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An Assessment of the Spatial Variability of Tropical Swamp Forest along a 300 km Long Transect in the Usumacinta River Basin, Mexico

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Abstract: The provision of valuable ecosystem services by tropical swamp forests (mainly carbon sequestration and storage in biomass and soil) explains their ecological importance. Current efforts toward the conservation of these ecosystems, however, face strong limitations as their spatial variation is largely unknown, particularly in regions where they occur over large areas. Here, we analyze the α -diversity (i.e., effective number of species or true diversity) and community structure variability of three tropical swamp forest communities distributed along an approximately 300 km long portion of the Usumacinta River Basin, southern Mexico. We sampled eighty-three 625-m² plots to characterize the diversity and structural attributes of the woody plant communities. We recorded 2302 individuals belonging to 60 species and 25 families. Both α -diversity and structural attributes differed significantly among the three communities. The most inland community stood out for having the highest α -diversity for three true diversity values. Interestingly, the mangrove *Rhizophora mangle* L. was one of the dominant species, both in the swamp forest located closest to the coast and in the community farthest away from the sea. Basal area and density of individuals also had their maxima in the most inland swamp forest. The diversity and structural differences observed among the examined swamp forests seem to be related to contrasting environmental conditions, such as water salinity, distance to the coastline, and the hydrological dynamics of the Usumacinta River. We emphasize the urgency to conserve *R. mangle* populations in the swamp forest located farthest away from the coast due to its unusual habitat association, which appears to be a relictual condition.

Keywords: forest structure; plant species conservation; *Rhizophora mangle*; San Pedro y San Pablo River; wetland forest

1. Introduction

Wetlands are important ecosystems that provide valuable environmental services (mainly carbon sequestration and storage in biomass and soil) and host high biodiversity [1–5]. This ecosystem type is characterized by the (almost) permanent presence of water-saturated soils [1]. Despite this common feature, wetlands comprise a large suite of plant communities, ranging from those dominated by herbs and shrubs to those where trees are the prevailing structural component [1,4].

Among the tree-dominated wetland plant communities, the tropical swamp forest is one of the most important and representative forms, as well as one of the most heterogeneous both in terms of floristic composition and structure [5,6]. Such heterogeneity is reflected across spatial scales [7] and has been related to variations in hydrological conditions (i.e., flood regime), chemical and physical water properties (e.g., salinity), soil attributes (e.g., organic matter content), and the relief of the terrain where they occur [6–9]. Most studies that have analyzed the variation of tropical swamp forest attributes have focused on coastal forests dominated by *Rhizophora mangle* L. and usually evaluate the effects of local environmental conditions on certain forest attributes (e.g., [9–17]). Such bias has resulted in substantial knowledge gaps regarding the magnitude and nature of the spatial variation of these forests across their large geographical range, and more importantly, its underlying causes.

The Usumacinta River Basin hosts the largest area of coastal and continental wetlands in Mesoamerica, including a large share of tropical swamp forests, mainly in the lower sector of the basin [18,19]. The Usumacinta is one of the largest sources of freshwater being discharged into the Gulf of Mexico, second only to the Mississippi River [20]. Within the Usumacinta River Basin, tropical swamp forests are mainly concentrated across extensive areas near the coastline, but they also occur further inland on the banks of the Usumacinta and its main tributaries [21]. The wide distribution of tropical swamp forests in this region, particularly the large gradient of distances to the sea encompassed within its geographic range, provides an ideal scenario to examine the spatial variability of community attributes, and to attempt to gain new insights on the environmental factors responsible for such heterogeneity. To this end, we focused on three representative communities located at increasing distances from the coast along the Usumacinta or its tributaries. Previous studies examined the spatial variation of wetland forest in this region in a much smaller area [22,23], but no attempt has been made to scale up this analysis to sites separated by hundreds of kilometers. Wetland forest literature provides much evidence for environmental effects related to the vicinity of the sea, in particular intrusion of seawater salinity, intense tidal regimes, and even disturbance from frequent coastal climatic phenomena (e.g., [9,13–16,24]). Yet, forests located far away from the coastline are clearly not influenced by the sea in any way, rather, they are subjected to particular hydrological regimes determined by the natural dynamics of rivers and the climatic seasonality (i.e., yearly precipitation patterns) across the basin. For these reasons, we anticipated that swamp forests across this large geographic range should display a larger heterogeneity than that observed in more restricted areas closer to the sea, in particular that reported by Chávez et al. [22] and Solórzano et al. [23] in the same area.

We emphasize that the knowledge on the heterogeneity of tropical swamp forest attributes is crucial for informing conservation strategies and supporting their proper management [23]. Therefore, our goal was to assess the spatial variation of community attributes of three tropical swamp forest communities distributed over a 300-km long sector of the lower Usumacinta River Basin in the Gulf of Mexico Coastal Plain, Mexico. We focused on the characterization of diversity and structural attributes in three communities: (1) a coastal tropical swamp forest dominated by *R. mangle*; (2) a tropical swamp forest associated to a lagoon complex fed by the frequent raisings and overflows of the Usumacinta River; and (3) the tropical swamp forest of the San Pedro River, a major tributary of the Usumacinta

that joins it in the final part of its course. This latter community bears particular relevance, given the presence of *R. mangle* in an area that is more than 300 km away from the coastline. Hence, a further objective of this study was to provide the first quantitative description of this community, as well as to assess how distinctly different it is relative to the other tropical swamp forests occurring in the region.

