From Marsh to Swamps: Vegetation Gradient Linked to Estuarine Hydrology

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INTRODUCTION

The distribution of ecosystems in coastal landscapes responds to environmental gradients generated by the continent-ocean interaction (Silva et al. 2017). The wetlands of the coastal zone are often influenced by the tide and receive input of saltwater from the ocean. However, since they are located in the lowest part of the basin, they continuously receive freshwater from the upper parts of the basin, either superficially or subsurface through the water table as well as from rainwater (Day et al. 2019). This interaction generates a mosaic with different types of coastal ecosystems, connected to each other by hydrology, and sharing species (Sheaves 2009). The excess of water and salinity are stressors for plant establishment (Perata et al. 2011; Rasool et al. 2013). In wetlands, hydrophytes have developed adaptations that allow them to tolerate or avoid these stressful conditions (Blom 1999; Howard and Mendelssohn 1999). This is especially true for plants growing in tidal saline wetlands (Tiner 2013). It is expected that, in a salinity and flood gradient, the greatest diversity or productivity will be present in the areas with less saline influence and less flooding.

In this study we sampled the vegetation, interstitial water salinity and water level in a coastal wetland system where there is a clear zonation between herbaceous and arboreal vegetation and, within the latter, different types of plant formations. Our objective was to determine the presence of a combined water level and salinity gradient in relation to the different observed plant formations.

STUDY SITE

The wetland system where the present study is located is in the south and southeast of Laguna La Mancha, in the central coastal region of the State of Veracruz, in Mexico. (Figure 1). The climate in this region is warm sub-humid with a summer rainy season and a Precipitation/Temperature quotient greater than 55.3 (type AW2; García 1970). Mean annual precipitation varies between 1200 and 1650 mm. The mean annual temperature is 25.5°C with a minimum of 17°C in January and a maximum of 27.3°C in June (Campos et al. 2011). There are three climatic seasons in the region: (a) the dry season (March to June) characterized by a mean monthly rainfall of 6 mm; (b) the rainy season (July to October) with a mean monthly rainfall from 200 to 400 mm; and (c) the *nortes* season (November to February) characterized by lower temperatures, strong northern winds (7 m/s on average at 10 m elevation), and a mean monthly rainfall of 24 mm (Castillo and Carabias 1982). The "La Mancha" lagoon has permanent and intermittent inputs of fresh water through streams, and also has input of salt water from the sea through intermittent communication with the Gulf of Mexico. The cold fronts of winter (*nortes* season) generate strong gusts of wind that lift the sand from the beach and the dunes, and deposit it at the mouth of the lagoon, forming a sandy bar that prevents communication with the Gulf of Mexico. During this season, the lagoon continues to receive freshwater through streams or by subsurface (Yetter 2004), which causes the water level of the entire system to rise (Moreno-Casasola et al. 2010). When the water level exceeds the level of the sand bar, it breaks through, so the lagoon once again communicates with the Gulf of Mexico, and the water level of the wetland system is offset by the sea level. The study site is within Ramsar Site 1336 "La Mancha y El Llano" and is partially within a private conservation area belonging to "Residencial Ecológico Diada La Mancha."

As shown in the map in Figure 1, The largest area of wetlands in the study site is covered by mangroves, but being located at the southern end of the lagoon, the distance to the mouth of the lagoon is two or more kilometers, and it is close to the mouth of the river called *Caño Gallegos*, which permanently carries water to the lagoon. Due to this location, the study site has a marked hydrological gradient, which is reflected in the presence of other types of vegetation, such as the flooded palm grove, the flooded freshwater forest and the freshwater herbaceous wetland.

METHODS

Sampling Design and Data Collection

We distributed 19 permanent monitoring units (MUs) in four types of wetlands in the system. We placed three MUs in the freshwater swamp (FWS, Figure 2), three in the palm forest swamp (PFS, Figure 3), and nine in the flooded grassland (FG, Figure 4). For this study we did not place MUs in the mangrove, but we used previous information gathered by our work team (Moreno-Casasola et al. 2009; Utrera López and Moreno-Casasola 2008) to select another four MUs from this wetland. The mangrove physiognomy at the site is shown in Figure 5. The geographical location and the characteristics of the vegetation type and main species of each MU are presented in Table 1. Figure 6 shows

