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ORIGINAL RESEARCH ARTICLE

Floristic and Structural Heterogeneity in a Neotropical Riparian Wetland: Conservation Implications

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Abstract

Despite the incontrovertible importance of wetland ecosystems, our understanding of the causes underlying the spatial heterogeneity of their attributes is still insufficient. Here, we assess the spatial variation of the floristics (species composition and their relative abundances) and quantitative structure (vegetation cover) of the San Pedro Mártir River riparian herbaceous wetlands (Tabasco, Mexico), and explore potential factors responsible for within- and among community variation. Vegetation was sampled at 10 sites along a 40-km stretch of the river. Per site cover of the recorded morphospecies was assessed with digital photography, and community diversity was analyzed using the Hill numbers framework. Total richness was 76 morphospecies (67 identified to some taxonomic category); the drastic decrease in true diversity with increasing q values indicated that few species dominate the community matrix, while numerous remaining species occupy the small interstices among them. Three Cyperaceae species had the largest importance in the community, with *Cladium jamaicense* being the most frequent and having the largest cover along the river. Ward's site classification and NMDS ordination indicated the existence of four floristically and structurally different vegetation groups. Within sites, GLMMs showed a weak inverse relationship between species richness and distance from the river, but no relationship for plant cover. Fluvial geomorphology, and possibly regional geological heterogeneity, are the main factors determining the spatial variation of these herbaceous wetlands. Deep understanding of the relationship of herbaceous riparian wetlands with their environment will improve the prediction of the effects of modifications of fluvial dynamics and support efficient conservation strategies.

Keywords Diversity · Floristic structure · Fluvial geomorphology · Herbaceous communities · Quantitative structure · Spatial heterogeneity

Resumen (Español)

A pesar de la incuestionable importancia de los humedales, no conocemos bien los factores responsables de la heterogeneidad espacial de sus atributos. Evaluamos la variación espacial de la estructura florística (composición de especies y sus

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abundancias relativas) y cuantitativa (cobertura vegetal) de los humedales herbáceos ribereños del río San Pedro Mártir (Tabasco, México) y exploramos factores potencialmente responsables de su variación dentro y entre comunidades. Se muestreó la vegetación en 10 sitios en un tramo de 40 km del río. La cobertura por sitio de las morfoespecies se evaluó con fotografía digital y la diversidad de las comunidades se analizó con números de Hill. La riqueza total incluyó 76 morfoespecies (67 identificadas hasta alguna categoría taxonómica); la drástica disminución de la diversidad verdadera al usar valores de *q* mayores indicó que pocas especies dominan la matriz comunitaria, mientras que las numerosas especies restantes ocupan los intersticios entre ellas. Tres especies de Cyperaceae fueron las más importantes en la comunidad, siendo *Cladium jamaicense* la más frecuente y la de mayor cobertura. La clasificación de Ward de los sitios y su ordenación por NMDS indicaron la existencia de cuatro grupos de vegetación diferentes florística y estructuralmente. Dentro de los sitios, los GLMM mostraron una relación inversa débil entre la riqueza de especies y la distancia al río, pero no así para la cobertura vegetal. La geomorfología fluvial y posiblemente la geología regional son los principales factores que determinan la variación espacial de estos humedales ribereños. La comprensión profunda de la relación de los humedales ribereños herbáceos con su ambiente mejorará la predicción de los efectos de modificaciones de la dinámica fluvial y dará sustento a estrategias eficientes de conservación.

Introduction

Wetlands are transitional ecosystems located at the boundaries of terrestrial and aquatic environments (Dodds 2002; Mitsch and Gosselink 2002; Keddy 2010). Despite their ecological significance for biodiversity conservation and the provision of ecosystem services to humans (Greeson et al. 1979; Keddy 2010; Clarkson et al. 2013; Betancur et al. 2016), these ecosystems face strong anthropogenic pressures which are rapidly forcing them towards disappearance (Turner et al. 2000; Mitsch and Gosselink 2002; Albert et al. 2021). By the early twenty-first century, these pressures had halved the original global coverage of wetlands (Zedler and Kercher 2005), making them one of the most threatened ecosystems on the planet.

Wetland plant communities exhibit high floristic, structural, and growth form diversity (Wheeler et al. 2002). Such diversity has been related to spatially contrasting environmental conditions such as microtopography, substrate characteristics including soil texture and nutrient availability, water chemistry, light exposure, oxygen levels in the water column, and flood depth and duration (Cronk and Fennessy 2001; Braddock and Berntsen 2007; Cherry 2011; van der Valk 2012; Meli et al. 2015; Chávez et al. 2020; Huang et al. 2022; Xu et al. 2024). The complex interplay of these factors often results in steep small- or mid-scale (i.e., meters to hundreds of meters) environmental gradients in these ecosystems that are responsible for their spatial heterogeneity (Flores-Verdugo et al. 2007; Chávez et al. 2020; Solórzano et al. 2020). Nonetheless, water depth, and in general flooding temporal dynamics, seem to be major factors affecting the spatial differentiation of wetland ecosystems, particularly in herbaceous communities, since the large variety of growth forms represented in them mainly differ from each other depending on whether they are rooted (either submerged or emergent) or free-floating (Sculthorpe 1967; Spence 1982; Cronk and Fennessy 2001; Thomaz et al. 2008; van der Valk 2012; Lot et al. 2015). Growth form diversity translates into large heterogeneity in vegetation physiognomy and structure, which has led to multiple wetland classification systems worldwide (Cowardin et al. 1979; Finlayson and van der Valk 1995; Scott and Jones 1995). Assessing the spatial heterogeneity of wetland ecosystems and understanding its underlying causes is crucial to designing efficient conservation actions for them.

Riparian wetlands are recognized as one of the most distinct wetland types in some of these classifications, yet they are one of the least studied ones despite accounting for a substantial fraction of total wetland area worldwide (Wantzen et al. 2008; Junk 2013; Rodríguez-González et al. 2022). Riparian zones are dynamic and complex habitats (Naiman et al. 1993) with varying characteristics largely depending on their location within the hydrological network, ranging from small forest-embedded areas at river headwaters to extensive floodplains with different plant communities adapted to seasonal flooding (Malanson 1993; Naiman and Décamps 1997; Stromberg et al. 2012). Constant changes in hydrological and geomorphological processes make riparian environments highly variable both spatially and temporally (Hamilton 2009; Park and Kim 2020). Thus, plant communities in these environments exhibit a high structural and compositional variability (Gregory et al. 1991). This variation may be observed not only along the river course but also perpendicular to it; for example, the axis orthogonal to the water course may be associated with a depth gradient related to differential species distributions, depending on their tolerance to floods and anaerobic soils, as well as their interactions with other species (Thomaz et al. 2008; Cherry 2011; Park and Kim 2020). Examination of such local variation in community attributes is necessary to fully understand the consequences of wetland spatial heterogeneity across scales.

Although over 50% of wetlands occur in tropical and subtropical regions worldwide (Cronk and Fennessy 2001), research on these ecosystems has mainly focused on temperate regions in North America and Europe (Barba-Macías et al. 2006; Junk et al. 2013). The conservation situation of wetlands

in Mexico, one of the world's megadiverse countries, is also critical (Moreno-Casasola et al. 2012). Approximately 70,000 km^2 of wetlands have already been lost in this country, which is equivalent to 61% of their original area (Landgrave and Moreno-Casasola 2012). Most of our knowledge about Mexican wetlands derives from taxonomic and ecological studies of coastal wetland floras (e.g., Olmsted 1993; Moreno-Casasola et al. 2010; Landgrave and Moreno-Casasola 2012; Mora-Olivo et al. 2013; Lobato-de Magalhães and Martínez 2018; López-Jiménez et al. 2020) and from research focused on the ecology and conservation of mangrove forests (Thom 1967; Flores-Verdugo et al. 1992; López-Portillo and Ezcurra 2002; López-Medellín and Ezcurra 2012; Rodríguez-Zúñiga et al. 2013; Chávez et al. 2020; Aburto-Oropeza et al. 2021). By contrast, the extensive areas of inland herbaceous wetlands found throughout Mexico, many of which are associated with rivers, are comparatively understudied.