2. Materials and Methods

2.1. Study Area

The study was conducted in the lower Usumacinta Basin (Figure 1). As a whole, the Usumacinta Basin is a naturally defined region stretching over 7 million hectares that includes a broad range of landscapes, from the cold Guatemalan Highlands in the Cuchumatanes region, where the headwaters of this complex fluvial network are located, down to the discharge zone in the Gulf of Mexico [25]. In the basin, three sectors (low, middle, and high) can be distinguished according to topographic, geomorphological, and hydrological features [25]. The lower sector corresponds to the region where the main rivers approach the Mexican coastline of the Gulf of Mexico; this sector is predominantly a discharge zone that encompasses extensive continental wetlands of the San Pedro river in Guatemala, along with large wetland areas across the deltaic plain of the Usumacinta in Mexico. This coastal region boasts the largest diversity of aquatic plants in Mesoamerica [26–28].

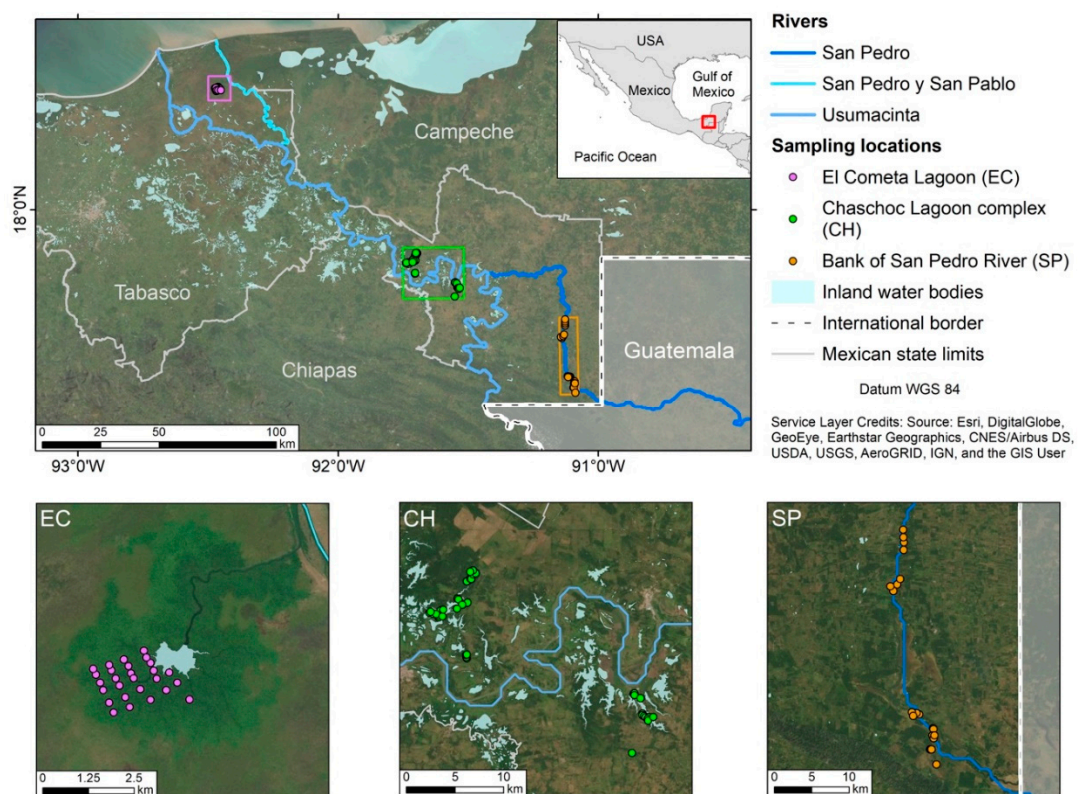


Figure 1. Study area in the Usumacinta River Basin, Tabasco, Mexico.

In this sector of the basin, we selected three sites along the course of the Usumacinta River and its tributary or distributary rivers. Each of these sites is representative of the most contrasting environmental conditions prevailing in the lower Usumacinta Basin regarding flooding regime, water properties, and substrates. These sites were (1) El Cometa Lagoon (EC), located in the vicinity of the San Pedro y San Pablo river and connected to it by a short canal; (2) the Chaschoc Lagoon complex (CH), located along the Usumacinta River; and (3) the inland bank of the San Pedro River (SP). EC is located in the Gulf of Mexico coastal plain within the Pantanos de Centla Biosphere Reserve, where the

most extensive and best-preserved tracts of *Rhizophora mangle*-dominated forests can be found in the basin. This forest community thrives in an almost permanently flooded condition. The most striking environmental feature in this latter area is the recurrent intrusion of a salt wedge that produces periodic changes in water salinity, in addition to very deep (>2 m) organic soils [29]. In turn, CH lies approximately 100 km away from the coast, in an area where the course of the Usumacinta is characterized by very wide meanders, along with a multitude of associated oxbow lakes of different shapes and sizes; most of these dry out seasonally and they only fill up when the river overflows and the water leaves its channel, creating a water column several meters in depth [30]. The substrate in this area is characterized by clayey soils and the accumulation of large volumes of sediment. Finally, SP is located much further inland, some 200 km in a straight line from the coast and around 300 km along the meandering course of the Usumacinta; at this site, swamp forest patches occur on river banks that are permanently flooded. For this region of limestone bedrock, there are earlier reports of the presence of isolated, relictual populations of *R. mangle*, which is clearly an ecological and geographical anomaly for this species [31].

