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Forested riparian belts as reservoirs of plant species in fragmented landscapes of tropical mountain cloud forest

Franjas ribereñas como reservorios de especies de plantas en un paisaje fragmentado de bosque de niebla

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Abstract
Background: Cloud forest in central Veracruz is highly fragmented. However, different arboreal elements are still present within the agricultural matrix, including small patches of secondary forest, isolated trees and forested riparian belts. These elements could be important for cloud forest species conservation.
Questions: What is the structure and composition of forested riparian belts within current anthropic landscapes, and what is their potential contribution as reservoirs of mountain cloud forest native plant species?
Studied species: Vegetation community of forested riparian belts of cloud forest.
Study site and dates: Eastern Mexico (central Veracruz), January to November 2018
Methods: Along 14 segments of riparian belts (≈400 m long), distributed across different tributary streams, six 50 × 2 m transects were placed (three per riverside) per segment. Every plant rooted within a transect and ≥ 1.5 m in height was identified and measured (height and DBH).
Results: A total of 2,062 plants from 161 species, 102 genera and 55 families were recorded in the 14 sites (8,400 m² sampled). Structural attributes and floristic composition varied widely amongst sites. Elevation and the amount of forest cover (*i.e.*, area) within 250 m of each sampling site were the most important factors underlying the spatial variation in species composition.
Conclusions: Riparian belts were remarkably heterogeneous harboring a notable richness of tree and shrub species many of them native of the original cloud forest. This diversity reveals that these arboreal elements are keystone structures for biodiversity conservation and also have a high potential as propagule sources for cloud forest restoration in anthropic landscapes.
Keywords: American sycamore, biodiversity reservoirs, forest fragmentation, riparian corridor.

Resumen
Antecedentes: En la región central de Veracruz el bosque de niebla está muy fragmentado. Sin embargo, aún encontramos elementos arbóreos en campos agropecuarios, incluyendo parches de vegetación secundaria, árboles aislados y franjas ribereñas. Estos elementos pueden ser relevantes en la conservación del bosque de niebla.
Preguntas: ¿Cuál es la estructura y composición de la vegetación de franjas ribereñas que cruzan potreros y cuál es su contribución como potencial reservorio de especies nativas?
Especies estudiadas: Vegetación de franjas forestales ribereñas del bosque de niebla
Sitio de estudio y fechas: Este de México (Veracruz, central). Enero a noviembre de 2018.
Métodos: En 14 segmentos de río (≈ 400 m), distribuidos en diferentes corrientes tributarias, se colocaron 6 transectos (50 × 2 m) por segmento. Toda planta enraizada en algún transecto y ≥ 1.5 m de altura fue identificada y medida.
Resultados: Un total de 2,062 plantas de 161 especies, 102 géneros y 55 familias se registraron en las 14 franjas (8,400 m²). La composición florística y estructura de la vegetación varió ampliamente entre franjas. La elevación y la cantidad de cobertura forestal 250 m a la redonda de cada franja muestreada fueron los factores que mejor explicaron la variación espacial de la vegetación.
Conclusiones: Las franjas ribereñas fueron muy heterogéneas, albergando una notable riqueza de árboles y arbustos nativos del bosque de niebla. La diversidad encontrada muestra que estos elementos arbóreos son componentes estructurales del paisaje cruciales para la conservación de la biodiversidad y constituyen valiosas fuentes de propágulos para la restauración del bosque original en paisajes antrópicos.
Palabras clave: Corredores riparios, fragmentación forestal, *Platanus mexicana*, reservorios de biodiversidad.

The tropical mountain cloud forest (hereafter: cloud forest) is one of the most important ecosystems worldwide, in particular due to their high proportion of endemic species or with restricted distribution and their remarkable heterogeneity in floristic composition (Rzedowski 1996). Cloud forest provides valuable environmental services, such as soil formation, water retention and infiltration, carbon sequestration, mitigation of both drought and flooding, among others. Besides, this forest provides local resources and benefits such as timber, firewood, edible plants, animals and fungi, as well as medicinal remedies (Hamilton *et al.* 1994, Williams-Linera 2012). However, these tropical forests are amongst the most threatened ecosystems in the planet (Hamilton *et al.* 1994, Aldrich *et al.* 2000). It is estimated that the total area of cloud forest amounts to 250,000 km², which represents only 0.14 % of emerged land and 1.14 % of tropical forest worldwide (Bruijnzeel *et al.* 2011).

Cloud forest in Mexico covers less than 1 % of the country (Williams-Linera 2012, Ponce-Reyes *et al.* 2012), where is drastically threatened by deforestation (Toledo-Aceves *et al.* 2011). For the central part of Veracruz State, Muñoz-Villers & López-Blanco (2008) estimated for 2003 that only 21 % of the region still was covered by cloud forest. Even though we still find some remnant fragments of cloud forest, without a doubt the current situation of this forest in the region is worse than 20 years ago, because deforestation has not stopped. Cloud forest in central Veracruz is highly fragmented, with forest remnants surrounded by an agricultural matrix in which different arboreal elements are still present, including small patches of secondary forest, treed living fences, isolated trees and forested riparian belts crossing pastures, crop-fields and urban areas (Williams-Linera 2012). These arboreal elements standing within the agricultural matrix in conjunction with the few and widely scattered fragments of remnant cloud forest play a critical role in the long-term conservation of different forest species. These organisms include not only trees and shrubs but also epiphytic plants, amphibians, mammals and birds (Pardini *et al.* 2005, Rodríguez-Mendoza & Pineda 2010, Toledo-Aceves *et al.* 2014). Forested riparian belts crossing the agricultural matrix, due to their lineal narrow shape and arboreal structure, represent biological corridors for forest animals that are crucial for connectivity in anthropic landscapes, but also provide extra food and temporary refuge or shelter for forest species within highly modified areas. These riparian belts are also important for soil stability and retention (*i.e.*, riverbed protection), aquifer recharge, nutrient cycling, pesticide and agrochemical retention and removal from run-off, as well as highly valuable for human recreation or outdoor activities (Naiman *et al.* 1993, Lees & Peres 2008).

Even though there are several studies on the richness and composition of cloud forest in America, including Mexico (Gual-Díaz & Rendón-Correa 2014), they usually are focused on the less disturbed remnants, and even when the study is carried out in fragmented landscapes, vegetation sampling is circumscribed to the largest and less disturbed forest fragments. Particularly for Mexico, as is the case for the rest of the Neotropical region, there is scant or null information on the vegetation structure and species composition of forested riparian belts in anthropic landscapes that were formerly covered by cloud forest. The present study is focused on providing reliable quantitative information on the floristic composition and community attributes of the vegetation of forested riparian belts in anthropic landscapes currently dominated by cattle-raising pastures, which originally were covered by cloud forest. The latter will allow us to assess the potential contribution of these arboreal elements as reservoirs of native tree and shrub species in the current modified landscape. Since the study region is highly deforested and severely fragmented due to extensive agricultural activities, then forested riparian belts may represent crucial structural elements for maintaining and increasing landscape connectivity and thus be keystone arboreal elements for the sustainable management of the landscape as well as for cloud forest restoration in agricultural areas, if they still harbor the native species of the original flora.

Materials and methods

Study area. This study was carried out in the upper basin of "La Antigua" river in the central part of Veracruz State in Mexico. The weather is temperate and humid with a mean annual temperature of 18 °C and total annual precipitation that varies from 1,500 to 2,000 mm. The original vegetation was tropical montane cloud forest, in which the most common species of woody plants were *Quercus lancifolia*, *Clethra macrophylla*, *Liquidambar styraciflua*, *Ilex discolor* var. *tolucana*, *Styrax glabrescens*, *Zanthoxylum* sp. and *Prunus rhamnoides* (Williams-Linera 2012). The sites selected for vegetation sampling were located within 19° 22' 05" and 19° 32' 31" latitude N and 96° 57' 31" and 97° 06' 08" longitude W (Figure 1) and ranged in elevation from 1,100 up to 1,800 m asl. Sampling sites corresponded to riparian forested belts that are part of anthropic landscapes in which cattle-raising pastures predominate. In this study, we defined forested riparian belts as the arboreal vegetation that grows on both sides of a river and that in our study area are usually 3 to 5 m wide in each riverbank.