Our goals were twofold. First, we aimed to assess the floristic and structural spatial variation of herbaceous riparian wetland communities along one river of southern Mexico (namely the San Pedro Mártir River), noted for its good water quality (Estrada Loreto 2011) but in need of conservation actions due to the expansion of intensive farming in the region (Isaac-Márquez et al. 2005). The second goal was to examine the factors underlying wetland vegetation spatial heterogeneity at two scales, namely among herbaceous wetland communities along the river, and within each of these communities. We hypothesized the existence of different factors driving herbaceous wetland community structure at these two scales. First, we hypothesized that fluvial geomorphology is a major driver of wetland differentiation as the migration of the river channel creates different habitats (e.g., sites dominated by erosional or depositional processes) along its course. Regarding within-site heterogeneity, we hypothesized that this is mainly related to the distance to the river, because of the factors that operate mainly near the river edge (e.g., more frequent disturbance related to river dynamics). Given the role of disturbance on community diversity, we expected a stronger differentiation in community species richness over this small-scale gradient. To test these hypotheses, we conducted vegetation surveys to record species occurring in the studied wetlands, assessed species diversity and distribution along the course of the river, and analyzed the spatial variability of vegetation cover by using multivariate techniques and mixed-effects modeling.

Methods

Study Region

The Usumacinta River is only second to the Mississippi in terms of its average annual discharge (3,727 $m^3 s^{-1}$) in the Gulf of Mexico (Kolb and Galicia 2012). Its basin covers an area of 73,192 km^2 and stands out as one of the most biodiverse regions in Mesoamerica (March Mifsut and Castro 2010; Meave et al. 2021; Jiménez-López et al. 2023). The San Pedro Mártir River (hereafter simply referred to as San Pedro River) is one of the most important transboundary tributaries (its headwaters is in Guatemala) of the Usumacinta (Saavedra et al. 2019; Fig. 1). This tropical lowland region's climate is warm and humid with abundant summer rainfall, an average annual temperature ranging from 26 to 28 °C, and total annual precipitation varying between 1,500 and 2,500 mm (Arriaga-Cabrera et al. 2000). The San Pedro River sub-basin is located on the southern margin of the Yucatán Peninsula, with its course flowing approximately along the boundary between two major geological formations, the Yucatán Platform and the Chiapas Highlands (Bauer-Gottwein et al. 2011).

In its Mexican portion, the San Pedro River is characterized by a wide channel (average width of 145 m), and its floodplains are allochthonous stream environments, with their sediments mainly coming from other regions (Estrada Loreto 2011; Solís-Castillo et al. 2014). Although its drainage pattern is overall straight for most of its course (Castillo-Acosta et al. 2019), anastomosed patterns are present in many sections, especially near its mouth. This drainage pattern, typical of a high-flow river flowing through very flat and low terrain, allows a very active lateral channel migration. The result is a complex fluvial geomorphology with pronounced meanders, side channels of varying widths, large changes in channel width, and the presence of oxbow lakes (Christopherson 2006; Charlton 2008).

The vegetation in the banks of the San Pedro is represented by several natural and man-made plant communities, including old-growth and secondary semi-deciduous tropical forest, evergreen *Haematoxylon campechianum* forest, shrubland, natural and cultivated grasslands, and aquatic and semi-aquatic (i.e., wetland) vegetation (Estrada Loreto 2011; Cámara Cabrales et al. 2019; Castillo-Acosta et al. 2019; Martínez-Camilo et al. 2020). Along the Mexican section of the San Pedro, wetlands cover an area of approximately 10,300 ha, reaching maximum widths from the river inland of over 1 km, but usually much less (Estrada Loreto 2011).

Study Sites and Vegetation Sampling

Ten sites along a 40-km long stretch of the San Pedro River were chosen, in areas without visible signs of disturbance. Vegetation was surveyed at the end of the dry season, in May 2018, to maximize access to the study sites and to avoid the peak flooding period (Vis et al. 2003). At each site, twelve 2×2 m (4 m^2) plots were used for vegetation sampling (Kent 2012), except at Site 7 where only six plots were sampled. The plots were placed at 5-m intervals along two 37-m long, parallel lines located 30 m apart and perpendicular to the river channel (Fig. S1 in Supplementary Information).

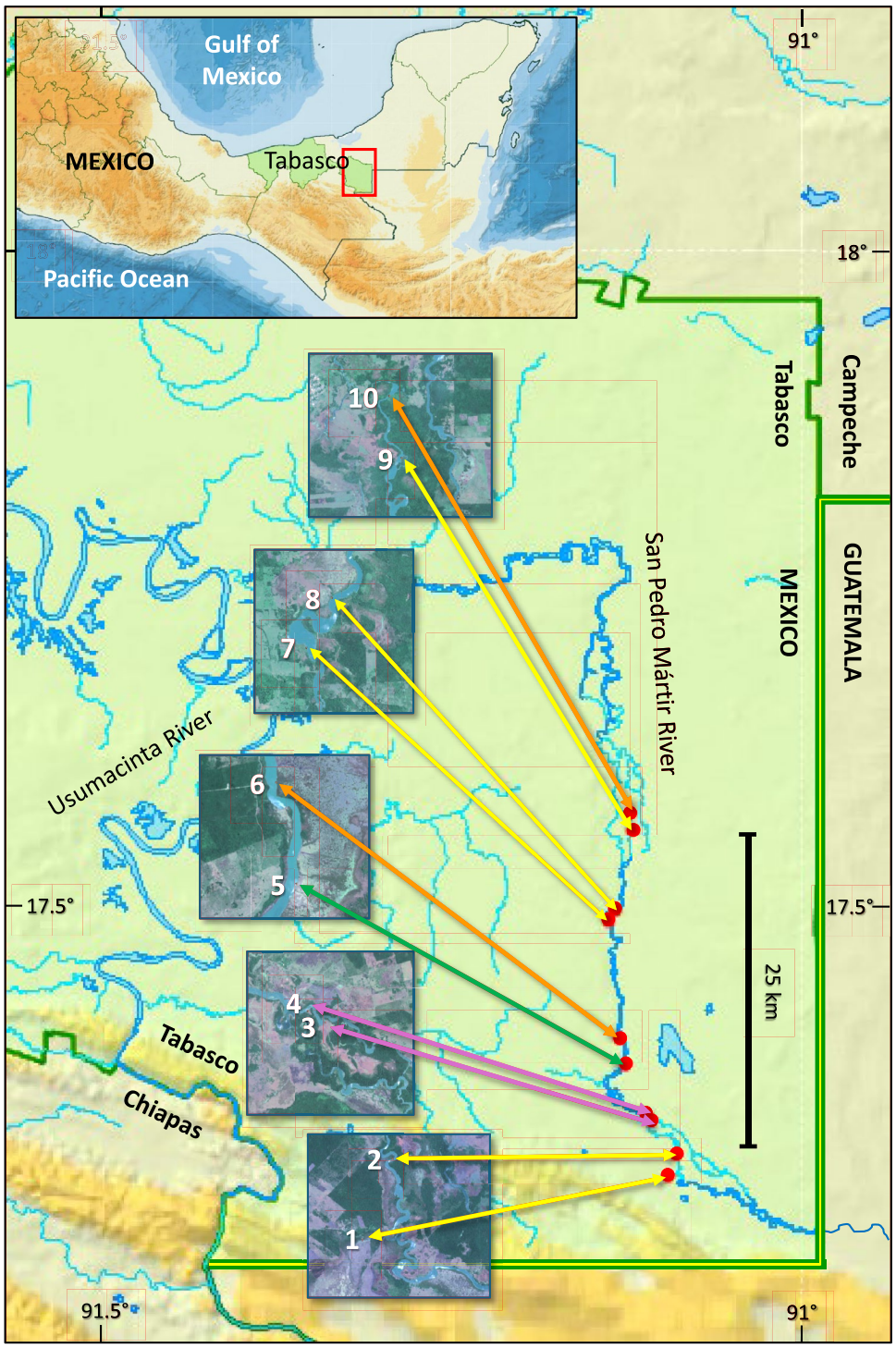


Fig. 1 Location of the study riparian herbaceous wetlands in Mexico and their classification based on multivariate methods. Inset: study region in Tabasco State, southern Mexico. The river sections where the study sites are located are represented by windows of Sentinel 2 images from the study period (May 2018). The arrows connecting sites (red circles) and site numbers are color-coded to reflect the site classification according to Ward's clustering and NMDS ordination. Color code: pink, Group 1; green, Group 2; yellow, Group 3; orange, Group 4

The presence of all plant morphospecies occurring at each plot was recorded. The morphospecies were determined to different taxonomic levels using taxonomic keys (Standley and Steyermark 1952; Davidse et al. 1994, 1995; Stevens et al. 2001; Lot et al. 2013). Vouchers were collected for later determination in the laboratory. Lack of reproductive structures prevented determination of some morphospecies, but this material was carefully examined to avoid overestimation of diversity due to duplication of unidentified species.