2.2. Data Collection

We used a total of eighty-three 625-m² (25 × 25 m) plots to characterize the tropical swamp forest; all plots were georeferenced with a GPS receiver (TrimbleGEO7). The plot distribution per community was EC = 27 plots, CH = 35 plots, SP = 21 plots. In each plot, we recorded all woody plants with a diameter at breast height (DBH) ≥ 10 cm. For each plant, we measured DBH with a diameter tape and maximum height with a Sndway SW-E80 range finder or a Vertex (Laser Technology TruPulse 200, Dongguan Sndway Co., Ltd., Dongguan, China). Although we tried to determine the taxonomic identity of every individual to species level, this was not always possible, and thus we recognized these entities as morphospecies. All names were verified and updated according to The Plant List database (<http://www.theplantlist.org/>).

2.3. Analysis

In order to compare α -diversity among sites, we calculated the effective number of species using the Hill numbers approach. Hill numbers allow for the determination of the sensitivity of effective species richness (D) to species' relative abundances (q) [32]. The three diversity orders calculated were order zero true diversity (0D), which is the absolute species richness; first order diversity (1D), which represents the number of abundant species (calculated as the exponential of Shannon's Index); and second order diversity (2D), which is interpreted as the number of dominant species (calculated as the inverse of Simpson's index) [32]. Given the differences in tree density between communities, the data were standardized by rarefaction before calculating the effective numbers of species [33,34]. To assess the significance of the differences in 0D , 1D , and 2D among communities, we calculated 95% confidence intervals for species accumulation curves through bootstrapping [35]. Additionally, for each community, we constructed a rank abundance curve to examine the abundance patterns of species and to ultimately identify the dominant species in each community.

We based the structural description of the three communities on three variables: (i) density of individuals; (ii) basal area, calculated as the sum of the individual basal area values in the plot; and (iii) community canopy height, calculated as the mean height of the ten tallest trees recorded in the plot [36]. Basal area for each stem was approximated to the area of a circle with radius equal to DBH divided by 2. Density of individuals and basal area values were scaled to 1 ha.

We analyzed the differences among the three communities' structural attributes through analysis of variance (ANOVA), after verification of normality of residuals. When significant, we then conducted post hoc pairwise Tukey tests. In all analyses, we used $\alpha = 0.05$ as the significance threshold. All analyses were conducted in R version 4.0.2 [37]; for diversity analyses, we used the iNEXT package [35].

3. Results

3.1. Overall Community Characterization

We recorded a total of 2302 woody individuals that represented 60 species and 25 families (Table 1). Leguminosae was the most speciose family (13 species), well above the following nine families, each one represented by two species only; all the remaining families were represented by a single species each (Table 1). Notable species given their high abundances across sites were *Pachira aquatica* Aubl. (430 individuals), *Haematoxylum campechianum* L. (316), *Terminalia buceras* (L.) C.Wright (299), *Rhizophora mangle* L. (241), and *Salix humboldtiana* Willd. (183) (Table 1). These five species alone accounted for 63.8% of all sampled individuals. We detected 12 species represented by 1 individual only (singletons).

Table 1. Checklist of woody species and their abundances in three tropical swamp forest communities in the Usumacinta River Basin, Mexico. EC, El Cometa Lagoon; CH, Chaschoc Lagoon complex; SP, San Pedro River.

Family	Species	Site		
		EC	CH	SP
Anacardiaceae	<i>Metopium brownei</i> (Jacq.) Urb.			2
	<i>Spondias mombin</i> L.		5	
Annonaceae	<i>Annona reticulata</i> L.		2	
Apocynaceae	<i>Tabernaemontana longipes</i> Donn.Sm.		1	
Arecaceae	<i>Attalea butyracea</i> (Mutis ex L.f.) Wess.Boer		1	
	<i>Sabal mexicana</i> Mart.		67	
Bignoniaceae	<i>Crescentia cujete</i> L.		2	
	<i>Tabebuia rosea</i> (Bertol.) Bertero ex A.DC.		2	39
Burseraceae	<i>Bursera</i> sp.			6
Capparaceae	<i>Crateva tapia</i> L.		1	
Chrysobalanaceae	<i>Chrysobalanus icaco</i> L.	15		14
	<i>Couepia polyandra</i> (Kunth) Rose		1	
Clusiaceae	<i>Calophyllum brasiliense</i> Cambess.			40
Combretaceae	<i>Terminalia buceras</i> (L.) C.Wright	154	1	144
	<i>Laguncularia racemosa</i> (L.) C.F.Gaertn.	4		
Fabaceae	<i>Acacia cornigera</i> (L.) Willd.			2
	<i>Albizia lebeck</i> (L.) Benth.		1	
	<i>Cynometra retusa</i> Britton & Rose		4	
	<i>Enterolobium cyclocarpum</i> (Jacq.) Griseb.		4	
	<i>Haematoxylum campechianum</i> L.		303	13
	<i>Inga vera</i> Willd.			2
	<i>Lonchocarpus guatemalensis</i> Benth.		52	
	<i>Lonchocarpus hondurensis</i> Benth.	80		74
	<i>Lonchocarpus</i> sp.			6
	<i>Pithecellobium lanceolatum</i> (Willd.) Benth.		17	
	<i>Swartzia cubensis</i> (Britton & Wilson) Standl.			2
	<i>Zygia conzattii</i> (Standl.) Britton & Rose		72	
	<i>Zygia recordii</i> Britton & Rose			8
Fagaceae	<i>Quercus oleoides</i> Schlttdl. & Cham.		5	
Malpighiaceae	<i>Malpighia</i> sp1.			5
Malvaceae	<i>Guazuma ulmifolia</i> Lam.		6	
	<i>Pachira aquatica</i> Aubl.	110		320
Meliaceae	<i>Cedrela odorata</i> L.		5	
	<i>Trichilia havanensis</i> Jacq.			2
Moraceae	<i>Ficus insipida</i> Willd.			21
Myrtaceae	<i>Eugenia acapulcensis</i> Steud.		57	
	Myrtaceae sp1.			2
Polygonaceae	<i>Coccoloba barbadensis</i> Jacq.		5	11
Primulaceae	<i>Bonellia macrocarpa</i> (Cav.) B.Stahl & Källersjö		4	
Rhizophoraceae	<i>Rhizophora mangle</i> L.	170		71

Table 1. Cont.