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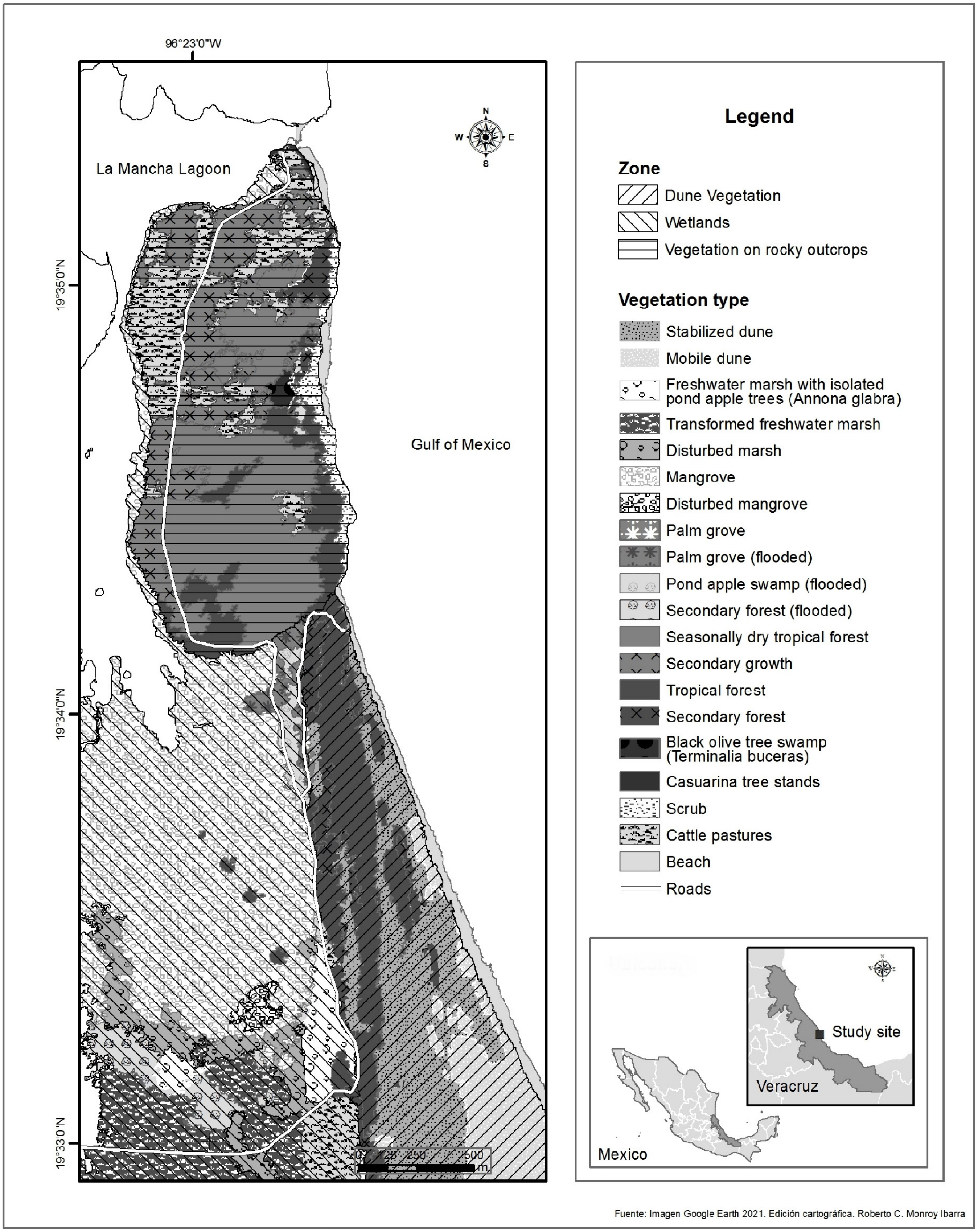

Figure 1. Map showing the different types of vegetation in the study site.

Monitoring Unit (MU)	Vegetation type	Geographic location		Dominant species	Accompanying species
		Latitude	Longitude		
FWS_01	Freshwater swamp	19.568587°	-96.379556°	*Annona glabra*	*None*
FWS_02	Freshwater swamp	19.566294°	-96.379593°	*Sabal mexicana, Conocarpus erectus*	*Laguncularia racemosa, Ficus cotinifolia*
FWS_03	Freshwater swamp	19.563870°	-96.379356°	*Annona glabra*	*Sabal mexicana*
PFS_01	Palm forest swamp	19.566827°	-96.380280°	*Sabal mexicana*	*Ginoria nudiflora, Pithecellobium* dulce
PFS_02	Palm forest swamp	19.567565°	-96.380106°	*Sabal mexicana, Conocarpus erectus*	*Avicennia germinans, Laguncularia racemosa*
PFS_03	Palm forest swamp	19.569334°	-96.380058°	*Sabal mexicana*	*Ginoria nudiflora, Avicennia germinans*
FG_01	Flooded grassland	19.555920°	-96.378484°	*Mimosa pigra, Echinochloa pyramidalis*	*Ipomoea tiliacea, Pontederia sagittata*
FG_02	Flooded grassland	19.555925°	-96.378770°	*Echinochloa pyramidalis*	*Mimosa pigra*
FG_03	Flooded grassland	19.555929°	-96.379065°	*Echinochloa pyramidalis*	*Eleocharis mutata,* Annona glabra
FG_04	Flooded grassland	19.554973°	-96.378509°	*Echinochloa pyramidalis*	*Mimosa pigra*
FG_05	Flooded grassland	19.554977°	-96.378786°	*Mimosa pigra, Eleocharis mutata*	*Fuirena simplex, Echinochloa pyramidalis*
FG_06	Flooded grassland	19.554990°	-96.379071°	*Mimosa pigra, Eleocharis mutata*	*Eclipta prostrata, Leersia hexandra*
FG_07	Flooded grassland	19.554025°	-96.378515°	*Echinochloa pyramidalis, Eleocharis interstincta*	*Leersia hexandra, Hymenocallis littoralis*
FG_08	Flooded grassland	19.554038°	-96.378810°	*Echinochloa pyramidalis*	*Mimosa pigra*
FG_09	Flooded grassland	19.554042°	-96.379105°	*Echinochloa pyramidalis*	*Annona glabra, Dalbergia brownei*
MS_01	Mangrove swamp	19.558693°	-96.379735°	*Rhizophora mangle, Laguncularia racemosa*	*Avicennia germinans*
MS_02	Mangrove swamp	19.557859°	-96.379530°	*Rhizophora mangle, Laguncularia racemosa*	*Avicennia germinans*
MS_03	Mangrove swamp	19.568718°	-96.389261°	*Rhizophora mangle*	*Laguncularia racemosa*
MS_04	Mangrove swamp	19.564902°	-96.388875°	*Avicennia germinans*	*Laguncularia racemosa, Rhizophora mangle*