Vegetation sampling. To determine community attributes and floristic composition of forested riparian belts, a total of

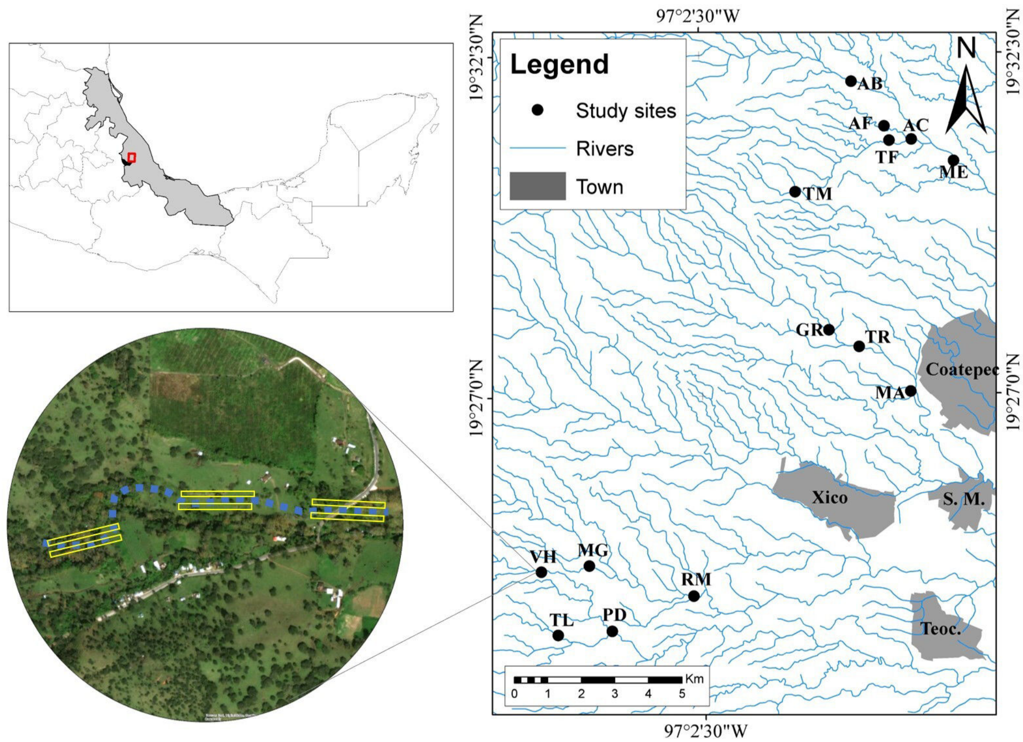

Figure 1. Study site and location of forested riparian belts sampled (black dots) in central Veracruz, Mexico. River courses are shown (blue lines) as well as urban areas (in gray). At the lower left an aerial image of the sampled site VH is shown in detail as an example of the spatial layout of the six transects (yellow rectangles) along the river (blue dotted line) in which vegetation was sampled. See Table 2 for study sites names. Urban areas are: Coatepec, Xico, San Marcos (S. M.) and Teocelo (Teoc.).

14 sampling sites were selected with a minimum separation of 1 km and a maximum of 18 km. Selected sites were 300 to 500 m long sections of the river (mean length of 400 m) having woody vegetation on both riverbanks. Belt transects modified from Gentry (1982) were placed along both riverbanks aligning its longest dimension parallel to the river. Six 50 × 2 m transects were placed at each selected site (three at each river side; Figure 1), for a total of 84 transects. Every plant rooted within each transect and having a total height ≥ 1.5 m was identified and measured (total height and diameter at breast height). Height was estimated with the help of a 6 m long post, graduated every 10 cm and for trees > 6 m an Abney inclinometer was used. Diameter at breast height (DBH) was measured with a diametric tape (in mm) at 1.3 m from the ground in trees and at the trunk base in shrubs. Additionally, the proportion of forest canopy cover was estimated at two sites within each transect using a spherical canopy densiometer. Herbaceous plants and other growth forms (*e.g.*, palms, ferns) taller than 1.5 m were also recorded.

Taxonomic determination was based on the Flora de Veracruz (Sosa & Gómez-Pompa 1994) and nomenclature on TROPICOS web site (Tropicos.org). Botanical specimens were deposited in the XAL-herbarium from the Instituto de Ecología, AC. Some collected specimens during field-work had no flower nor fruit, and for many of them botanist experts on the flora of Veracruz were able to identify them to genus or family level, being impossible to determine its species name.

Data analysis. Sampling completeness based on Hill numbers was assessed using the software iNEXT (iNterpolation and EXTrapolation; Hsieh *et al*. 2016), estimating the individual-based species accumulated curve of the 14 riparian belts sampled. Diversity profiles were drawn for each riparian belt (n = 6 transects/belt), estimating Hill numbers (q0, q1, q2) per belt, expressed in units of effective number of species (Chao *et al*. 2014) for all species (q0 = observed richness), for typical species (q1 = Shannon diversity) and for very abundant species (q2 = Simpson diversity). The importance value index (IVI) for each species was estimated by combining its relative abundance, relative frequency and relative basal area recorded in all 84 transects. To compare species composition among the 14 riparian belts the Jaccard distance or dissimilarity (Jost *et al*. 2011) was estimated between each pair of belts using incidence data. Jaccard distance varies from 0 (*i.e.*, identical composition) to 1 (*i.e.*, no shared species between sites).

Additionally, a multivariate ordination by canonical correspondence analysis (CCA) was used to summarize the spatial variation in floristic composition amongst the 14 belts and to explore the environmental factors that could explain the detected variation. The CCA and permutation tests (to assess the statistical significance of the CCA ordination axis) were run in the software R v. 3.4.3 (R Core Team 2017) using the 'vegan' package (Oksanen *et al.* 2019).

Remote sense images from Google Earth Pro v. 7.3.2 (year 2017; 2.5 m/pixel resolution) were used to estimate different landscape attributes or metrics of the sampled riparian belts and its surroundings. These images were processed in ArcGis v 10.4.1 as follows: a central point was defined for each tract of sampled riparian belt as the centroid of the 6 geo-referenced (with a Garmin-GPS) vegetation transects placed at each belt; then a circular area with 250 m radius centered on this centroid was defined; and finally, within each circular area three land cover categories were distinguished and their areas estimated in hectares: a) area covered by forest, b) area covered by agriculture (*i.e.,* non-forest cover with open pastures or crop-fields), and c) area covered by urban or rural settlements including roads and streets. Each of these three areas was used as indicators of human disturbance in the vicinity of the sampled belts and were incorporated as environmental variables in the CCA ordination. Other environmental variables included in the CCA were the average value of arboreal canopy cover along the sampled belt estimated with the canopy densiometer; the elevation m asl of the centroid of each sampled belt; the distance to the nearest town and finally the distance to one of the 14 sampled belts located in the SW corner of the study area (shown in Figure 1 as the TL site). The latter was done to assess if proximity between sampling sites was related with similarity in composition or not. All environmental variables used in the CCA ordination are shown for each riparian belt in Supplementary material, Table S1. Only non-auto-correlated environmental variables were included in the CCA. The abundance matrix data in the CCA only included tree and shrub species identified at least to the genus level. The distinct species of *Solanum* that we recorded were grouped into a single category: *Solanum* spp. and the same was done for *Piper* spp. The latter was a consequence of the difficulty in identifying sterile individuals of these genera in the field.