Family	Species	Site		
		EC	CH	SP
Rubiaceae	<i>Alseis yucatanensis</i> Standl.		28	
Salicaceae	<i>Salix humboldtiana</i> Willd.		183	
	<i>Xylosma</i> sp.			1
Sapindaceae	<i>Sapindus saponaria</i> L.		5	
Sapotaceae	<i>Manilkara zapota</i> (L.) P.Royen	1		41
Solanaceae	<i>Cestrum nocturnum</i> L.		1	
Not determined	Morphospecies 1	1		
	Morphospecies 2			62
	Morphospecies 3			10
	Morphospecies 4			4
	Morphospecies 5			5
	Morphospecies 6			5
	Morphospecies 7			2
	Morphospecies 8			3
	Morphospecies 9			1
	Morphospecies 10			2
	Morphospecies 11			2
	Morphospecies 12			2
	Morphospecies 13			1
	Morphospecies 14			1
	Morphospecies 15			1

SP was the community hosting the largest richness (58% of all species), in strong contrast with EC, which was the most species-poor community (eight species, or 13% of the total; Table 2). On the other hand, CH was the community hosting the largest diversity at the family level, slightly higher than that observed in SP (19 vs. 16 families, respectively). Furthermore, in EC, six families were recorded, among which only Combretaceae was represented by two species. Regarding density of individuals, SP ranked first (44.4 ± 17.8 individuals), while CH ranked second (23.9 ± 16.5 individuals), and EC ranked third (19.8 ± 8.0 individuals). The sampling effort for the three sites was insufficient according to the rarefied species accumulation curve (Figure 2). For CH and SP communities, this situation was particularly evident (Figure 3).

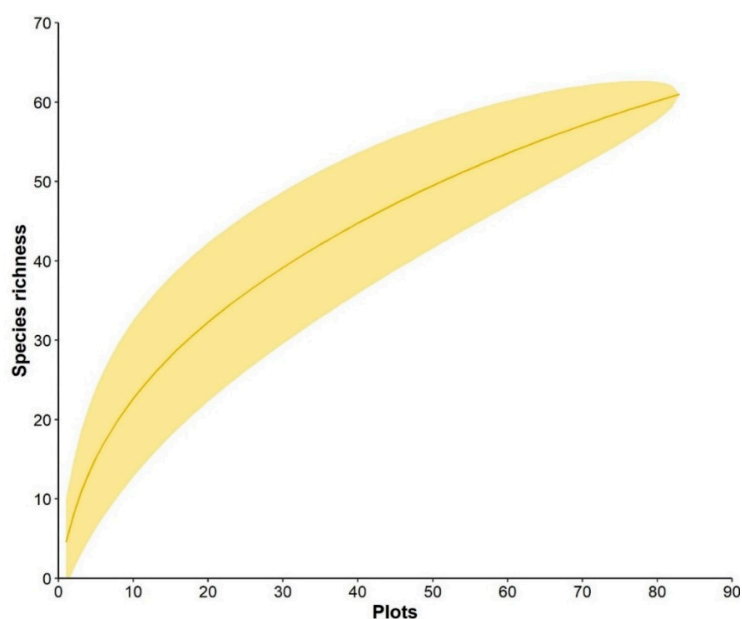


Figure 2. Smoothed species accumulation curve for all plots of swamp forest communities in the Usumacinta River Basin, Mexico. The shaded area represents the 95 % confidence envelope.