At the center of each plot, we took between five and eight photographs to assess the cover of each species. We used a 20-megapixel *Evorok Adventure III* camera with a wide-angle lens that was mounted on a support fixed to

an L-shaped structure made of PVC pipes, which allowed maintaining the camera height 3 m above the vegetation (Fig. S1 in Supplementary Information). Additionally, the cover of some species was visually estimated and recorded in the field. In the laboratory, the photographs taken in the field were corrected using *Adobe Photoshop CC 2018* to reduce the spherical distortion produced by the wide-angle lens. Next, to estimate the cover of each morphospecies, the images were divided into four equal sections to facilitate the use of the Ordinal Transfer Value (OTV), a modification to the nine-value ordinal scale proposed by van der Maarel (2005), which uses the mean value of the extremes of each cover interval (Table S1 in Supplementary Information). The percent cover of each plant was transformed into cover values expressed in area (m^2), with the maximum value being 4 m^2 in a plot.

Data Analyses

Community diversity was assessed through the Hill numbers framework (Hill 1973), i.e. effective number of species, for three diversity q orders: $q=0$ (^0D), $q=1$ (^1D), and $q=2$ (^2D), which differ from each other in the relative weights they give to species abundances (no weight in $q=0$ and maximum weight in $q=2$) (Jost 2006). Because we were unable to count individuals in the field (mainly due to the clonal growth of many wetland species), we used the fraction of total cover corresponding to each species instead of the fraction of total abundance. The equations of Chao et al. (2014) were used to calculate the diversity values of order 1 and 2, following the modifications of the Shannon and Simpson indices proposed by López-Olmedo et al. (2006).

$$^1D = exp(H) = exp\left[-\left(\sum_{i=1}^{S}\left(\frac{COV_i}{COV_{tot}}\right)ln\left(\frac{COV_i}{COV_{tot}}\right)\right)\right]$$

$$^2D = \frac{1}{\sum \frac{(COV_i)(COV_i-1)}{(COV_{tot})(COV_{tot}-1)}}$$

where COV_i = cover fraction of the i_{th} species, and COV_{tot} = total cover of all species.

Rarefaction curves were constructed for the entire herbaceous wetland community (i.e., all sites together) and for the local communities at each site separately, using the R package iNEXT (Hsieh et al. 2024) with order 0 (^0D) diversity. For Site 7, where only half of the plots were sampled, an extrapolation curve was used to estimate the number of species in an area equal to that sampled at the other sites.

The quantitative structure of the wetland vegetation at each site was calculated based on cover estimates of all individual plants present in the plots. Individual cover values were summed to calculate the total cover by species and site. Then, cover values of each species were transformed into relative cover. In addition to these values, the relative frequency of each species at each site was calculated based on their occurrence in the 12 sampling plots. Finally, the relative cover and frequency values of each species at each site were summed to obtain their relative importance values (RIV).

To examine the floristic and structural heterogeneity in the study wetland and explore the potential existence of groups of sites based on their similarities, we first conducted a site classification using Ward's method with Euclidean distances as linkage distances. Two classifications were done: one using binary (presence-absence) data of species, and the second one using species' RIVs to explore both the qualitative and quantitative aspects of community structure. Next, to visualize the floristic relationships among sites, Non-metric Multidimensional Scaling (NMDS) was employed (ter Braak 1995). This method involves a non-parametric ordination based on the ranks of distances (floristic dissimilarity) between sites. To detect significant differences in species composition among sites, Permutational Multivariate Analysis of Variance (PERMANOVA) was used. Finally, to identify those sites that showed significant differences in their species composition with others, we conducted a multiple comparisons analysis with the *pairwise.adonis* function in R (Martínez Arbizu 2020); *p*-values were adjusted using the Bonferroni method (Dunn 1961). Due to the random nature of this permutational analysis, the results of this test represent the mean of 20 runs. The species making the strongest contribution to the observed dissimilarity between sites were identified using the Similarity Percentages (SIMPER) procedure. We used the default (1,000) number of permutations.

To evaluate the effect of distance to the river channel on wetland vegetation attributes we used linear mixed-effects models and generalized linear mixed-effects models. Two model types were used because the error distribution family varies according to the response variable (Y): Gaussian for cover (continuous variable) and Poisson for richness (count variable). For each response variable, five models were constructed, including the null model (Model 1, without the distance to the river effect) and four models that included this effect:

$$Y \sim \beta_0 + (\beta_0|Site) \quad \text{(Model 1)}$$

$$Y \sim \beta_0 + \beta_1 X + (\beta_0|Site) \quad \text{(Model 2)}$$

$$Y \sim \beta_0 + \beta_1 X + \beta_2 X^2 + (\beta_0|Site) \quad \text{(Model 3)}$$

$$Y \sim \beta_0 + \beta_1 X + \beta_2 X^2 + \beta_3 X^3 + (\beta_0|Site) \quad \text{(Model 4)}$$

$$Y \sim \beta_0 + \beta_1 lnX + \left(\beta_0 | Site\right) \quad \text{(Model 5)}$$

In the latter four models, the explanatory variable X (distance to the river) was used in four forms: its original form, i.e. as measured in the field (Model 2), squared (Model 3), cubed (Model 4), or ln-transformed (Model 5), to allow the possibility of non-linear relationships. In all five models the Site was included as random factor $\left(\beta_0 | Site\right)$. Models were compared with the sample corrected Akaike Information Criterion (AICc) using the `aictab` function of the **AICcmodavg** package (Mazerolle 2023); models with ΔAICc ≤ 2 were considered indistinguishable, i.e., equally supported (Burnham and Anderson 2002). When equally supported models were found, an average model was constructed with the *model.avg* function in the **MuMIn** package (Bartoń 2023). The models were fitted using the `lmer` (cover) and `glmer` (richness) functions from the **lme4** package (Bates et al. 2015) in R (R Core Team 2024).

Results

Floristic Composition

The checklist of taxa recorded in all sampling sites of the San Pedro River wetland vegetation includes 76 morphospecies, of which 45 (58.4%) were determined to species, 12 (15.5%) to genus, and 10 (13.2%) to family level only (Appendix 1 in Supplementary Information). The group of taxa determined to any of these taxonomic levels includes 31 families, 45 genera, and 45 species; the classification of plant groups uses the taxonomic classification systems APG IV (2016) for Angiosperms and PPG I (2016) for ferns. Nine morphospecies (11.8%) remained undetermined and are listed as unknown species. The majority (95.5%) of the 67 morphospecies determined to any taxonomic level were Angiosperms, whereas a much smaller fraction (4.5%) were ferns. The Angiosperms included large fractions of eudicots (54.7%) and monocots (43.7%), but a single member only of the Nymphaeales order (1.6%) (Table 4.1). The most speciose family was Cyperaceae, with 12 species representing six genera, followed by Poaceae (11 species, 4 genera), and Fabaceae (6 species, 5 genera). Most remaining families were represented by one or two species each, except Convolvulaceae (4 species), and Asteraceae and Verbenaceae (3 species each) (Fig. S2 in Supplementary Information). In turn, the richest genera were *Eleocharis* (Cyperaceae), *Fuirena* (Cyperaceae), *Ipomoea* (Convolvulaceae), and *Phyla* (Verbenaceae), with three species each.