Results

Total sampling effort amounted to 8,400 m² in the 84 transects, where a total of 2,062 plants were recorded and they belonged to 161 species, from 102 genera and 55 families (Table S2). The individual-based species accumulation curve pooling all transects showed that overall sampling effort reached 98 % of the estimated species richness (Figure S1). Families with the highest number of species were Asteraceae (18 spp.), Solanaceae (13), Rubiaceae (10), Fabaceae (9), Piperaceae and Melastomataceae (8 spp., each). The richest genera were *Piper* and *Solanum* (8 spp., each), *Clethra* (6), *Quercus* (5), *Cestrum*, *Hoffmannia*, *Miconia* and *Oreopanax* (each with 4 spp.). Of all plant species 66 were trees and 65 shrubs, the rest (19 % of total richness) had different growth forms, including herbs, palms and ferns. Regarding their dispersal syndrome, 112 species (69 %) were zoochorous (*i.e.,* animal dispersed), 34 species (20 %) were anemochorous (wind-dispersed), and the remaining 15 species (11 %) had other dispersal syndromes (Figure 2).

The species with the highest IVI was *Platanus mexicana* with a value (0.95) much higher than any of the other species (IVI < 0.09), in great part due to the very large size of their trees (DBH > 1 m) and also because it was present in most transects and was very abundant (Table 1). Thus, we regard this tree species as over-dominant in the sampled riparian belts. The next most important species had IVI values that ranged between 0.086 and 0.040; in descending order, these species were *Liquidambar styraciflua*, *Palicourea padifolia*, *Styrax glabrescens*, *Perrottetia longistylis*, *Alnus acuminata*, *Miconia minutiflora*, *Piper auritum*, *P. hispidum*, *Conostegia arborea*, *Clethra* sp. and *Meliosma alba* (Figure 3).

Community attributes. More than 80 % of recorded plants ranged in size from 1.5 to 5 m tall (Figure 4A), while 70 % of all plants had a DBH smaller than 10 cm (Figure 4B). The tallest individual was a *P. mexicana* tree with 41 m recorded in the GR site and the one with the largest DBH (257 cm), was another tree recorded in the AB site (Table 2). The overall average of plant height was 6.3 ± 7.0 (s.d.) m and overall DBH average was 14.8 ± 29.1 cm. Vegetation physiognomy and plant sizes varied widely between as well as within riparian belts. Average plant height per sampled site varied from 4.4 ± 4.6 m in the AB site to 12.4 ± 11.8 m in TR. Average DBH per site varied from 7.9 ± 17.8 cm in AF up to 33.5 ± 43.8 cm in the TR site (Table 2).

Overall basal area adding the 14 riparian belts amounted to 190 m² in 0.84 ha of sampling area (*i.e.,* 223.5 m²/ha). The TL site had the highest basal area with 27.9 m², while the lowest value was 2.6 m² recorded in the MG site. The percent proportion of tree canopy cover within the riparian belts, had a global average of 80 %, being the densest belt AF with 89 % and the least dense was PD with 72 % (Table 2). Plant abundance also varied widely, varying from only 79 plants in the LM and ET sites up to 327 plants in AF, with an overall average of 147 ± 68 plants per site (*i.e.,*

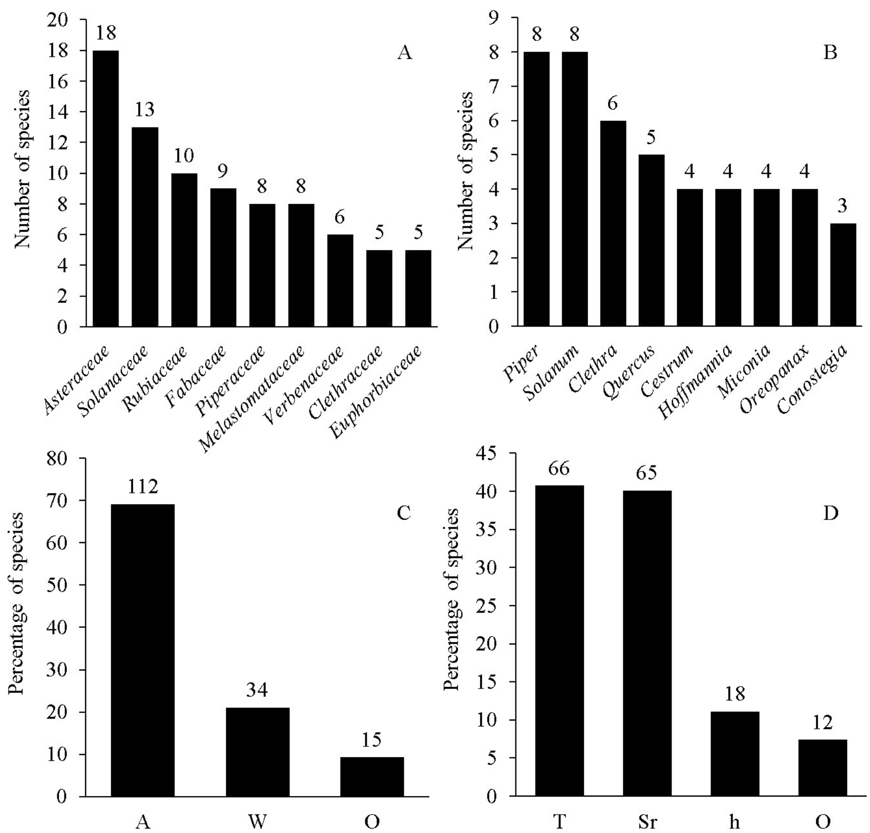

Figure 2. Richest families (A) and genera (B) of plants recorded in the 14 forested riparian belts sampled, and proportion of species for each of three types of seed dispersal vector (C): A = animal, W = wind and O = other vector; and for each of three growth forms (D): T = tree; Sr = shrub; h = herb; O = other (number of species per category are shown above each bar).

2,450 plants/ha). Species richness per site varied from 22 species in MA and also in TR, up to 55 species in AF, with an average richness of 37 ± 9 species per site. Diversity profiles for each riparian belt, showed that the AF and TF sites were not only the richest in observed species (*i.e.,* q0 = 55 and 49 species, respectively), but also in the number of typical species (Shannon diversity; q1 > 30 spp.) and also of very abundant species (Simpson diversity; q2 > 20 spp.). Whereas the TR belt was the site with the lowest number of typical (q1 = 12) and very abundant (q2 = 7) species of all sampled belts (Figure S2).

Variation in floristic composition. The Jaccard distance index showed that the highest dissimilarity was recorded between the MA and BA belts and also between VH and TR, being 0.92 in both comparisons, sharing only 4 and 5 species, respectively. While the least dissimilar sites were AF and TF with 0.61 in Jaccard distance, sharing 29 species. Overall dissimilarity between the sampled riparian belts was very high surpassing 0.7 in Jaccard distance between most paired comparisons (Table 3).

The CCA ordination of the 14 riparian belts in the species abundance space summarized 46 % of variation in floristic composition along the two most important ordination axis (*i.e.*, eigenvalues for CCA-axis 1 = 0.36 and for axis 2 = 0.31). CCA scores for each sampled belt along axis 1 were significantly and positively related with site elevation (F = 1.95; P < 0.003), while those of axis 2 were significantly related (F = 1.65; P < 0.001) with forest cover area within 250 m around the sampled site and also with distance between sites. Riparian belts at highest elevation (MG, VH, TM; higher than 1,650 m asl.) were grouped towards the right part of the CCA plot (*i.e.*, high positive values for axis 1), while those at lower elevations (MA, TR, ME, GR) were grouped towards the left of the graph (Figure 5). Most sites having less than 10 ha of forest cover within 250 m around them (RM, PD, TL and MG) had high negative values along CCA axis 2 (lower part of graph), while sites located in areas with higher forest cover in their surroundings and thus in less disturbed areas (MA, AF, GR, AB) had positive values along this axis (upper part of the graph).