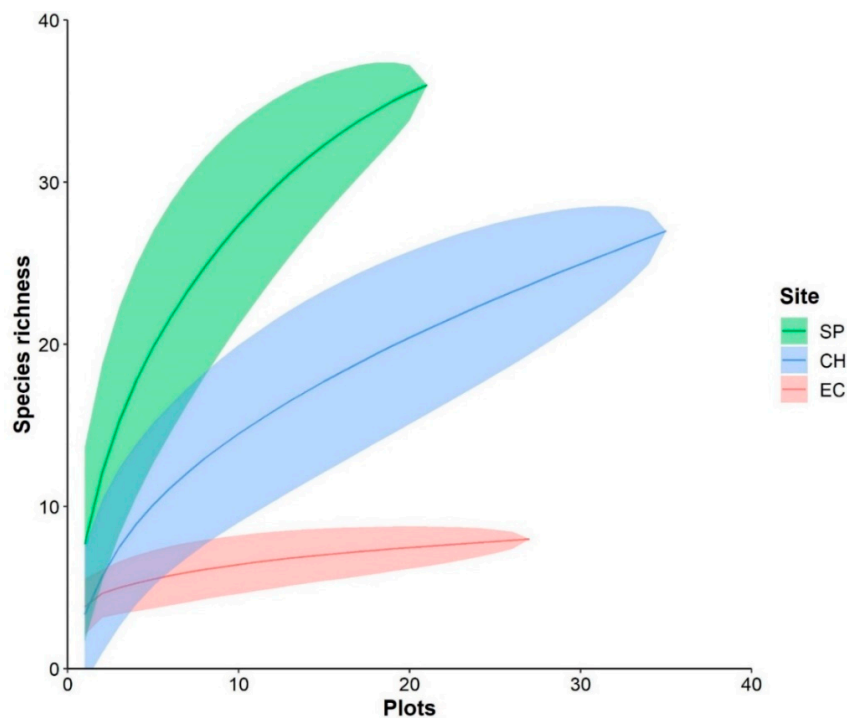


Figure 3. Species accumulation curve for three tropical swamp forest communities in the Usumacinta River Basin, Mexico. EC = El Cometa Lagoon, CH = Chaschoc Lagoon complex, SP = San Pedro River. The shaded areas represent 95 % confidence envelopes.

Table 2. Number of plots, individuals, and species in three tropical swamp forest communities in the Usumacinta River Basin, Mexico.

Site	Plots	Abundance	Families	Species
El Cometa Lagoon	27	535	6	8
Chaschoc Lagoon complex	35	835	19	27
San Pedro River	21	932	19	35

3.2. Diversity and Dominance

SP was the community with the highest α -diversity according to the three true diversity values, although the values differed depending on the relative contribution of species abundances (Figure 4). According to 0D , SP (37 species) and CH (36 species) were not significantly different (Figure 4a) from each other, but both differed significantly from EC (10 species). Regarding 1D , SP was significantly higher than both EC and CH (Figure 4b). Finally, the differences became attenuated after considering the effect of dominant species; for 2D , SP (6.3 species) and CH (5.3 species) did not differ significantly, whilst EC was significantly lower than the former two communities (4.4 species; Figure 4c).

The rank abundance curves of CH and SP showed a similar pattern, which consisted in a gradual reduction in the abundance of the most frequent species, as well as a good share of singletons and doubletons (Figure 5b,c, respectively). Singletons and doubletons are important community components in SP and CH, with 14 and 10 species, respectively, all of which occurred exclusively in one community. The pattern observed in EC was notably different, as half of the few species recorded here were very abundant (Figure 5a). Importantly, the identities of the most abundant species differed between sites. Although EC and SP hosted more species in common, their composition differed greatly from CH. In EC, the most abundant species were, in decreasing order (Figure 5a), *R. mangle*, *T. buceras*, and *P. aquatica*; in CH, *H. campechianum*, *S. humboldtiana*, and *Zygia conzatti* had the highest abundances (Figure 5b); lastly, for SP, the group of abundant species comprised *P. aquatica*,

T. buceras, and *Lonchocarpus hondurensis*. Notably, in this inland site, *R. mangle* ranked fourth in terms of abundance (Figure 5c).

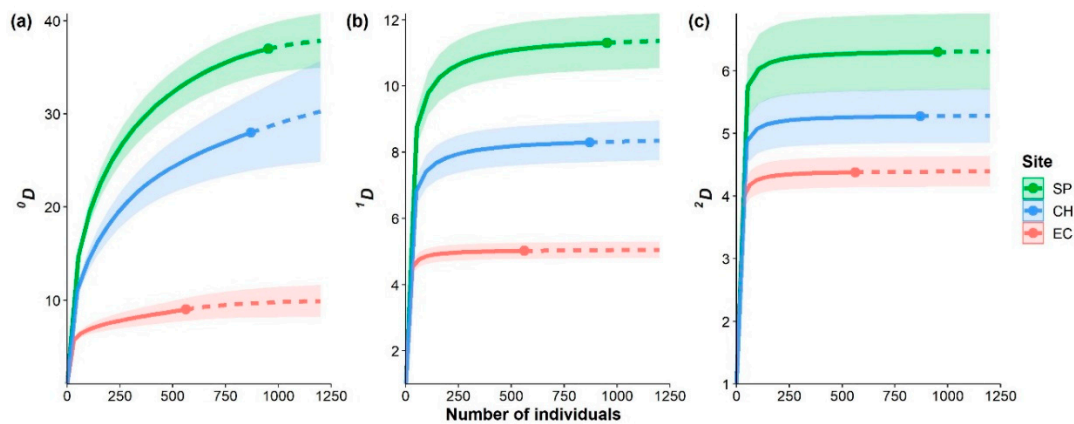


Figure 4. Cumulative woody species accumulation curves for three tropical swamp forest communities in the Usumacinta River Basin, Mexico. (a) 0D , species richness; (b) 1D , number of common species (Shannon exponential); (c) 2D , number of dominant species (inverse Simpson's index). Continuous lines indicate interpolation, discontinuous lines indicate extrapolation. Species richness was rarified to 1200 individuals in order to standardize tree densities among communities. The shaded areas represent 95% confidence envelopes.