Wetland Community Diversity

The slope of the species rarefaction curve for the entire sampled area (456 m^2) did not stabilize (Fig. S3 in Supplementary Information), suggesting that increasing sampling area would reveal a larger number of species in the community. In contrast to the total richness (${}^0D$) recorded in the entire sampling (76 species), the asymptotic diversity estimate (average total richness), calculated using the *ChaoRichness* function from the iNEXT package, was 115.65 species (95% confidence interval: 76 to 181.55), indicating a moderate sampling completeness (65.72%). The diversity measures that weigh abundant species more heavily (${}^1D$ and ${}^2D$) were 11.89 and 4.99 species, respectively, which imply that this community is characterized by the strong dominance of a few species. Similarly, the species rarefaction curves calculated for each site separately indicated that the sampled area was insufficient to reach theoretical asymptotes despite a large variation in their slopes (Fig. S4 in Supplementary Information). Even so, completeness was $< 60\%$ in only two sites and it was $> 70\%$ in four sites (Table 1).

In more than half of the sampling sites, the recorded richness was ≥ 20 species, whereas the remaining four sites had 15 or 16 species each. Notably, the true diversity values (Hill numbers) showed, again, drastic reductions in the effective number of species when giving increasingly larger weights to abundant species (${}^1D$ and ${}^2D$), confirming the presence of a high number of rare species and a marked dominance by a few species locally (Table 1).

Quantitative Structure of the Community

In the entire sampled area, total plant cover was 361.22 m^2 (i.e., $< 80\%$ of the sampled area), reflecting the existence of large gaps in this community's canopy in the dry season. The species with the largest cover was *Cladium jamaicense* (149.3 m^2; 41.3% of the total cover). This species was also the most frequent in all sampling, as it was recorded at all sites and in a high proportion (67.0%) of the sampling plots.

Only two species, both of them Cyperaceae, had relative importance values (RIV) > 10, but with a remarkable gap between them; the highest value corresponded to *Cladium jamaicense* (46.08), distantly followed by *Eleocharis interstincta* (16.68). Beyond this latter species, RIVs were less discontinuous, with a prevalence of species having very low values (Appendix 2 in Supplementary Information). In most species, relative frequency contributed more to their RIV than their cover, except for *Cladium jamaicense*, *Eleocharis interstincta*, and *E. cellulosa*, for which cover contributed more than 85% to their RIVs. These figures reveal the large asymmetry in the contributions of species to overall community structure.

Table 1 Diversity and structure in the riparian wetlands of the San Pedro Mártir River, Mexico. The data shown for each site are the mean number of species per plot (± SD), true diversity values (species richness, ${}^0D$; the effective number of common species, ${}^1D$; and the effective number of dominant species, ${}^2D$), asymptotic richness, completeness, and total percentage of plant cover

Site	Mean number of species per plot	${}^0D$	${}^1D$	${}^2D$	Asymptotic richness	Completeness (%)	Cover (%)
Site 1	11.17 (± 2.07)	27	7.11	3.76	35.25	76.60	80.48
Site 2	7.50 (± 1.32)	20	3.28	2.00	32.37	61.79	86.17
Site 3	5.43 (± 2.25)	16	2.92	1.69	29.75	53.78	67.50
Site 4	6.67 (± 2.43)	21	2.47	1.52	30.78	68.23	71.63
Site 5	5.42 (± 2.18)	16	3.15	2.44	27.46	58.27	74.96
Site 6	9.17 (± 1.52)	26	10.28	7.94	41.67	62.40	73.27
Site 7*	6.67 (± 1.60)	16	2.50	1.57	22.80	70.18	82.67
Site 8	8.75 (± 2.13)	29	4.13	2.21	40.09	72.34	84.67
Site 9	6.25 (± 1.42)	15	2.48	1.59	18.82	79.70	92.02
Site 10	8.00 (± 1.83)	20	10.00	9.16	31.23	64.04	77.35

Patterns of community dominance were similar at the site level. In more than half of the sites, *Cladium jamaicense* was the dominant species, generally with > 60% of the site's total plant cover (Fig. 2). Notwithstanding such strong dominance by this sedge at many sites, it is notable that in other sites this species made a very minor contribution to community structure (albeit it was always present). For example, at Site 10 three species shared dominance (*Ipomoea carnea*, *Scleria macrophylla*, and *Wedelia acapulcensis*), together accounting for 56.3% of the site's total plant cover. In turn, at Sites 3 and 4 the dominant species was *Eleocharis interstincta* (RIVs > 90), accounting for > 70% of total cover at these sites. At these two latter sites, the second most important species was *Phyla stoechadifolia*, which had low cover values but high frequencies, Finally, at Site 5 the most important species was *Eleocharis cellulosa* (RIV = 80; 58% of site's total cover); interestingly, the species with the second highest RIV (44) was *Cladium jamaicense*, where it accounted for slightly more than 30% of the total cover at this site.

Site Classification and Ordination

Figure 3 shows the site classification obtained with Ward's Method and Euclidean distances based on species' RIVs at each site. The dendrogram based on presence-absence data (not shown) was very similar, with only two sites changing group position and the groups being less clearly defined. This dendrogram indicates the existence of three groups of sites with similar internal structure and homogeneity plus a fourth group comprising a single site (Site 5). In both classifications Sites 3 and 4 were the most similar to each other and the first ones to join, forming a single group.

The NMDS ordination based on species cover data from the 114 plots at the ten sites (Fig. 4a) revealed a discontinuous distribution along the primary axis (NMDS1), indicating a clear separation between two sets of sites. On the right side of the ordination space lies a group comprising Sites 3 and 4; in turn, on the left side of the ordination there is a greater site overlap, particularly for Sites S1, S2, S7, S8 and S9. Regarding NMDS2, Sites 3 and 4 were highly homogeneous and overlap almost completely, whereas the remaining sites are more amply dispersed along this axis. Site 5, located at the lower sector of the ordination space, appears to represent a distinct community that differs from all others, as it does not overlap with any other site in the ordination, in consistency with its position as a separate group in the quantitative classification. Finally, in the upper part of the ordination space (and centrally located on NMDS1) Sites 6 and 10 form a distinct group although relatively close to the larger group that contains all remaining sites. This means that the NMDS ordination confirmed the four floristically different communities that were distinguished by Ward's clustering. The vectors representing the weights of the different species on the NMDS ordination axes (Fig. 4b) reveal the identities of the species contributing the most to this pattern: *Eleocharis interstincta* for the group in the far right (hereafter referred to as Group 1), *Eleocharis cellulosa* for the group only containing Site 5 (Group 2), *Cladium jamaicense* and *Ageratina malacolepis* for the large group of the left side (Group 3), and *Ipomoea carnea*, *Typha domingensis* and *Scleria macrophylla* for the group located toward the top of the ordination plot (Group 4).

Generally, the results of the PERMANOVA were consistent with the NMDS ordination, although with some notable differences. According to this analysis, Sites 3 and 4 differed significantly from all other sites but not from each other (Table S2 in Supplementary Information). Also, Site 7 did not differ significantly from any other site included in Group 3, which is the largest one in the ordination. However, almost all other pairwise comparisons involving sites in this group produced significant differences, except between Sites 1 and 8. In turn, Sites 6 and 10 also showed a different pattern than that observed in the ordination: although they were recognized as a single group both in the ordination