Table 1. Abundance, basal area (m^2) and frequency (n = 84 transects) for all species sampled in 14 segments of forested riparian belts, showing their respective Importance Value Index (I.V.I). Species are grouped by growth form and ordered alphabetically.

	Abund.	Basal Area (m^2)	Frec.	I.V.I
Trees				
Aiouea effusa	7	0.002	4	0.007
Alchornea latifolia	16	0.743	13	0.025
Alnus acuminata	47	2.891	30	0.068
Annona cherimola	15	0.390	13	0.022
Ardisia compressa	2	0.139	2	0.004
Ardisia liebmannii subsp. *jalapensis*	3	0.001	2	0.003
Bernardia dodecandra	38	1.451	12	0.038
Bocconia frutescens	3	0.004	3	0.004
Brunellia mexicana	3	0.061	2	0.004
Bunchosia lindeniana	3	0.001	3	0.004
Carpinus caroliniana var. *tropicalis*	7	0.345	5	0.010
Cestrum dumetorum	1	0.003	1	0.002
Cestrum miradorense	7	0.004	6	0.009
Citharexylum cf. *mexicanum*	2	0.001	2	0.003
Citharexylum mocinoi	14	0.122	8	0.015
Clethra aff. *costaricensis*	10	0.421	8	0.015
Clehtra aff. *vicentina*	6	0.288	3	0.007
Clethra macrophylla	7	0.668	4	0.011
Clethra schlechtendalii	9	1.544	5	0.017
Clethra sp.1	21	1.638	9	0.028
Clethra sp.2	22	0.617	5	0.019
Cnidoscolus multilobus	14	0.024	11	0.018
Cojoba arborea	5	0.114	5	0.008
Erythrina breviflora	16	0.460	8	0.018
Eugenia sp.	2	0.053	1	0.002
Ageratina espinosarum var. *subintegrifolia*	15	0.030	10	0.017
Frangula discolor	2	0.002	2	0.003
Guarea sp.	1	0.024	1	0.002
Gymnanthes longipes	3	0.041	1	0.003
Hedyosmum mexicanum	16	0.217	9	0.018
Heliocarpus appendiculatus	10	0.138	8	0.014
Ilex tolucana	1	0.009	1	0.002
Inga aff. *paterno*	8	0.297	6	0.011
Inga inicuil	8	0.043	7	0.011
Liquidambar styraciflua	65	4.368	31	0.086
Lonchocarpus aff. *orizabensis*	3	0.014	3	0.005
Lonchocarpus sp.2	1	0.385	1	0.004
Lysiloma microphylla	13	0.268	4	0.012
Meliosma alba	13	4.715	9	0.040
Myrsine coriacea	20	0.160	16	0.027
Ocotea psychotrioides	9	0.015	5	0.009

	Abund.	Basal Area (m^2)	Frec.	I.V.I
Oreopanax echinops	6	0.061	4	0.007
Oreopanax xalapensis	11	0.124	6	0.012
Parathesis melanosticta	27	0.348	11	0.026
Perrottetia longistylis	61	2.066	29	0.070
Perrottetia ovata	1	0.015	1	0.002
Persea americana	2	0.016	2	0.003
Platanus mexicana	163	155.672	60	0.955
Prunus aff. *brachybotria*	6	0.046	5	0.008
Prunus tetradenia	2	0.012	2	0.003
Quercus corrugata	12	0.737	8	0.018
Quercus lancifolia	17	2.008	6	0.025
Quercus paxtalensis	21	0.250	7	0.019
Quercus pinnativenulosa	5	0.064	2	0.005
Quercus sapotifolia	3	0.023	1	0.003
Rhamnus longistyla	2	0.001	2	0.003
Sambucus nigra	7	0.167	6	0.010
Saurauia leucocarpa	2	0.005	2	0.003
Saurauia pedunculata	9	0.317	9	0.015
Saurauia sp.	1	0.011	1	0.002
Roldana angulifolia	6	0.011	3	0.006
Styrax glabrescens	81	0.737	23	0.066
Trema micrantha	2	0.082	2	0.003
Trichilia havanensis	5	0.011	4	0.007
Vernonanthura patens	4	0.040	3	0.005
Viburnum tiliifolium	9	0.134	8	0.013
Zinowiewia integerrima	1	0.125	1	0.002
Shrubs				
Arachnothryx bourgeai	5	0.092	4	0.007
Arachnothryx capitellata	17	0.041	11	0.020
Baccharis conferta	1	0.018	1	0.002
Boehmeria caudata	18	0.099	10	0.019
Brugmansia suaveolens	27	0.231	12	0.026
Cestrum fasciculatum	2	0.001	1	0.002
Cestrum nocturnum	1	0.000	1	0.001
Colubrina celtidifolia	1	0.008	1	0.002
Conostegia arborea	66	0.175	20	0.053
Conostegia icosandra	9	0.048	2	0.007
Conostegia xalapensis	19	0.040	9	0.018
Deppea grandiflora	21	0.037	10	0.020
Gaultheria odorata	3	0.001	1	0.002
Hampea integerrima	7	0.060	2	0.006
Hoffmannia excelsa	4	0.002	4	0.006
Hoffmannia orizabensis	4	0.002	4	0.006
Hoffmannia psychotriifolia	19	0.006	7	0.016

	Abund.	Basal Area (m^2)	Frec.	I.V.I
Hoffmannia sp.	7	0.004	5	0.008
Hybanthus elatus	1	0.000	1	0.001
Lantana sp.	1	0.001	1	0.001
Lantana camara	1	0.007	1	0.002
Lantana hirta	1	0.000	1	0.001
Leandra subseriata	7	0.005	4	0.007
Lozanella enantiophylla	19	0.301	9	0.020
Malvaviscus arboreus	19	0.021	7	0.016
Miconia glaberrima	39	0.070	17	0.036
Miconia minutiflora	74	0.144	22	0.059
Miconia oligotricha	1	0.000	1	0.001
Miconia sylvatica	1	0.000	1	0.001
Moussonia deppeana	2	0.000	2	0.003
Myriocarpa longipes	15	0.167	4	0.012
Odontonema callistachyum	38	0.022	12	0.031
Palicourea padifolia	91	0.217	36	0.081
Piper aduncum	2	0.002	2	0.003
Piper auritum	82	0.063	18	0.058
Piper disjunctum	1	0.005	1	0.002
Piper hispidum	67	0.328	21	0.055
Piper lapathifolium	40	0.066	16	0.036
Piper sanctum	5	0.007	3	0.005
Piper schiedeanum	14	0.015	5	0.012
Piper sp.	2	0.003	1	0.002
Psychotria nervosa	7	0.036	3	0.007
Psychotria trichotoma	31	0.042	13	0.028
Senna septemtrionalis	1	0.000	1	0.001
Siparuna thecaphora	1	0.003	1	0.002
Solanum aphyodendron	34	0.097	20	0.037
Solanum chrysotricum	1	0.001	1	0.001
Solanum erianthum	7	0.015	4	0.007
Solanum nigricans	13	0.022	8	0.014
Solanum schlechtendalianum	4	0.002	4	0.006
Solanum umbellatum	1	0.050	1	0.002
Solanum sp.1	8	0.033	4	0.008
Solanum sp.2	5	0.004	5	0.008
Telanthophora grandifolia	11	0.040	6	0.012
Telanthophora sp.	3	0.012	3	0.005
Tournefortia glabra	3	0.008	3	0.005
Triumfetta sp.	4	0.002	4	0.006
Turpinia insignis	5	0.048	5	0.008
Verbesina greenmanii	3	0.001	3	0.004
Verbesina turbacensis	1	0.001	1	0.001
Vernonia sp.	4	0.013	3	0.005