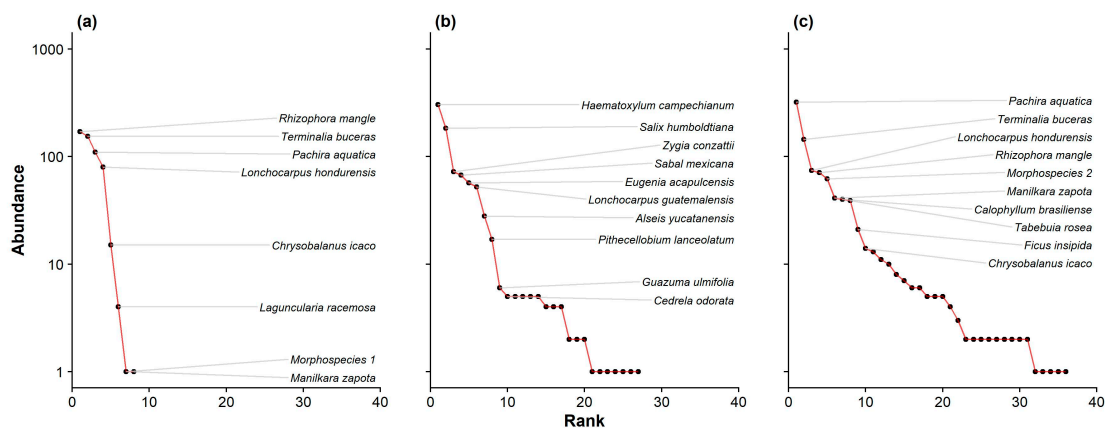


Figure 5. Rank abundance curves for three tropical swamp forest communities in the Usumacinta River Basin, Mexico. (a) El Cometa Lagoon; (b) Chaschoc Lagoon complex; (c) San Pedro River.

3.3. Forest Structure

The structural attributes evaluated differed considerably among the three communities. The largest community basal area values were recorded at SP (mean = 28.84 m² ha⁻¹) and CH (27.03 m² ha⁻¹). These two mean values differed significantly from that recorded at EC (mean = 17.27 m² ha⁻¹; $p < 0.05$; Figure 6a). On the other hand, SP had the largest density of individuals (710 ind. ha⁻¹), a value more than twice as large as those recorded in EC and CH (317.04 and 381.71 ind. ha⁻¹, respectively; $p < 0.05$; Figure 6b). Similarly, for canopy height, we found significant differences among sites ($p < 0.05$; Figure 6c), with EC having the tallest mean canopy height (15.1 m).

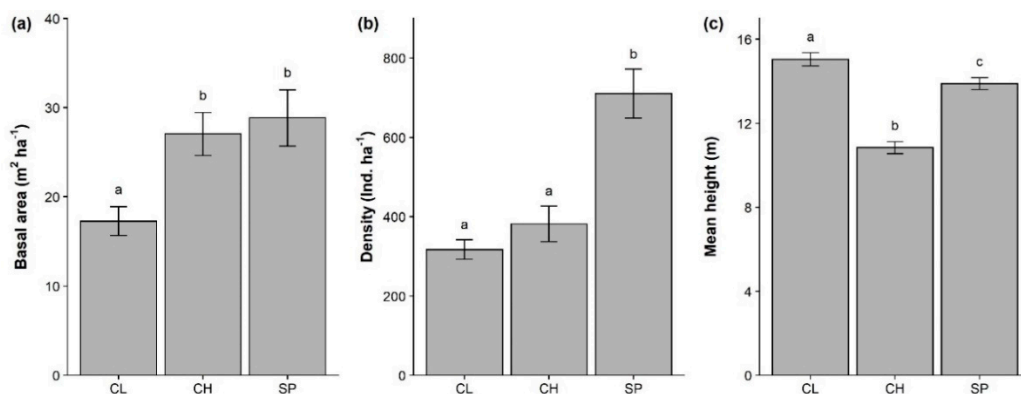


Figure 6. Comparison of structural attributes in three tropical swamp forest communities in the Usumacinta River Basin, Mexico. (a) Basal area; (b) density of individuals; (c) mean canopy height. Different letters indicate significant differences according to post hoc Tukey pair-wise tests ($p < 0.05$). EC, El Cometa Lagoon; CH, Chaschoc Lagoon complex; SP, San Pedro River.

Woody plant species contributed differentially to the structural attributes of the three communities (Table 3). Species with the largest contributions were *R. mangle* and *T. buceras* in EC, *H. campechianum* in CH, and *T. buceras* and *P. aquatica* in SP. Notably, *R. mangle* made the largest contributions to basal area and tree density. The tallest species recorded in the study (i.e., those species attaining heights >15 m) were *R. mangle* at EC, and *Enterolobium cyclocarpum* and *Cedrela odorata* at CH; in fact, some trees of the latter species were taller than 30 m. A comparison of mean height for *R. mangle* between EC and SP revealed that the trees in EC were twice as tall as the tallest trees recorded in SP (8.25 m vs. 17.42 m, respectively; Table 3). The tallest *R. mangle* trees reached heights around 26 m at EC.

Table 3. Basal area, tree density, and mean height by species in three tropical swamp forest communities in the Usumacinta River Basin, Mexico. For basal area and tree density, the total values by species are shown.

Site	Species	Basal Area (m ² ha ⁻¹)	Density (Ind. ha ⁻¹)	Height (m)
El Cometa Lagoon	<i>Rhizophora mangle</i>	210.58	100.74	17.42
	<i>Terminalia buceras</i>	200.97	91.26	12.66
	<i>Lonchocarpus hondurensis</i>	26.06	47.41	8.19
	<i>Pachira aquatica</i>	21.39	65.19	5.76
	<i>Chrysobalanus icaco</i>	5.02	8.89	5.96
	<i>Laguncularia racemosa</i>	1.84	2.37	10.32
	Morphospecies 1	0.25	0.59	6.47
	<i>Manilkara zapota</i>	0.14	0.59	6.19
	Chaschoc Lagoon complex	<i>Haematoxylum campechianum</i>	420.42	138.51
<i>Sabal mexicana</i>		122.07	30.63	8.48
<i>Lonchocarpus guatemalensis</i>		79.12	23.77	12.15
<i>Salix humboldtiana</i>		56.68	83.66	9.79
<i>Alseis yucatanensis</i>		47.62	12.80	11.36
<i>Enterolobium cyclocarpum</i>		40.65	1.83	22.00
<i>Eugenia acapulcensis</i>		40.05	26.06	10.68
<i>Zygia conzattii</i>		38.19	32.91	8.69
<i>Cedrela odorata</i>		30.75	2.29	25.00
<i>Cynometra retusa</i>		10.77	1.83	14.00
<i>Coccoloba barbadensis</i>		9.18	2.29	12.60
<i>Quercus oleoides</i>		8.67	2.29	16.0
<i>Spondias mombin</i>		7.90	2.29	12.60
<i>Pithecellobium lanceolatum</i>		7.81	7.77	8.59