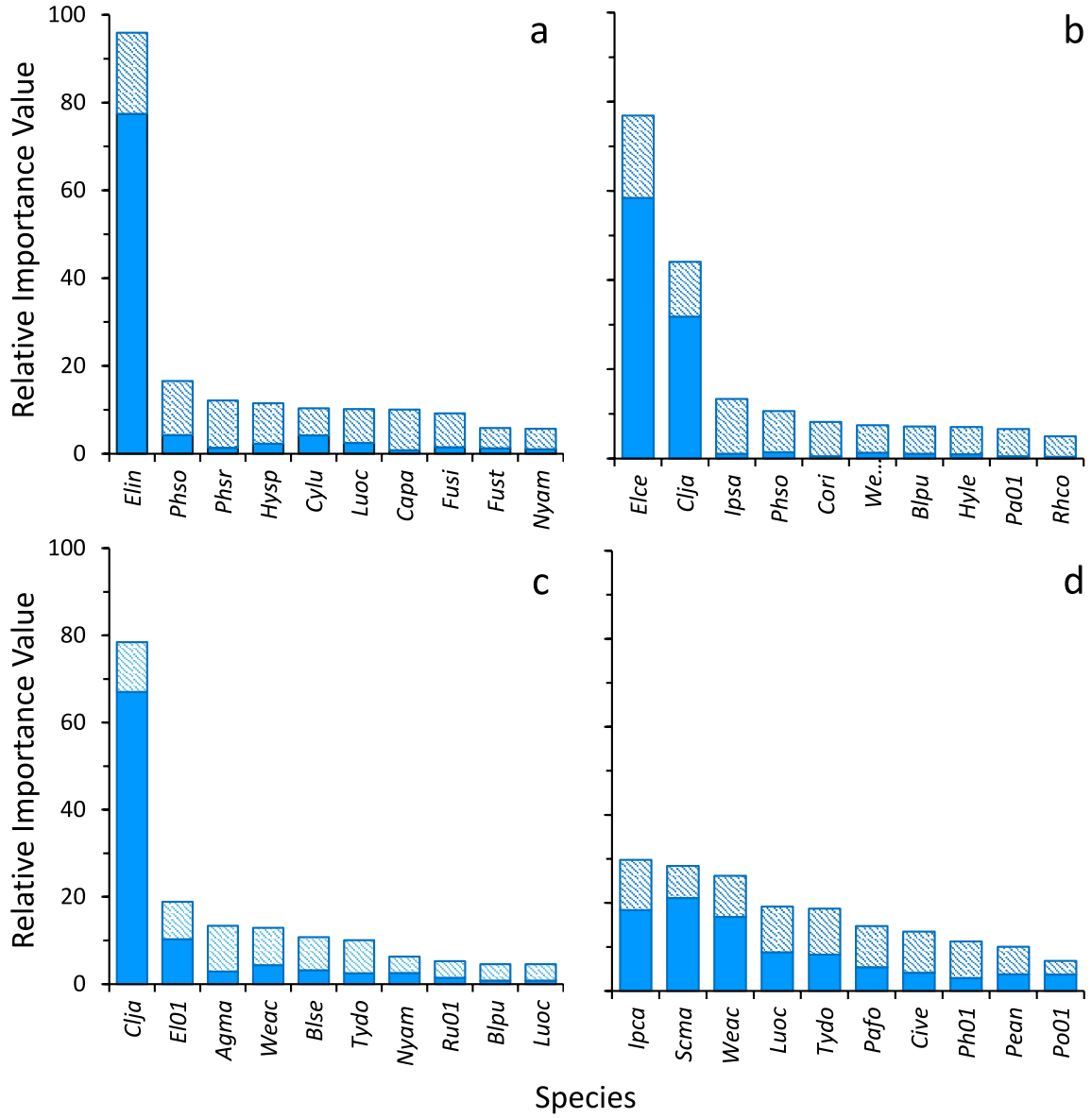


Fig. 2 Relative importance values (RIV) of the ten most important species at four sites representing different riparian wetland groups (according to Ward's classification and NMDS ordination) along the San Pedro Mártir River, Mexico. The RIV of each species is dissected to show the fraction corresponding to the relative cover (solid bar) and the relative frequency in the site (dashed bar). (a) Site 3, dominated by *Eleocharis interstincta*; (b) Site 5, dominated by *Eleocharis cellulosa*; (c) Site 8, dominated by *Cladium jamaicense*; (d) Site 10, without strong dominance of any species. Species abbreviations: Agma, *Ageratina malacolepis*; Blse, *Blechnum serrulatum*; Blpu, *Bletia purpurea*; Capa, *Caperonia palustris*; Cive, *Cissus verticillata*; Clja, *Cladium jamaicense*; Cori, *Coleataenia rigidula*; Cylu, *Cyperus lundellii*; Elce, *Eleocharis cellulosa*; Elin, *Eleocharis interstincta*; El01, *Eleocharis* sp01; Fusi, *Fuirena simplex*; Fust, *Fuirena stephani*; Hyle, *Hydrocotyle leucocephala*; Hysp, *Hydrolea spinosa*; Ipca, *Ipomoea carnea*; Ipsa, *Ipomoea sagittata*; Luoc, *Ludwigia* aff. *octovalvis*; Nyam, *Nymphaea ampla*; Pafo, *Passiflora foetida*; Pa01, *Panicum* sp01; Phso, *Phyla stoechadifolia*; Phsr, *Phyla strigulosa*; Ph01, *Physalis* sp01; Pean, *Pentalinon andrieuxii*; Po01, Poaceae sp01; Rhco, *Rhynchospora* aff. *colorata*; Ru01, Rubiaceae sp01; Scma, *Scleria macrophylla*; Tydo, *Typha domingensis*; Weac, *Wedelia acapulcensis*

and the site classification, they differed significantly from each other, while Site 6 did not differ significantly from Sites 1 and 7. Notably, the results for some pairwise comparisons were inconsistent across runs. For example, comparisons between Sites 6 and 1 showed an average adjusted p-value of 0.06, although only 4 out of 20 runs had adjusted p-values > 0.05. Contrastingly, in comparing Sites 6 and 7, 12 out of 20 runs had an adjusted p-value > 0.05. Finally, the PERMANOVA showed that Site 5 significantly differed from almost all sites but Site 7. However, although the average adjusted p-value was 0.065, only 7 out of 20 runs had adjusted p-values > 0.05. The group of species making the

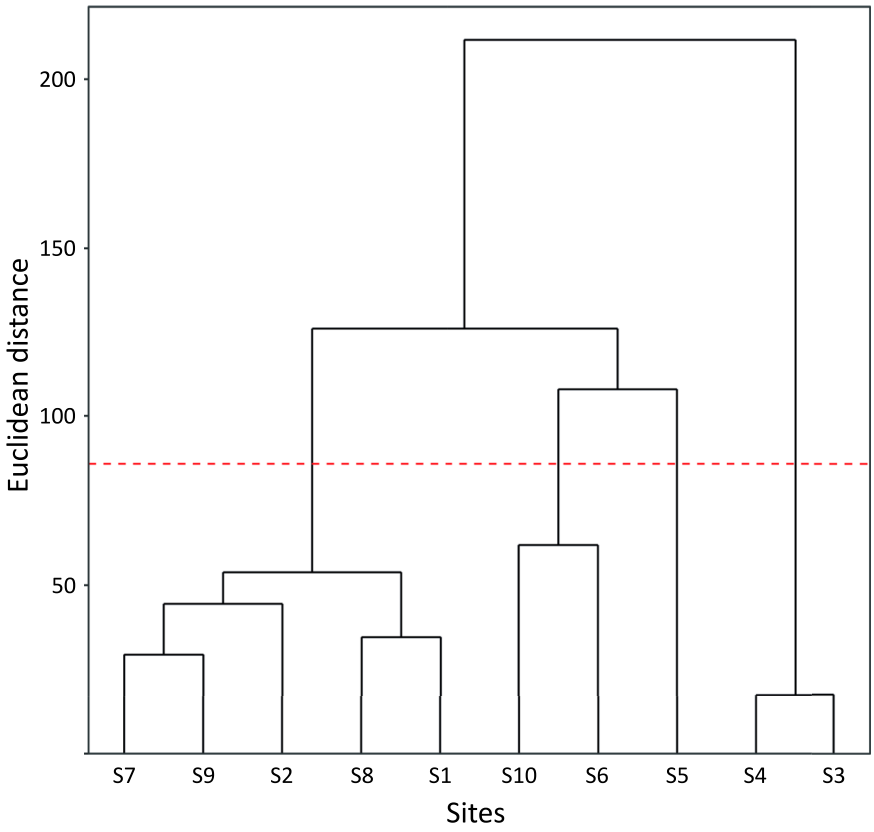


Fig. 3 Cluster analysis (Ward's Method) of ten riparian herbaceous wetland sites along the San Pedro Mártir River, Mexico. Linkage distances are Euclidean distances based on a matrix containing species and their Relative Importance Values (RIVs). The broken red line shows the linkage threshold separating four groups of sites

largest contributions to between-site floristic differences included, in decreasing order, *Cladium jamaicense* and *Eleocharis interstincta*, and less frequently *Eleocharis cellulosa*, *Scleria macrophylla*, and *Ipomoea carnea*, with the latter two species mainly defining the differences between Site 10 and the remaining sites (Table S2 in Supplementary Information).