	Abund.	Basal Area (m²)	Frec.	I.V.I
Xylosma flexuosa	6	0.022	5	0.008
Xylosma panamensis	7	0.066	6	0.010
Zanthoxylum aff. *melanostictum*	1	0.007	1	0.002
Zapoteca portoricensis	8	0.007	3	0.007
Herbs				
Acalypha schiedeana	6	0.003	4	0.007
Asteraceae (Gen. no det.) sp.1	6	0.012	5	0.008
Asteraceae (Gen. no det.) sp.2	2	0.002	2	0.003
Asteraceae (Gen. no det.) sp.4	2	0.016	2	0.003
Asteraceae (Gen. no det.) sp.5	2	0.004	2	0.003
Asteraceae (Gen. no det.) sp.6	1	0.007	1	0.002
Asteraceae (Gen. no det.) sp.7	3	0.003	2	0.003
Asteraceae (Gen. no det.) sp.8	3	0.036	2	0.004
Duranta repens	1	0.013	1	0.002
Gunnera mexicana	1	0.002	1	0.002
Heliconia schiedeana	3	0.014	2	0.004
Odontotrichum goldsmithii	41	0.078	9	0.029
Rumfordia guatemalensis	5	0.037	3	0.006
Salvia mexicana	1	0.001	1	0.001
Salvia sp.	1	0.001	1	0.001
Solenophora insignis	2	0.001	1	0.002
Stenostephanus haematodes	23	0.040	8	0.019
Urticaceae (Gen. no det.) sp.	1	0.004	1	0.002
Ferns				
Alsophila firma	21	0.813	10	0.025
Cyathea microdonta	26	0.435	14	0.029
Dennstaedtia sp.	7	0.123	4	0.008
Diplazium sp.	1	0.018	1	0.002
Lophosoria quadripinnata	1	0.007	1	0.002
Polystichum hartwegii	1	0.034	1	0.002
Pteris muricata	1	0.002	1	0.002
Epiphytes				
Clusia sp.	1	0.008	1	0.002
Oreopanax capitatus	9	0.141	9	0.014
Oreopanax liebmannii	23	0.372	15	0.028
Palms				
Chamaedorea schiedeana	9	0.002	4	0.008

The separation between sampling sites as denoted by the distance of each sampled belt to the TL belt (see Methods) also had a strong influence in the CCA results, since those sites far away from TL and located towards the NE corner of our map (Figure 1) were grouped relatively close together in the upper left corner of the CCA graph (Figure 5), while sites close to TL and located towards the SW corner of our map, were grouped towards the lower right corner of the CCA graph, albeit there was a relatively high floristic variation among them as revealed by the wide spread in their placement within the CCA graph. Other site variables related with the CCA ordination of riparian belts,

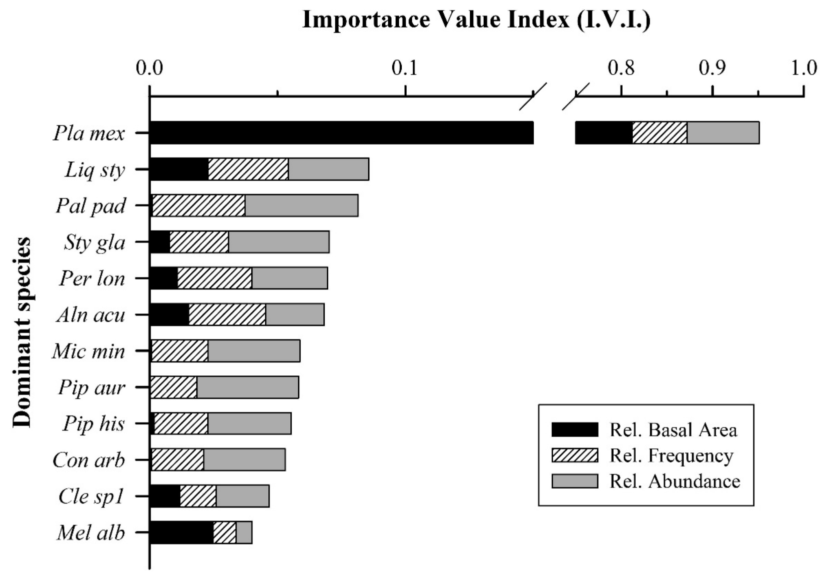

Figure 3. Importance value index (IVI) of the most important (*i.e.,* dominant) species within the sampled riparian belts, showing for each species the contribution of its relative basal area, frequency and abundance. Only the three first letters of the genus and species names are shown (see full names in Table S2). Note that the X-scale is cut from 0.2 to 0.8 and is different below and above those values due to the over-dominance of *P. mexicana* (*i.e.*, extremely high IVI value).

were the distance to the nearest town or settlement and the amount of urban area within 250 m of the sampled site, albeit their relationship with the CCA scores (*i.e.*, axis values) was much lower than that of the previous three variables (as shown by the length of their vectors in the CCA graph of Figure 5). The rest of the environmental variables measured for each sampled site (see Methods) was not related with the floristic variation summarized in the CCA graph or were auto correlated with at least one of the previous five variables mentioned.

Discussion

The recorded plant richness (161 species) in the 14 riparian belts sampled represents 2.4 % of total floristic richness for the national inventory of Mexican cloud forest (Villaseñor 2010), and 5.0 % of total richness for the cloud forest of the Veracruz State (Villaseñor & Ortiz 2017). For the central part of Veracruz in relatively well-preserved areas of cloud forest, García-Franco *et al.* (2008) found 67 tree species and 35 shrub species in 0.3 ha of total sampling area. While for the same area but within cloud forest remnant fragments of 1.2 up to 40 ha, Toledo-Aceves *et al.* (2014) found 45 tree species in 0.48 of sampling area and Williams-Linera (2002) found 71 tree and 24 shrub species in 0.7 ha of sampling area. In other states of the country with cloud forest, different studies have reported between 76 and 121 tree species and 59 to 151 shrub species (Mayorga *et al.* 1998, Alcántara-Ayala & Luna-Vega 2001, Cartujano *et al.* 2002), reaching 300 or more species of woody plants in some regions (Ramírez-Marcial 2001), albeit these studies covered larger areas and were carried out mostly in well preserved cloud forest. For the case of riparian habitats, other studies have found between 34 to 70 tree species and 33 to 49 shrub species in sampling areas ranging from 0.2 up to 1 ha, although these studies were carried out in deciduous oak forest of Morelos (Camacho-Rico *et al.* 2006) and tropical rain forest in SE Mexico (Moreno-Jiménez *et al.* 2019). Given that our total sampling effort amounted to less than 1 ha (0.84 ha) and that the 14 riparian belts sampled are narrow habitats completely subjected to intense edge-effects within human disturbed landscapes, the richness that they harbor (66 tree species and 65 shrub species) is remarkable. Even though riparian belts cover a relatively small area within our sampling sites (8 ha pooling the 14 sites) in comparison with open areas under agricultural activities (77 ha, mostly pastures) and the extent of secondary forest (184 ha) within 250 m of our sampling sites, these riparian belts are widespread within the studied landscape and as our results show they concentrate a relatively high density of native species of trees and shrubs.