Table 3. Cont.

Site	Species	Basal Area (m ² ha ⁻¹)	Density (Ind. ha ⁻¹)	Height (m)
San Pedro River	<i>Guazuma ulmifolia</i>	5.21	2.74	11.83
	<i>Crescentia cujete</i>	4.41	0.91	7.50
	<i>Crateva tapia</i>	2.92	0.46	8.00
	<i>Couepia polyandra</i>	2.80	0.46	15.00
	<i>Attalea butyracea</i>	2.48	0.46	12.00
	<i>Albizia lebbek</i>	2.12	0.46	15.00
	<i>Sapindus saponaria</i>	1.70	2.29	8.20
	<i>Bonellia macrocarpa</i>	1.62	1.83	8.00
	<i>Tabebuia rosea</i>	1.02	0.91	11.50
	<i>Annona reticulata</i>	0.89	0.91	10.00
	<i>Cestrum nocturnum</i>	0.48	0.46	8.00
	<i>Terminalia buceras</i>	0.42	0.46	15.00
	<i>Tabernaemontana longipes</i>	0.25	0.46	10.00
	<i>Terminalia buceras</i>	219.68	109.71	12.84
	<i>Pachira aquatica</i>	188.71	243.81	10.54
	<i>Lonchocarpus hondurensis</i>	31.29	56.38	10.42
	<i>Rhizophora mangle</i>	24.77	54.10	8.25
	<i>Manilkara zapota</i>	22.36	31.24	9.39
	Morphospecies 2	19.43	47.24	9.46
	<i>Tabebuia rosea</i>	17.38	29.71	10.83
	<i>Calophyllum brasiliense</i>	14.90	30.48	12.02
	<i>Ficus insipida</i>	11.18	16.00	9.71
	<i>Haematoxylum campechianum</i>	10.93	9.90	9.00
	<i>Swartzia cubensis</i>	9.99	1.52	12.64
	<i>Chrysobalanus icaco</i>	7.11	10.67	6.41
	Morphospecies 3	4.34	7.62	11.55
	<i>Coccoloba barbadensis</i>	3.69	8.38	9.10
	<i>Zygia recordii</i>	1.92	6.10	7.88
	Morphospecies 4	1.91	3.05	10.31
	Morphospecies 5	1.75	3.81	9.89
	<i>Malpighia</i> sp.	1.70	3.81	7.20
	<i>Bursera</i> sp.	1.51	4.57	10.61
	<i>Lonchocarpus</i> sp.	1.16	4.57	9.49
	<i>Metopium brownei</i>	1.05	1.52	10.24
	<i>Inga vera</i>	0.98	1.52	7.08
Morphospecies 6	0.92	3.81	9.01	
<i>Acacia cornigera</i>	0.68	1.52	9.16	
Morphospecies 7	0.52	1.52	5.38	
Morphospecies 8	0.50	2.29	8.40	
<i>Trichilia havanensis</i>	0.43	1.52	7.05	
Morphospecies 9	0.42	0.76	17.88	
Morphospecies 10	0.40	1.52	8.25	
Morphospecies 11	0.39	1.52	11.19	
Morphospecies 12	0.33	1.52	6.01	
Morphospecies 13	0.23	0.76	10.04	
Morphospecies 14	0.18	0.76	10.42	
<i>Xylosma</i> sp.	0.15	0.76	8.62	
Morphospecies 15	0.13	0.76	9.70	

4. Discussion

To our knowledge, this is the first study to examine the variation of α -diversity and structural attributes of three tropical swamp forest communities in the Usumacinta River Basin at a regional level. In addition, this is also the first report of the structure and diversity of a tropical swamp forest with

R. mangle located more than 300 km away from the sea. The three swamp forest communities analyzed occur in floodplains, but they differ in their proximity to the coast.

4.1. Diversity and Dominance

Interestingly, EC, the community most closely located to the coastline, had the lowest α -diversity. This result agrees with the frequently reported pattern where plant communities closer to the coast tend to have lower species richness in comparison to communities located further inland [9,10,12,13,16,38,39]. Additionally, communities closer to the coast usually host one or few mangrove species. This pattern has been reported in the regions of Western Africa, Western Atlantic and The Caribbean, and Eastern Pacific [11]. All mangrove species of different genera have morphological and physiological adaptations that enable them to tolerate stressing conditions derived from water saturation and salinity [8,11,40]. In the case of our study, although the EC site was the one closer to the coast, it showed a non-pure mangrove species composition, which suggests that this site can be seen as an ecotone between pure mangrove communities and tropical swamp forest communities [22,23]. This probably explains the difference between the dominant species in EC (*R. mangle*, *T. buceras*, and *P. aquatica*) and those recorded in areas closer to the coast, where in addition to *R. mangle*, other mangrove species have been reported such as *Avicennia germinans* and *Laguncularia racemosa* [22,29,41–43]. For the same region, besides water salinity, there is a significant influence of the geomorphological and topographic variation of the terrain that drives the occurrence of different tree associations in Tabasco's coastal plain [22,23,42]. This variation results in the presence of highly heterogeneous forests across the lower portion of the Usumacinta Basin, particularly within the Pantanos de Centla Biosphere Reserve [42].