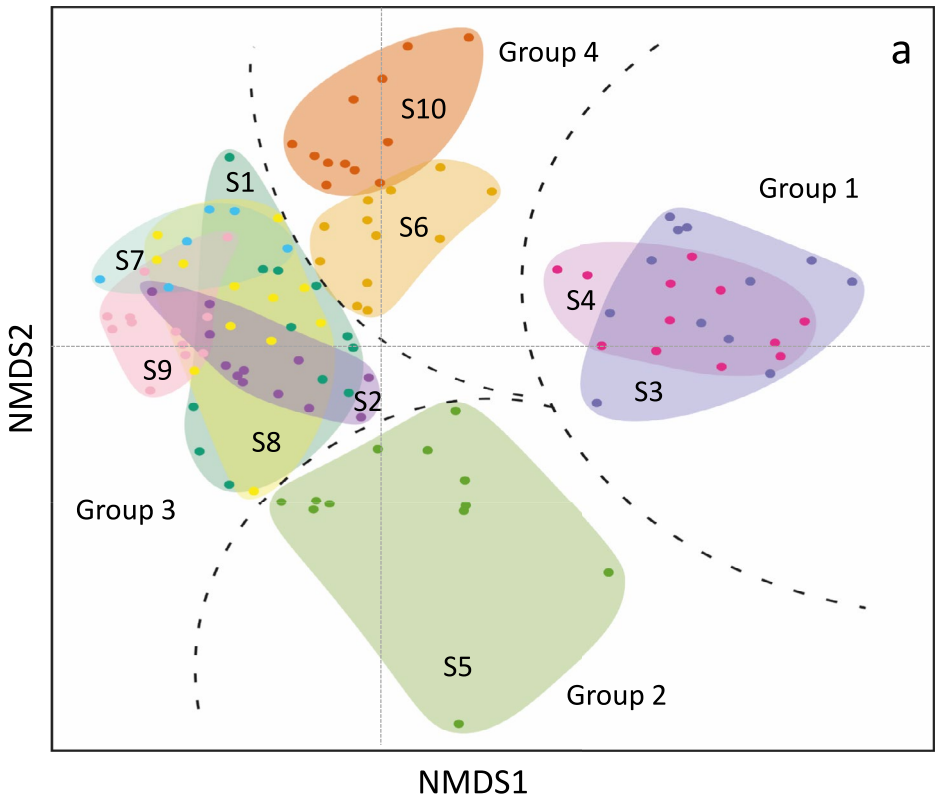
Within-Site Differentiation Related to the Distance from the River Channel

Within the set of models evaluated to analyze the variation of plant cover and species richness as functions of distance from the river channel, no single model was identified as the best fit for species richness. Therefore, an average model was constructed for this response variable based on the coefficients of the models with the best fits (Fig. 5).

For plant cover, Model 1 (the null model) was the best fit ($\Delta AIC = 0$), suggesting that distance from the river channel does not have a significant effect on this response variable (Fig. 5a). Unlike cover, however, when species richness was the response variable, the null model was not among the models best supported by the data; all best models (Model 5 or logarithmic, $\Delta AIC = 0$; Model 2 or linear, $\Delta AIC = 0.10$; and Model 3 or quadratic, $\Delta AIC = 1.66$) clearly showed that richness peaks right at the river edge and then gradually decreases until reaching its lowest value in the wetland portion that is furthest inland (Fig. 5b).

Discussion

In this study, we analyzed the structure and floristic composition of riparian herbaceous wetlands along the San Pedro Mártir River (S Mexico) to gain insights into community assembly of these wetlands and to test the hypotheses that the spatial variation of these communities is related to fluvial geomorphology and to within-site (distance to river) factors. Overall, our results support these hypotheses, as they revealed substantial heterogeneity in these riparian wetlands at two scales. At the regional scale, despite the frequent dominance of the sedge *Cladium jamaicense*, we identified four vegetation groups, mainly differentiated by their composition, with this species making a minor contribution to community structure at some sites. In addition, we also found evidence of within-site heterogeneity related to the distance to the watercourse (for species richness only), but this variation was much smaller than that observed among sites. Although the large plant community heterogeneity in these riparian wetlands is clearly related to fluvial geomorphology, we found some evidence that the lithological diversity in the area may also contribute to this heterogeneity.



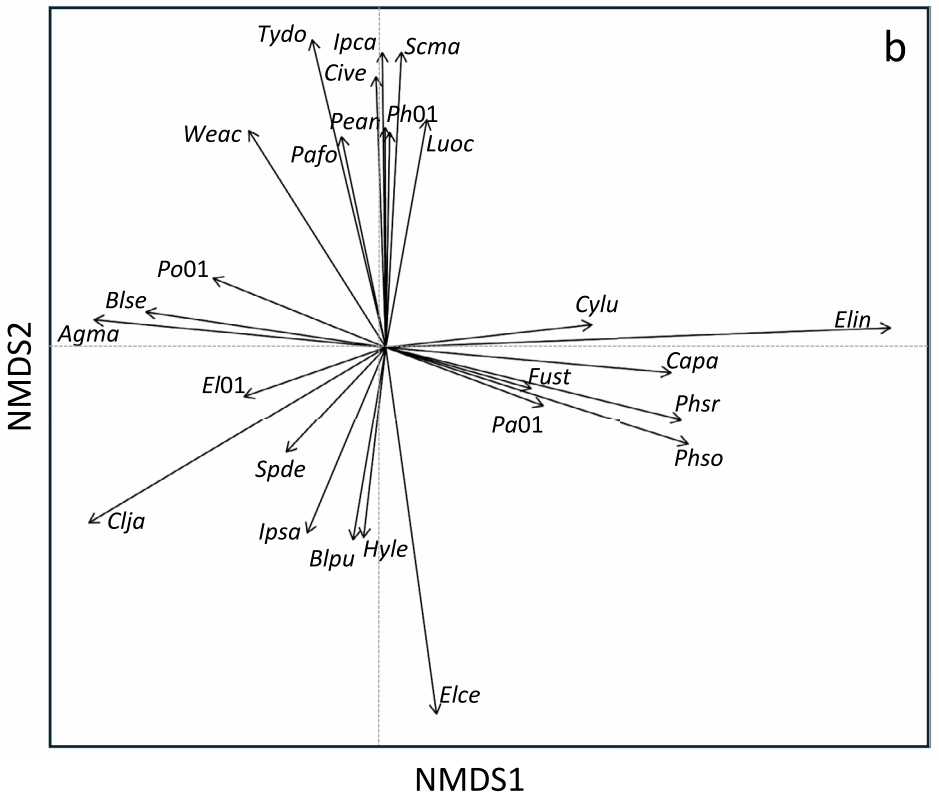


Fig. 4 NMDS ordination of ten riparian herbaceous wetland sites along the San Pedro Mártir River (Stress = 0.183). (a) Distribution of all 4-m^2 quadrats sampled at ten sites along the river on the ordination space. Group definition and number derived from the Ward's clustering of these sites. (b) Vectors of the species determining the distribution of sites on the ordination space. Species abbreviations as in Fig. 2, except for Spde, *Spermacoce densiflora*