Vegetation structure and composition of riparian belts. The structural features and floristic composition of the sampled riparian belts shows some similarity with cloud forest remnant fragments of central Veracruz. Total basal area in the 14 sampled riparian belts was 217.8 m²/ha (trees with

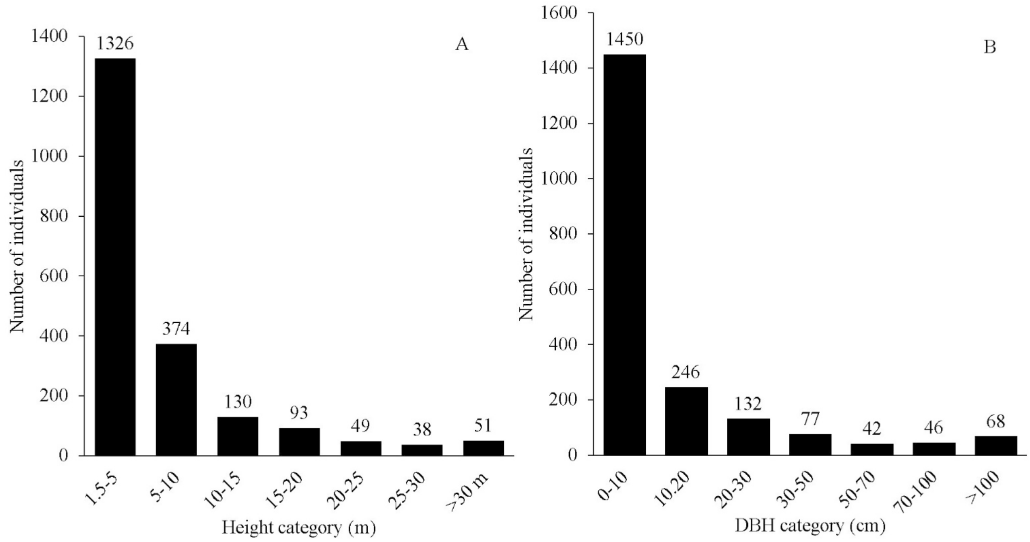

Figure 4. Number of plants taller than 1.5 m and rooted within the transects of all riparian belts sampled arranged by plant height category (A) and by DBH category (B).

DBH ≥ 10 cm), which is higher than the values reported by Williams-Linera (2012) in remnant cloud forest fragments of different sizes (58 to 100 m²/ha). However, the density of trees with DBH ≥ 10 cm in riparian belts (580 trees/ha) was lower than in cloud forest remnant fragments (900 trees/ha; Williams-Linera 2012). Tree canopy height in cloud forest remnants varies between 25 and 30 m, with some emergent trees reaching up to 40 m, having wide trunks with 1 m of DBH or more, which could be regarded as the giants of these forests (Williams-Linera 2002). Most of the plants recorded in the 14 riparian belts were smaller than 5 m tall, however they were part of the understory, because trees having 20 to 30 m in height were widespread along the riparian belts and many of them had wide trunks (DBH ≥ 1 m). Even though most of the tallest and largest trees in the riparian belts belonged to *P. mexicana*, we also found very large trees of other species such as *M. alba*, *Quercus lancifolia*, *Alnus acuminata* and *Clethra* spp.

Plant families with highest number of species in riparian belts were Asteraceae, Solanaceae, Rubiaceae, Piperaceae, Fabaceae and Melastomataceae, which together contribute with 47 % of total richness reported so far for the cloud forest of Mexico (Gual-Díaz & Rendón-Correa 2014). Other important families in Mexican cloud forest are Fagaceae, Clethraceae, Actinidaceae, Lauraceae, Gesneriaceae, Aquifoliaceae, Lamiaceae, Betulaceae, Clusiaceae and Styracaceae (Rzedowski 1996, Gual-Díaz & Rendón-Correa 2014), all of which were also found in the riparian belts. The genera with most species recorded in our study were *Piper*, *Solanum*, *Quercus*, *Clethra*, *Hoffmannia*, *Miconia*, *Oreopanax*, *Ardisia* and *Cestrum*, many of which correspond to the richest genera in cloud forest of Mexico (Rzedowski 1996, Williams-Linera 2012, Gual-Díaz & Rendón-Correa 2014). Trees and shrubs were the richest and most common growth forms recorded in riparian belts, however we also found some species of palms, ferns, herbs and epiphytes that were taller than 1.5 m within our sampled sites, in spite of the high density of cattle and frequent weeding with machete by farmers. However, it is important to remark that our sampling criteria (*i.e*., plant height > 1.5 m) was not adequate for sampling these latter growth forms, which are usually small plants or grow on top of trees and that could be an important and rich component of cloud forest (Rzedowski 1996, Flores-Palacios & García-Franco 2008).

As many as 70 % of the plant species that we found in riparian strips have edible fleshy fruit corresponding to the zoochorous dispersal syndrome (*i.e.,* plant species whose seeds are dispersed by frugivorous animals). Riparian belts are elongated and narrow arboreal elements that cross open areas converted into pastures or different types of crop-fields, which farmers left uncut to protect both riverbanks and thus are integrated into agricultural management, but as our results show they are also important reservoirs of plant species that might provide important edible fruit for different forest animals (Griscom *et al*. 2007). Given that the studied landscape is dominated in extension by open agricultural areas, these narrow arboreal elements along rivers also provide crucial perching sites and movement corridors for different animals, ensuring and enhancing landscape connectivity (Pardini *et al*. 2005). Within anthropic landscapes, arboreal riparian belts connect forest fragments from upper to lower areas and represent the most important venues for the displacement of forest animals across the landscape. Thus, riparian belts are not only important for the conservation of native species of woody

Table 2. Vegetation structure of the 14 sampled riparian belts (abbreviation used in Figure 1). Average (±s.d.), maximum and third quartile values for plant height (m) and DBH (cm) are shown, as well as total basal area (cm²) and average percent of forest canopy cover estimated with the canopy densiometer (see Methods).

Riparian belt sampled	Height (m)			D.B.H. (cm)			Basal area (m^2)	Can. Cover (%)
	Avg.	Max	3rd Qrt.	Avg.	Max	3rd Qrt.		
Acuario (AC)	6.5 ± 6.7	32.2	< 7.8	15.2 ± 23.4	123.1	< 17.3	10.03	79.59
Agua Bendita (AB)	4.4 ± 4.6	40.5	< 4.7	8.0 ± 20.9	257.0	< 6.0	9.34	83.40
Aguita Fría (AF)	5.3 ± 6.1	37.31	< 5.2	7.9 ± 17.8	213.2	< 5.9	10.89	89.08
Trianon (TR)	12.4 ±11.8	38.0	< 23.6	33.5 ± 43.8	168.7	< 61.9	20.88	86.83
Granada (GR)	6.0 ± 9.3	40.9	< 4	13.7 ± 33.9	154.3	< 5.5	20.94	83.45
Marina (MA)	9.3 ± 9.8	35.8	< 12.8	29.4 ± 42.5	157.5	< 41.9	16.92	75.64
Mariano Escobedo (ME)	7.0 ± 7.3	34.6	< 8.0	13.6 ± 25.2	210.4	< 11.6	9.80	88.99
Monte Grande (MG)	5.9 ± 5.0	20.0	< 6.8	8.7 ± 11.6	69.4	< 9.4	2.65	75.11
Puente de Dios (PD)	5.8 ± 6.9	34.0	< 5.9	17.1 ± 39.2	203.3	< 9.1	21.99	72.05
Río Matlacobatl (RM)	7.7 ± 6.3	28.9	< 9.0	23.3 ± 29.3	130.1	< 24.2	10.78	72.54
Tlalchy (TL)	6.4 ± 5.7	31.3	< 8.0	25.4 ± 42.1	197.9	< 21.3	27.98	78.03
Trucha Feliz (TF)	6.0 ± 5.6	27.9	< 8.0	16.8 ± 34.9	249.8	< 13.0	19.41	87.65
Truchas Martín (TM)	6.0 ± 5.2	25.1	< 8.0	12.3 ± 12.9	64.2	< 20.4	2.83	85.52
Vista Hermosa (VH)	6.6 ± 4.8	22.2	< 9.0	15.7 ± 15.7	81.8	< 23.3	5.58	74.54

plants but also for forest animals (Crome *et al*. 1994). In particular, they are important for those animals that found edible fruit or other food sources (*i.e.*, insects associated with tree foliage or their epiphytes) in them, as well as nesting sites, temporal refuge or perching sites in the middle of open areas with scant or null tree cover outside these narrow belts (Griscom *et al*. 2007). Therefore, riparian belts are also crucial for the maintenance of the ecological interaction between zoochorous woody plants and frugivorous animals, without which forest regeneration is impossible.