Our results show that α -diversity is twice as large in swamp forest communities located far from the coast, which are also more complex in species composition. Moreno-Casasola et al. [6] reported a similar increase in α -diversity with increasing distances to the coast in river bank communities. It has been frequently reported that forest communities are less diverse when they are subjected to high water salinity, in comparison to those under fresh water conditions [6,43]. Moreover, it is important to highlight that tropical swamp forest communities in SP and CH are located in the vicinity of hilly areas where non-flooded tropical forest communities occur; these upland forests may act as sources of propagules of many other species, which explains at least in part the presence of floristic elements from those communities such as *Alseis yucatanensis*, *Calophyllum brasiliense*, *Manilkara zapota*, *Tabebuia rosea*, and *Z. conzattii*. Infante-Mata et al. [43] reported a similar finding for floodplain tree communities.

Notably, the most similar communities by floristic composition and species dominance were the most distant ones, i.e., EC and SP, with a good number of shared species between them, mainly *R. mangle*, *T. buceras*, *P. aquatica*, *L. hondurensis*, and *Chrysobalanus icaco*. The presence of a *R. mangle* population in SP continues to be intriguing, given its geographical location, approximately 300 km away from the sea. Actually, we have recorded the presence of *R. mangle* individuals further inland on the banks of the San Pedro River, closer to the Mexico–Guatemala border. However, we acknowledge that this is not a unique example of this situation; in the USA, the range of this species in some extensive wetland regions (e.g., Everglades National Park, Florida, USA) extends well beyond the limit of the coastlines by dozens of kilometers inland [44–46]. Yet, in these cases, distances from the coast are not as large as in the case of the *R. mangle* population of the San Pedro River. The peculiarity of this community is also related to the presence of mangrove companion species, such as *P. aquatica*, which also has adventitious roots and physiological adaptations that enable it to grow in flooded conditions but with low salinity [38]. The occurrence of *R. mangle* in the swamp forest along the San Pedro river has been intermittently mentioned since the second half of the 20th century [31,47–49], but we are still lacking an estimate of the time when these populations became isolated from other coastal tropical swamp forests in the region, and ignore how this separation took place.

4.2. Community Structure

Both basal area and density values were higher in those sites further away from the coast. This may be related to the effects of salinity and other environmental variables that create stressing conditions near the sea. These variables play an important role in other flooded forests dominated by mangrove species, where salinity and geomorphology shape the structural attributes of the community [9,14,43,50]. Increasing salinity has also been related to reductions in stem diameter and density of individuals [14,16]. Therefore, the high basal area and density values in CH and SP may be favored by the absence of salt in the water.

Mean canopy height was the only structural attribute for which the community at EC had the highest values (even though the tallest trees were recorded in CH). Overall, mean canopy height in both CH and SP never exceeded 12 m, in strong contrast to the heights recorded at EC. Across all three sites, only 75 trees were taller than 20 m, among which 50 were recorded at EC, most of them being *R. mangle*. This suggests a considerably more homogeneous canopy height for EC, and ultimately a better developed mature forest, relative to the other study sites. Canopy heights at EC are similar to those reported for other swamp forests dominated by *R. mangle* [13] or even higher than other communities located in Mexico [9] and in South America [14], but they are considerably shorter than the mangroves located in the Soconusco region (Pacific Coast Plain in Chiapas), which are considered the tallest mangrove communities in Mexico [51,52]. Nevertheless, close to the EC sampling site, along the San Pedro y San Pablo River, higher values of both canopy height and biomass have previously been reported [22]. The heights of *R. mangle* trees growing on the banks of the SP were always lower than 12 m (mean height = 8.45 m). In general, these are short trees compared with those from other analogue communities in southern Mexico, except for those found in some localities along the coasts of Quintana Roo, Yucatán [7], and Baja California [53,54] states, where dwarfed mangrove forest never reaches heights above 5 m.

Finally, we highlight the importance of comparing two distinct flooded forest communities characterized by the presence of *R. mangle* in the lower Usumacinta River Basin, each of them having its own diversity and structure. Although certainly the two communities are important for biological conservation and their provision of ecosystem services, we emphasize our concern for the future of the community located on the San Pedro River, given its relictual condition and the extremely small area it occupies, probably < 11 ha [49].

5. Conclusions

The swamp forest communities of the lower Usumacinta Basin exhibit a high structural and diversity heterogeneity across space. Such heterogeneity is determined by multiple environmental factors, among which water salinity and geomorphology seem to be of particular importance, although the ecological neighborhood may also play a considerable role. Most studies that emphasize the importance of swamp forests have focused on communities located in the close vicinity of the river mouths, in areas where large coastal lagoons exist or in saline or brackish environments with high sediment deposition. However, swamp forests located in continental areas distant from the coast have received much less attention, despite the fact that they are also highly threatened, if not more so, by human activities, which has resulted in a worrisome large shrinkage of their original extent. No single tract of the San Pedro flooded forest is currently included in any nature protection area, which makes its conservation even more uncertain.

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