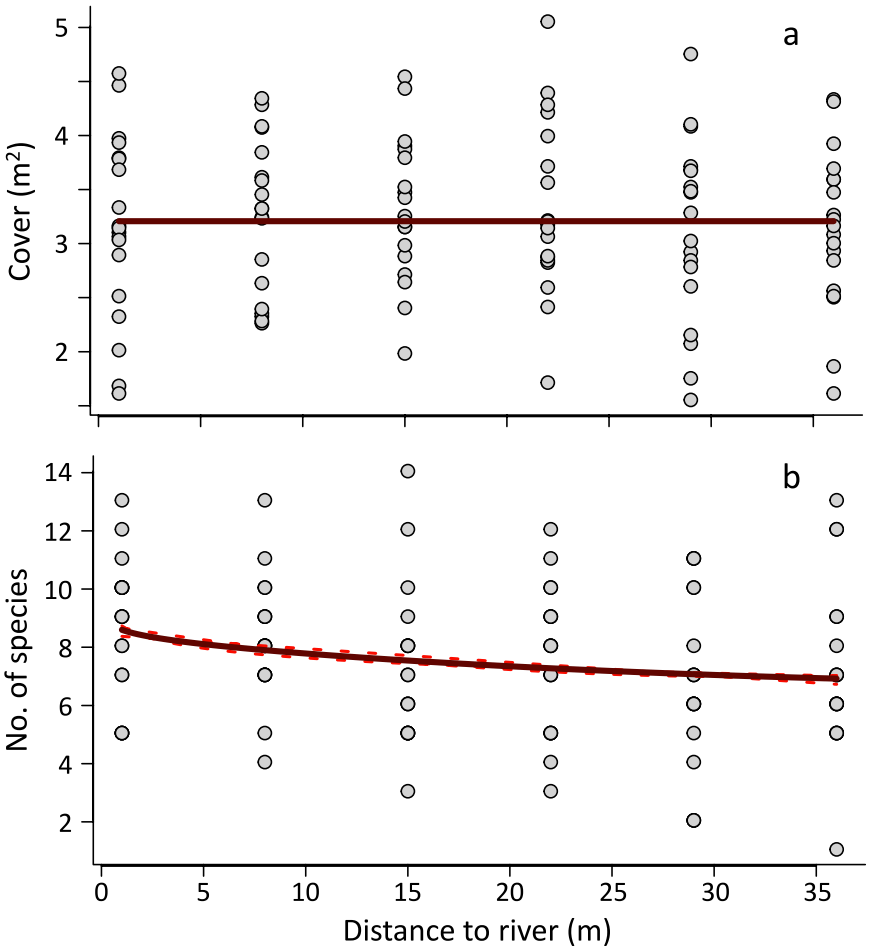


Fig. 5 Relationship between vegetation cover (a) and species richness (b) with distance to the edge of the San Pedro Mártir River. The dark red solid line represents the model with the highest support based on the data. The light red dashed lines represent models with a ΔAICc < 2, which were averaged to obtain the final model, if present. Each gray dot corresponds to a sampled plot within each site

In the following sections these results will be discussed at greater depth.

Floristic Composition and Dominance in the San Pedro Mártir River Riparian Wetlands

The peculiar semi-aquatic environment that characterizes wetlands is challenging for plant establishment; this condition has fostered the emergence of fine adaptations that enable plant species to thrive in frequently or permanently flooded environments (Duarte et al. 1994; Colmer and Voesenek 2009; Sand-Jensen et al. 2022). The floristic composition of the studied riparian wetlands is dominated by Angiosperms, while ferns are less common, in agreement with floristic patterns observed not only in modern wetlands but also in paleo-communities of this type since the Lower Cretaceous (Martín-Closas 2003). Interestingly, although dicots were slightly more diverse than monocots among Angiosperms, the most species-rich families, namely Cyperaceae and Poaceae, are monocots. The large richness of these two families concurs with reports for other tropical wetlands that point to the concentration of species and genera in them (Córdova et al. 2022; Khan et al. 2022).

The strong dominance of Cyperaceae (e.g., *Cladium jamaicense*, *Eleocharis interstincta*, and *E. cellulosa*) in this riparian herbaceous wetland is likely related to their ability to reproduce vegetatively (i.e., clonal expansion), a key trait behind their colonization success (Grace 1993; van Groenendael et al. 1996; Honnay and Jacquemyn 2010; van der Valk 2012), along with the presence of long, tuberous rhizomes that function as storage or resistance structures (Reznicek 2023). Clonal expansion may be largely responsible for the typical monodominated pattern of herbaceous riparian wetlands, which consists of a single or a few dominant species that are accompanied by numerous rare species that take advantage of the interstices amidst the dominant community elements (Boutin and Keddy 1993). Intriguingly, however, one of our study sites (Site 10) deviates considerably from this pattern, with more than half (56.3%) of its plant cover being shared among three species, none of which is hyper-dominant (here, hyper-dominant species are defined as those accounting for > 50% of plant cover, in analogy to Draper et al.'s [2021] definition based on density of individuals). As discussed later, local disturbance may be involved in the lack of dominance at this site.

Another interesting aspect of these riparian wetlands' composition is that grasses are nowhere dominant despite being represented by numerous species. Herbaceous terrestrial plant communities are commonly dominated by grasses and their structural patterns are similar to the one reported here: many rare species occupying minor positions in the community living in the few spaces left by the dominant taxa (López-Olmedo et al. 2006). Unlike terrestrial herbaceous vegetation, sedges are the dominant element in herbaceous wetlands (Goetghebeur 1998; Larridon 2011; but see Xu et al. 2024 for an example of riparian wetlands dominated by Poaceae and Asteraceae), and in fact over one quarter of Mexican Cyperaceae are aquatic or sub-aquatic species (Diego-Pérez and González-Elizondo 2013).

Regional-Level Heterogeneity of the Riparian Herbaceous Wetlands

The riparian herbaceous wetlands along the San Pedro are not uniform across the study region, as they encompass at least four distinct plant communities differing in structure and composition attributes. Although a variety of environmental factors may be involved in the regional spatial variation of these riparian wetlands (Naiman et al. 2005; Lawson et al. 2015), our results support the hypothesis that this heterogeneity is at least partly related to this river's fluvial geomorphology. Along its course, the San Pedro River is characterized by typical features of a high-energy fluvial flow, such as wide meanders and oxbow lakes, which are created during its lateral channel migration over the floodplain due to differential erosion and sediment deposition (Charlton 2008; Bogoni et al. 2017). Such river dynamics creates distinctive habitats across the alluvial floodplain (Fig. 1), leading to the creation of mosaics of contrasting plant communities (Kalliola and Puhakka 1988; Gregory et al. 1991; Naiman and Decámps 1997; Hamilton 2009). This agrees with our finding that the species composition at most sites located in different functional zones of the river course (e.g., deposition vs. erosion-dominated) differed significantly according to PERMANOVA, whereas sites apparently located in similar functional zones supported relatively similar wetland communities (e.g., Sites 1, 7, 8, and 9, all located in erosion zones). However, the correspondence between vegetation group distribution and the different functional zones was not perfect. For example, Site 2, not located in an erosional habitat, was included in a large group of sites associated with erosional conditions. The most likely explanation for these inconsistencies is that the different functional habitats that may be distinguished at a given time in the riparian habitat are not permanent in the landscape, precisely because the river migration processes that create them also destroy them constantly. For this reason, migrating rivers are commonly associated with ever-changing, highly complex and dynamic habitats; thus, it is likely that some present-day communities are associated with a given habitat that no longer exists. The result of these dynamic fluvial geomorphological processes are intricate vegetation mosaics along the course of the river (Kalliola and Puhakka 1988) that should not be interpreted as resulting from the river's current shape in a given year. Moreover, the presence of additional habitat variability on the floodplains might explain why the regional rarefaction curve did not reach asymptotic diversity, as geomorphological units excluded from our study like the edges of oxbow lakes and paleochannels with different times of successional development (many of which also support herbaceous wetland vegetation) may host an array of species not detected in our sampling (Madsen et al. 2001; Larsen and Alp 2015).