The most important or over-dominant species in the sampled riparian belts was the tree *P. mexicana*, whose I.V.I. was notoriously much higher than that of all the other species. Other important tree species were *L. styraciflua*, *S. glabrescens*, *P. longistylis*, *A. acuminata*, *M. alba* and *Clethra* sp., while important shrub species include *Palicourea padifolia*, *Miconia minutiflora*, *Piper auritum*, *P. hispidum* and *Cojoba arborea*. The over dominance of *P. mexicana* is explained by its high frequency (*i.e.,* recorded in most transects), its high abundance, and mainly due to its impressive basal area in riparian strips, related with the large size of their trunks whose DBH were usually larger than 80 cm. Mayorga *et al*. (1998) and Williams-Linera (2012) mention that *P. mexicana* and *L. styraciflua* are tree species strongly associated with riparian zones in cloud forest of Mexico. The latter coupled with the management practice of not cutting the trees along both sides of permanent rivers that cross the plots of farmers or cattle ranchers, explains the over-dominance of the first species and the high importance of the second within the sampled riparian belts. In riparian forest of the state of Puebla, Aguilar-Luna *et al*. (2018) have also found *P. mexicana* as the most important and dominant tree species, together with *Alnus acuminata* and *Quercus rugosa*.

Other plant species that are also known to be associated with riparian zones in cloud forest include *Deppea grandiflora*, *Boehmeria caudata*, *S. glabrescens*, and *A. acuminata* (Mayorga *et al*. 1998, Gual-Díaz & Rendón-Correa 2014), all of which were found in this study. Trees of different species of *Quercus* are also abundant in riparian zones as well as in sites far away from rivers, being one of the most important genus of trees in cloud forest of Mexico and Central America (Johnson & Jones 1977, Granados-Sánchez *et al*. 2006, Nur *et al*. 2008). Several species of *Quercus* are exclusive or quasi-exclusive of cloud forest, for example *Q. sapotifolia*, *Q. corrugata* and *Q. pinnativenulosa*, the last one being endemic to Mexico (Valencia-A & Gual-Díaz, 2014). These three *Quercus* species together with other two more were found in the riparian belts sampled. Additionally, the genus *Quercus* is regarded as an important functional group, very useful for the restoration of native cloud forest in fragmented

Table 3. Jaccard distance (dissimilarity index; upper-right values in Table) and number of shared species (*lower left*) among the 14 riparian belts sampled (see abbreviations in Table 2). Total number of species per sampled belt are shown in the diagonal of the Table (black cells). Cells shaded in gray show the highest and lowest values in dissimilarity (above diagonal) and the respective number of shared species (below diagonal) between those riparian belts.

	AC	AB	AF	TR	GR	MA	ME	MG	PD	RM	TL	TF	TM	VH
AC	**42**	0.69	0.76	0.81	0.76	0.88	0.68	0.79	0.75	0.79	0.78	0.66	0.84	0.84
AB	*21*	**46**	0.62	0.85	0.72	0.92	0.68	0.75	0.72	0.82	0.86	0.72	0.83	0.85
AF	*19*	*28*	**55**	0.83	0.77	0.88	0.75	0.78	0.72	0.81	0.77	0.61	0.80	0.84
TR	*10*	*9*	*11*	**22**	0.67	0.74	0.88	0.76	0.77	0.78	0.86	0.84	0.89	0.92
GR	*16*	*19*	*18*	*16*	**42**	0.81	0.81	0.73	0.76	0.85	0.83	0.80	0.84	0.89
MA	*7*	*5*	*8*	*9*	*10*	**22**	0.91	0.91	0.86	0.83	0.90	0.85	0.84	0.89
ME	*20*	*21*	*19*	*7*	*13*	*5*	**41**	0.82	0.80	0.84	0.87	0.71	0.83	0.89
MG	*14*	*17*	*17*	*12*	*17*	*5*	*12*	**39**	0.65	0.80	0.79	0.78	0.83	0.70
PD	*17*	*19*	*21*	*12*	*16*	*8*	*14*	*21*	**42**	0.71	0.72	0.72	0.80	0.76
RM	*13*	*12*	*14*	*10*	*10*	*8*	*10*	*12*	*17*	**33**	0.76	0.79	0.89	0.88
TL	*14*	*10*	*17*	*7*	*11*	*5*	*9*	*13*	*17*	*13*	**35**	0.76	0.90	0.84
TF	*23*	*21*	*29*	*10*	*15*	*9*	*20*	*16*	*20*	*14*	*16*	**50**	0.78	0.84
TM	*11*	*11*	*14*	*5*	*10*	*7*	*10*	*10*	*12*	*6*	*6*	*14*	**29**	0.84
VH	*10*	*10*	*11*	*4*	*7*	*4*	*7*	*16*	*14*	*7*	*9*	*16*	*9*	**30**

landscapes (Ramírez-Marcial 2001, Williams-Linera 2012, Gual-Díaz & Rendón-Correa 2014). Lastly, is important to remark that the species of *Quercus* found in the riparian belts of this study are classified under some risk category or as threatened, together with other tree species such as *Persea americana*, *M. alba*, *Carpinus caroliniana* var. *tropicalis*, among others. The presence of endemic or threatened species also highlights the importance of riparian belts for the conservation of native species of the cloud forest.

On the other hand, in the riparian belts sampled it was also notorious the presence of numerous species that are favored by disturbance, and that are abundant in large canopy gaps or along forest edges with open areas. Among the latter, we recorded different species of the genera *Piper*, *Solanum*, *Miconia*, *Conostegia*, *Rubus*, *Cnidoscolus*, *Telanthophora*, *Psychotria*, *Hampea*, *Trema*, *Ageratina*, *Sambucus*, *Bocconia*, *Alnus*, *Hedyosmum* and *Heliocarpus* (Hamilton *et al*. 1994, Mayorga *et al*. 1998, Alcántara-Ayala & Luna-Vega 2001, Bruijnzeel *et al*. 2011, González-Espinosa *et al*. 2011, Muñiz-Castro *et al*. 2012, Williams-Linera 2012, Toledo-Aceves *et al*. 2014). The early establishment of these pioneer heliophile species favors the arrival, establishment and further growth of intermediate or late successional species such as *Saurauia*, *Myrsine*, *Liquidambar*, *Clethra*, *Quercus*, *Perrottetia*, *Cestrum*, *Turpinia*, and *Carpinus* (Nadkarni & Wheelwright 2000, Muñiz-Castro *et al*. 2012). As stated before, arboreal riparian belts crossing agricultural matrices in fragmented landscapes, are exposed to human activities and this intense disturbance is notable in vegetation structure and composition, however, these arboreal elements are formed by trees that were part of the original forest canopy and were left uncut to protect the riverbanks, but also represent sites that provide opportunities for the establishment and growth of late successional tree and shrub species, which explains the heterogeneous mixture of species typical of different successional stages within these belts. Even though riparian belts show clear signs of intense human disturbance they are not poor in forest species, genera and families as our data demonstrate, on the contrary they harbor a notable diversity of native plants of the cloud forest, including *L. styraciflua*, *M. alba*, *C. tropicalis*, *Oreopanax xalapensis*, as well as species from the genera *Quercus, Clethra, Alnus, Prunus* and *Cinnamomum* (Mayorga *et al*. 1998, Muñiz-Castro *et al*. 2012, Gual-Díaz & Rendón-Correa 2014). Due to their wide distribution in current anthropic landscapes and their richness of woody plants, riparian belts crossing agricultural matrices if managed properly, could represent the most important and accessible source of propagules for the restoration of native cloud forest in agricultural fields.

