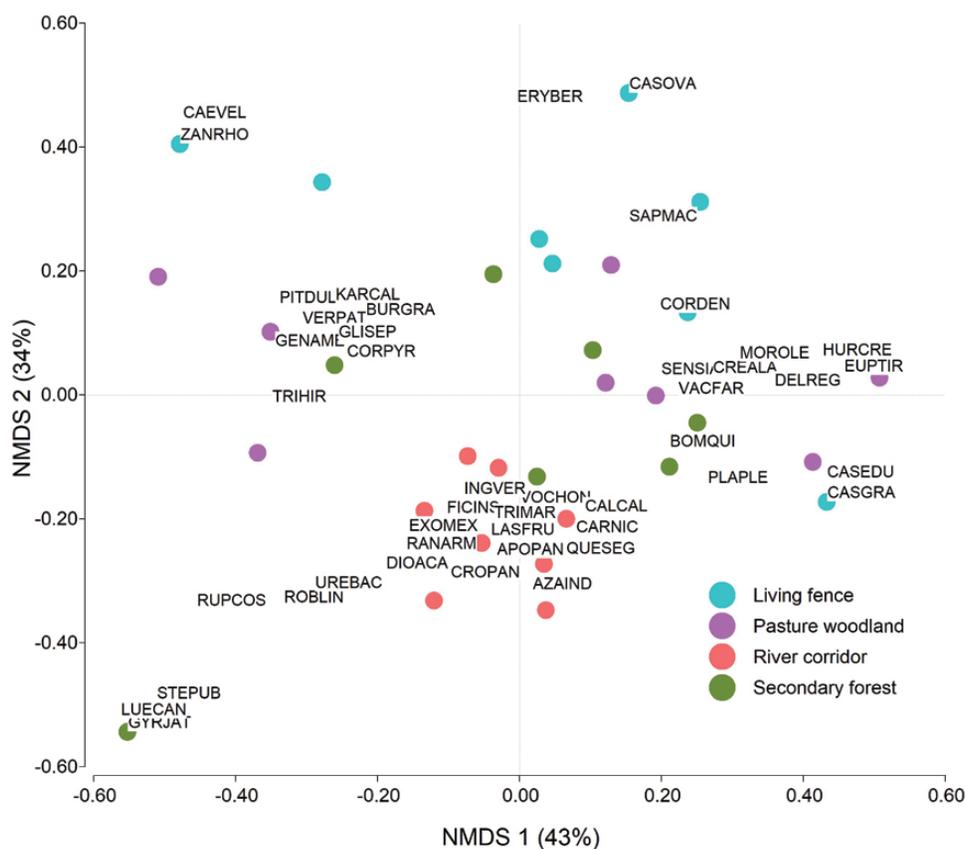


Figure 6: Non-metric multidimensional scaling (NMDS) ordination analysis of the differences in composition between each of the four tropical dry forest types in the study area. Only the most representative tree species of each forest type, i.e. those with correlation coefficients >0.20 on each axis, are shown. See [Supplementary Table S1](#) for species abbreviations.

2005). The Niche-Preemption model selected in RC ([Supplementary Fig. S2](#)) shows that a few abundant species occupy a large proportion of the niche hyperspace, whereas the remaining species—the vast majority—are generally rare, thereby suggesting a lack of evenness in the distribution of resources compared to the other rank-abundance models ([Whittaker 1965](#)). The most dominant species in RC (*I. vera* and *F. insipida*) are specifically adapted to this forest type, in which water availability is typically greater than in the other assessed habitats ([Stevens et al. 2001](#)). Thus, this dominance could also be related to their hydrochoric dispersal syndrome and the fact that they are not valued as timber. On other hand, *V. collinsii* is a common pioneer species in the early stages of secondary succession in Neotropical dry forests ([Hurka and Heinrich 2004](#)), although its presence in the RC could also be the result of seeds having been dispersed by rain or birds.

The most abundant species in SF were also dominant in pasture woodlands (PW), which reveals a strong connection between these two types of forest communities. The Zipf-Mandelbrot model selected

for SF and PW ([Supplementary Fig. S2](#)) demonstrates that the presence of a species in such forest types is dependent on previous physical conditions. Although pioneer species typically require few prior conditions, the needs of late-successional species are usually greater due to the organization, time and energy accumulated in the ecosystem before their establishment ([Wilson 1991](#)). Therefore, establishment costs are usually lower for pioneer species (*V. pennatula* and *V. collinsii*), which allows them to be dominant in early stages of succession. On the other hand, the dominance of *V. pennatula* and *G. ulmifolia* at these sites is associated with their edible fruits with many hard-coated seeds that are well adapted to endozoochoric dispersal by cattle ([Janzen and Martin 1982](#); [Peguero and Espelta 2014](#)). Germination in these species can increase by up to 15% after the frequent pasture fires, which enhances their colonization capacity in these anthropized landscapes ([Esquivel et al. 2008](#); [Peguero and Espelta 2011](#); [Peguero and Espelta 2014](#)).