Fluvial geomorphology, however, may not be the only cause of the observed regional community heterogeneity; we found evidence of a potential effect of geological differentiation in this region, a factor originally not foreseen in this study. The boundary between the Yucatán Peninsula limestone platform and the volcanic Chiapas Highlands is located in the vicinity of the San Pedro River (Islas-Tenorio et al. 2006; Bauer-Gottwein et al. 2011). The NMDS ordination segregating Sites 3, 4, and 5 from other sites might reflect this additional geological and edaphic variability. The distinctly different visual soil characteristics at these sites (greenish hue with whitish crusts adhered to the substrate with the appearance of biofilms), along with the presence of *Fuirena stephani*, a sedge endemic to the Yucatán Peninsula (Ramos Álvarez and Diego-Pérez 2002), suggest a different parent material. This unusual soil formation, which apparently results from the weathering of limestone in the Yucatán Platform (Sedov et al. 2008; González-Elizondo et al. 2018; Hulshof and Spasojevic 2020), could be responsible for the presence of distinct plant communities dominated by species of *Eleocharis*, unlike most other sites where *Cladium jamaicense* dominates. The precise mapping of the geological contact between Yucatán limestone and the Chiapas Highlands in the future will allow testing this possibility.

Unlike the potential underlying cause for the segregation of Sites 3, 4 and 5 (geological differentiation), the less-marked differentiation between Group 4 (Sites 6 and 10) and Group 3 in the NMDS ordination may be related to the lingering effects of a past disturbance. The largest difference between Groups 3 and 4 is a much lower importance of *Cladium jamaicense* in the latter, particularly at Site 10, where this species is not among the 10 species with the largest RIVs. Herndon et al. (1991) reported high mortality of this species caused by fires and subsequent flooding, followed by its gradual recovery in Florida wetlands. Therefore, it is likely that such a disturbance reduced dominance of this species at Site 10 sometime in the past, whereas Site 6 might exemplify a community where this species is on its way to recover dominance. Future studies should examine the

long-term impacts of human disturbances on these riparian wetlands to gain a comprehensive explanation of among-site variation and to guide management practices.

In this study, we observed large differences in species richness among the distinguished communities, with the *Cladium jamaicense*-dominated community having the largest species richness. These differences may be related to the adaptive strategies of many wetland plants to cope with a frequently flooded environment. One such strategy is the acquisition of a climbing habit in some species, which improves their access to light and oxygen in high vegetation cover and hypoxic conditions (Gianoli 2015; Lin et al. 2018). In our study riparian wetlands, this is exemplified by *Pentalinon andrieuxii* (Apocynaceae), *Passiflora foetida* (Passifloraceae), *Cissus verticillata* (Vitaceae), along with other Convolvulaceae and Cucurbitaceae species, in agreement with previous reports (Stevens 2007; Ocampo Pérez and Coppens d'Eeckenbrugge 2017; Wood et al. 2020). These species appear to benefit from the structural support provided by *C. jamaicense*, which forms dense systems of fibrous roots (Richards and Olivas 2020). This structural role likely contributes to the maintenance of high plant diversity in *C. jamaicense*-dominated communities, in contrast to communities dominated by other Cyperaceae, particularly *Eleocharis cellulosa* and *E. interstincta*, both of which possess a less rigid structure and consequently form communities hosting fewer species. In *Cladium*-dominated communities of the San Pedro River, the terrestrial orchid *Bletia purpurea* displays a particular association with the dominant *Cladium,* as it was always recorded growing mounted on the *C. jamaicense* dense clumps. In forest wetland communities, this species often establishes just above the water level, either on stumps, floating logs, or at the base of cypress trees (Brown 2002; Johnson and Kane 2012), but in herbaceous wetlands a similar facilitative plant-plant association has been documented between *B. purpurea* and rushes and emergent grasses (Hellmuth 2018). Other species found growing on *C. jamaicense* clumps included *Wedelia acapulcensis*, *Ageratina malacolepis*, and *Ludwigia* aff. *octovalvis*. Although these species have not been reported to have epiphytic or climbing habits, their establishment on *C. jamaicense* may enable them to keep their roots out of the water, thereby improving access to oxygen.

Within-Site Heterogeneity of the San Pedro River Riparian Wetland

In addition to the hypothesized regional-scale relationship between riparian wetland heterogeneity and fluvial geomorphology, in this study we also predicted the existence of within-site heterogeneity related to nearness to the watercourse. In support of this hypothesis, the best models evaluating the effect of distance from the river showed a slightly higher species richness near the river channel than in quadrats located farthest from it. This pattern, which is opposite to the findings of Xu et al. (2024) in riparian wetlands of Zhejiang Province, eastern China, likely reflects the response of the plant community to soil physicochemical gradients (Xia et al. 2018; Xu et al. 2024) or natural disturbances associated to the riverbank like erosion or flooding, both of which are more frequent and intense in this zone (Ward 1998; Abernethy and Willby 1999; Nakamura et al. 2000; Lite et al. 2005; Formann et al. 2014; Sharpe and Kemp 2021). Acting in isolation or synergistically, such disturbances may reduce, or even prevent, competitive exclusion by the hyper-dominant clonal species, with a consequent positive effect on community diversity in disturbed areas (Huston 1994; Pollock et al. 1998). Although the mechanisms involved in this local floristic differentiation seem rather weak, as shown by the relatively minor differences in richness along this gradient, it is interesting that they are detectable at such small spatial scale, considering that efforts to assess wetland heterogeneity related to disturbance gradients usually focus on processes occurring at much larger scales (e.g., Sparks et al. 1990; van Eck et al. 2005; Arias et al. 2018; Xia et al. 2024).

Future Challenges and Conservation Implications

Despite the progress made by this study in understanding the spatial variation of the San Pedro Mártir River herbaceous wetlands, several questions remain. Future research should prioritize the study of the physico-chemical environment of these communities by assessing soil and water properties, as well as river dynamics, including seasonal changes in water depth, the duration of the flooded state or substrate properties, to clarify how these factors contribute to the observed heterogeneity. In particular, the study suggests that limestone-derived soils possess unique properties affecting these communities differently than other soils (Hulshof and Spasojevic 2020). Another area for further research is related to the hyper-dominance of a few species, primarily from the genera *Cladium* and *Eleocharis*. While the dominance of these taxa in herbaceous wetlands is well-documented (Herndon et al. 1991; Baksh and Richards 2006), the mechanisms behind the dominance-subordination relationships among species are not well understood. Furthermore, the recognition of "rare" plant communities recorded at only a few sites, such as the one dominated by *Eleocharis interstincta*, points to the need for accurate mapping of the different plant communities within this riparian wetland system to determine whether these rare communities are truly restricted or just require more extensive sampling.

The high heterogeneity observed indicates that conservation efforts for these wetlands should ensure the inclusion of all plant communities present along the river's course,

particularly those identified as restricted, to prevent their disappearance. If *Eleocharis*-dominated communities are indeed rare, conservation efforts should prioritize them due to their unique characteristics and environmental relationships. However, a comprehensive conservation strategy should not only focus on the rare communities but also consider the widely spread *Cladium* communities, as their disappearance would result in the loss of many species that rely on the dominant one for their establishment. Importantly, future conservation efforts to safeguard the riparian herbaceous wetlands in this region must consider the disturbance caused by wildfires associated with agricultural activities and the hunting of freshwater turtles (Reyes-Grajales et al. 2024).

Conservation strategies of these endangered riparian herbaceous wetlands must be comprehensive and acknowledge the fluvial dynamics of the river, which results in continuous change in the spatial distribution and characteristics of these communities. Failure to do so may lead to unsuccessful, inflexible conservation actions that may rapidly reduce their efficacy. Given the current degradation of the riparian vegetation along the San Pedro Mártir River and the potential threats due to modifications in its hydrological system due to climate change (González Villela and Montero Martínez 2017), this analysis provides tools to improve the management and conservation of these ecosystems, hopefully ensuring their future preservation.

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Author Contributions The study conceptualization was performed by Diana Jimeno, J. Alberto Gallardo-Cruz, Rubén Martínez-Camilo and Jorge A. Meave. Investigation was performed by Diana Jimeno, Daniel Chávez, Rubén Martínez-Camilo, Rosa María Fonseca and Jorge A. Meave. Diana Jimeno, Moisés Enríquez and Jorge A. Meave conducted formal analysis. The first draft of the manuscript was written by Diana Jimeno, Daniel Chávez and Jorge A. Meave and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Data Availability The data that support the findings of this study are openly available in Dryad at https://doi.org/10.5061/dryad.5tb2rbpdq (Jimeno et al. 2025).

Declarations

Competing Interests The authors have no relevant financial or non-financial interests to disclose.

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