Spatial variation among riparian belts. Floristic composition varied notoriously as shown by the relatively high values of Jaccard distance (*i.e.,* dissimilarity index) amongst the 14 riparian belts, due to a high spatial

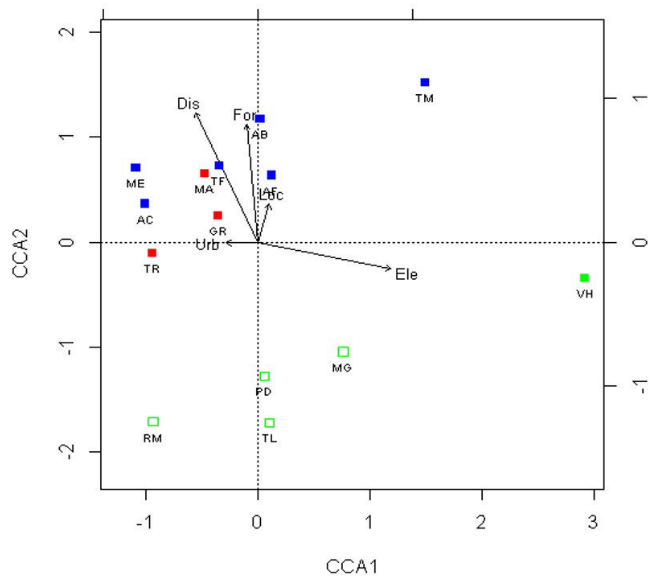

Figure 5. Multivariate CCA ordination of the 14 riparian belts in the species abundance space summarized in two axis. Environmental variables per sampled site correlated with CCA-scores for any of the CCA-axis are shown as vectors (the length and orientation of the vector depict the strength, direction and magnitude of the relationship with each axis). Empty symbols correspond to riparian belts having less than 10 ha of forest cover within 250 m; filled symbols had > 10 ha within 250 m. Symbol color indicates the general location of the riparian belt (see Figure 1), towards the NE corner of our study site (blue squares), towards the SW corner (green) or in the middle between them (red). Ele = elevation; For = forest cover area within 250 m; Dis = distance to the TL belt (see Methods); Urb = urban area within 250 m; Loc = distance to nearest town.

heterogeneity and species turnover (*i.e.,* beta diversity). Across the elevation gradient of central Veracruz where the cloud forest is found, a heterogeneous composition has been reported even in short distances along this gradient (Rzedowski 1996, Alcántara-Ayala & Luna-Vega 2001, Ruiz-Jiménez *et al*. 2012, Williams-Linera *et al*. 2013), and this explains in part the high spatial heterogeneity that we detected. The multivariate ordination (CCA) showed that sites at the same elevation level had higher floristic similarity amongst them than with sites at different elevation. Also the CCA results showed that the amount of forest cover in the vicinity of the sampled site (*i.e.*, within 250 m) was important, since those sites having less than 10 ha of forest cover around, had higher similarity in composition amongst them and were dissimilar to those sites having more than 10 ha of forest cover around. Additionally, another important factor explaining the spatial variation in floristic composition amongst the 14 riparian belts was their separation and location in a given sub-basin, since those sites closer together and forming part of the same sub-basin had a comparatively higher similarity among them than with riparian sites that were part of a different sub-basin and were more distant. It is important to remark that several other factors also affect the spatial variation in composition of cloud forest and of riparian belts, such as topographic and edaphic differences, natural and anthropic disturbance regimes. The latter varies widely from site to site in accordance with different practices of agricultural management followed by each farmer, including the frequency of cutting woody plants with machete to favor the growth of grasses, cow density and rotation regime, intensity of firewood extraction, among others (Williams-Linera 2012), and all of these influenced the spatial variation in composition that we detected.

The management of riparian belts by each farmer has a strong effect on the spatial heterogeneity in vegetation structure and composition. In the sampled transects we detected a sharp variation in abundance of favored tree or shrub species that were planted by the farmer or that were spared from cutting or weeding. Some farmers are very selective in the species that they prefer as firewood and thus protect and favor these species within their riparian belts (pers. obs. OAHD). Others plant different fruit trees (particularly citric fruits and guava), or highly valuable crops such as coffee shrubs or macadamia nut trees, or lumber trees such as non-native pines. A widespread (almost universal) management practice in the region is to leave uncut only a single line of trees at each river bank, as a result the riparian belts are very narrow, usually less than 5 m from the maximum water level at each riverbank, in order to maximize pasture area and fit in more cows within their properties. The actual width of riparian belts is much less than the requirements of Mexican law (Ley de Aguas Nacionales en Mexico; CONAGUA 1992), which states that for rivers wider than 5 m, the federal zone at each riverbank should be at least 10 m from the maximum water level and in this zone the native original vegetation must be left untouched; for rivers less than 5 m wide, the width of natural vegetation at each side must be at least 5 m. This law is neither respected nor enforced in our study site or in any other region in Mexico. The mentioned law was written to protect the river and water quality, but it would also have a great positive effect on the biodiversity of forest plants and animals if respected, as our results show, because even when this belts are narrower than the width stated in the law they harbor a notable diversity of native species of woody plants. The role of riparian belts as reservoirs of native plant species and sources of propagules for forest regeneration would be greatly enhanced if the width stated in the law is enforced and also their importance as extra habitat and corridor for forest fauna would be enhanced. Thus, national programs and campaigns to benefit those farmers that respect the law and make wider the riparian belts crossing their properties should be promoted to increase the positive role of arboreal riparian belts in highly fragmented landscapes in order to increase the potential of biodiversity conservation of the cloud forest in transformed landscapes. In particular, the preservation of native flora and fauna of the cloud forest as well as their ecological interactions will be encouraged if riparian belts were of the width stated in the law, this in turn will ensure and enhance landscape connectivity and forest resilience within these anthropic landscapes.

In conclusion, vegetation structure and floristic composition of the arboreal riparian belts that we sampled showed a relatively high similarity with the vegetation of large fragments of cloud forest in Central Veracruz, however in riparian belts the tree *Platanus mexicana* is over-dominant and this species is absent or extremely rare in sites far away from rivers. Overall the spatial heterogeneity in composition was very high among the river belts sampled, mainly due to differences in the management regime of each belt by farmers, but also due to the high spatial heterogeneity and beta diversity of the original cloud forest, which is still very high in the current anthropic landscape, at least within the riparian belts that cross agricultural areas. This study shows that these arboreal elements that cross the agricultural matrix of the landscape do contain a remarkably high diversity of plant species (161 species 80 % of which are trees and shrubs), many of which are pioneer or secondary species of disturbed sites, but also they have many others that are late-successional or old-growth forest species. These riparian belts not only harbor a high diversity of plants but also offer extra habitat, temporal perching sites and edible resources for animals, which could be directly produced by the plants (*i.e*., fruits or leaves) or indirect resources associated with their foliage (*i.e.,* insects and other invertebrates), that will not be there if the riparian belts were absent. In particular, frugivorous vertebrates (*i.e.,* birds and bats) that feed on these riparian belts are crucial for seed dispersal and forest regeneration in the fragmented landscape. These riparian belts are arboreal elements of current landscapes already incorporated in the management of pastures and crop-fields but that should be added to conservation plans or programs of the cloud forest of the region, by explicitly recognizing their value in biodiversity preservation and landscape connectivity and thus by implementing a reward system or incentives for those farmers that maintain their riparian belts with a high plant diversity and as wide as the Mexican law states. We regard riparian belts crossing agricultural matrices as a critical arboreal element of the landscape that is crucial for the long-term conservation of the cloud forest, particularly in highly fragmented landscapes in which their presence and proper management would surely enhance forest resilience.

Acknowledgments

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Supplemental data

Environmental variables for each sampled riparian belt used in the CCA analysis (Table S1). Species list of recorded plants with data on life form, dispersal mode, conservation status and I.V.I. (Table S2). Individual-based species accumulation curve and sample coverage for all 14 riparian belts sampled (Figure S1). Individual-based diversity profiles (Hill numbers; q0= observed richness; q1= Shannon diversity; q2= Simpson diversity) for each riparian belt sampled (Figure S2).

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