Unlike RC, species richness was lowest in living fences (LF), where abundances are best explained by a log-normal function; in this forest type, *B. simaruba*,

V. pennatula and *T. stan* are the most abundant species. This pattern was probably due to artificial selection by landowners, who favor these species since they perform well during vegetative propagation (Zahawi 2005). Nevertheless, *B. simaruba* is also an important resource for many bird species that eat its fruit and disperse its seeds (Graham *et al.* 2002). The additional habitat and increase in spatial connectivity provided by LF often play a key role in biodiversity in tropical areas by increasing seed dispersal and fomenting faunal movement, and thus, its composition and structure must be taken into account in fragmented landscapes (Arroyo-Rodríguez *et al.* 2020; Harvey *et al.* 2004; Medina *et al.* 2004).

The distribution of the DBH classes, with a paucity of trees in the highest diameter classes, suggested that all forest types were in early stages of succession, irrespective of their diversity and composition (Sabogal 1992). This bias toward younger cohorts is usually associated with greater resilience in forest patches before repeated disturbances (Lamprecht 1990; Oliver and Larson 1990; Vargas and Hidalgo-Mora 2013). Although individuals with DBH <2.5 cm were not included in our forest inventory, visual inspections revealed that our plots had low rates of sapling recruitment. This was likely due to the herbivorous pressure exerted by cattle, which typically move around freely in forest patches. The lack of any control of cattle grazing and trampling are sources of forest degradation that jeopardize any possible ecological restoration in this threatened tropical ecosystem (Hester *et al.* 2006; Quisehuatl-Medina *et al.* 2020). Our results, nevertheless, indicate that both SF and RC conserve a high level of tree diversity, and that RC also had an especially distinct community composition.

RCs connect aquatic and terrestrial systems and play an essential ecological role in protecting water resources, biodiversity and carbon stocks due to their high net primary productivity (Bennett *et al.* 2014; Giese *et al.* 2003; Tibbets and Molles 2005). These RCs are of great conservation value as they can increase connectivity in treeless matrices (Arroyo-Rodríguez *et al.* 2020). However, the impact of human activities on land adjacent to riparian forests has seriously affected the ecological conditions and properties of such habitats (Zermeño-Hernández *et al.* 2020). The contribution of riparian forests to landscape-scale conservation will probably change as environments become increasingly modified, so the protection and restoration of these communities should be a high

priority in anthropogenic environments (Bennett *et al.* 2014). Therefore, improving the matrix quality by designing biodiversity-friendly landscapes with greater coverage of riparian and secondary forests (Arroyo-Rodríguez *et al.* 2020; Reider *et al.* 2018) will provide species with additional resources and refuges, and facilitate their dispersal and survival, thereby helping us to reduce the impact of the loss of native forests (Boesing *et al.* 2018).

CONCLUSIONS

The SF fragments and RC were the most diverse forest types at all the evaluated sites. Overall, the largest share of the local pool of species was found in RC. These habitats have key ecological roles to play, even if their contributions to landscape-scale conservation will surely change as human activity increases. The protection and restoration of these habitats—especially riparian vegetation—are therefore priorities in these anthropogenic ecosystems as a means of increasing the structural and functional connectivity between surrounding protected areas (Arroyo-Rodríguez *et al.* 2020; Reider *et al.* 2018). Finally, these forest ecosystems need to be analyzed in greater detail, so they can be used as reference ecosystems in future restoration programs at landscape scale and to advance toward more mature successional states. This will enrich them with late-successional and/or endangered species and contribute to modifying the distribution of diametric classes by promoting the largest individual tree sizes.

Supplementary Material

Supplementary material is available at *Journal of Plant Ecology* online.

Table S1: Number of trees with a DBH ≥ 2.5 cm by forest remnant type, and proportions (%) relative to the total number of trees recorded.

Table S2: Results of the GLMs to identify differences in alpha diversity among forest types using Hill numbers ($q = 0, 1, 2$).

Figure S1: Rank-abundance curves for the four types of TDF remnants: (A) river corridor, (B) secondary forest, (C) living fence and (D) pasture woodland.

Figure S2: Rank-abundance curves of each habitat type adjusted to 1 of 5 model (Null, Preemption, Lognormal, Zipf, and Mandelbrot) using the Akaike Information Criterion (AIC).

Acknowledgements

We would like to thank Delver Francisco Pérez, Hanier Roberto Herrera and Jorge Arlington Palacios for their invaluable assistance with the fieldwork, as well as the landowners who collaborated with the setting up and running of this project. We thank Mike Lockwood for editing and revising the English version of the manuscript.

Conflict of interest statement. The authors declare that they have no conflict of interest.

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