Table 1. Geographical location, characteristics of the vegetation type, and main species of the monitoring units in this study.

Figure 2. Freshwater swamp with a mix of species that include *Annona glabra*, *Sabal mexicana, Ficus cotinifolia,* and the terrestrial *Pithecellobium dulce*. (Photo by Hugo López Rosas)

Figure 3. Palm forest swamp dominated by *Sabal mexicana*. (Photo by Hugo López Rosas)

Figure 4. Flooded grassland dominated by the African invader grass *Echinochloa pyramidalis.* (Photo by Hugo López Rosas)

Figure 5. Mangrove swamp with *Rhizophora mangle*. (Photo by Hugo López Rosas)

the location of these MUs in the system. The minimum distance between contiguous MUs was 30 m in herbaceous vegetation and 80 m in arboreal vegetation

The MUs were 10 x 10 m (100 m^2) squares, with two 4 x 4 m (16 m^2) sub-squares and four 1 x 1 m (1 m^2) sub-sub-squares, according to the methodology proposed by Valdez Hernández (2002). In the 10 x 10 m squares, we measured the diameter at breast height (DBH) and the height of trees with DBH greater than 2.5 cm, using the clinometer methodology (Brower et al. 1998). We use the 4 x 4 m squares to measure the percent cover (Kent 2011) and average height of shrubs and juvenile trees (i.e., those with height greater than 30 cm and DBH less than 2.5 cm). In the 1 x 1 m squares we estimated the percent cover and determined the average height for woody seedlings (less than 30 cm tall) and herbaceous species. In the center of each MU we installed a water table well (Peralta Peláez et al. 2009) to a depth of 50 cm to measure the water level and obtain interstitial water samples, from which we measured the salinity with Ultrameter II (Mod. 6PFC, Myron L). We did the vegetation and water sampling in October 2018. In addition to water table wells, to monitor hydrology, in June 2018 we installed level loggers (HOBO® model U20L) in three MUs: FWS_01, FWS_03, and FG_01. We programmed these probes to measure the water level every 30 min for slightly more than two years (until August 2020).

Relative Importance Value (RIV)

We obtained de RIV of each species in each MU. For tree species, we obtained the RIV using the formula:

$$\mathrm{RIV}_{\mathrm{trees}} = \frac{\text{Relative basal area} + \text{Relative height}}{2}$$

For shrub and herb species:

$$\mathrm{RIV}_{\mathrm{shrub\ and\ herbs}} = \frac{\text{Percent cover} + \text{Relative height}}{2}$$

We obtained the relative basal area of each tree species by adding the basal areas (in m^2) of the individuals of the same species in the MU and dividing by 100. To obtain the relative height, we divide the average height of the species in the MU by the maximum height obtained in the sampling, which was 14.4 m (López Rosas et al. 2021; Moreno-Casasola et al. 2016).

DATA ANALYSIS

With the values of each species, we constructed a data matrix with 19 MUs and 30 species. We transform these data with square root, to later create Bray-Curtis similarity matrices that we use to place each MU in groups (CLUSTER analysis; Legendre and Legendre 1998) or in an ordination space (MDS; Faith et al. 1987; Minchin 1987). To detect differences between groups of MUs, we applied an analysis of the percentage of similarity using permutation and randomization methods of the similarity matrix (SIMPROF test; Clarke et al. 2008). To identify the determining species of each group formed, we described the groups with statistical significance obtained from SIMPROF with the support of the technique of analysis of similarity between percentages and species contribution (SIMPER test; Clarke 1993). We constructed a second matrix (abiotic) with the salinity and water level data. We transformed these data through standardization before running an indirect gradient analysis (BEST/BIOENV test; Clarke et al. 2008) to interpret the CLUSTER or MDS in relation to environmental variables. We used PRIMER 6.0 to run the CLUSTER, SIMPROF,

Figure 6. Distribution of the monitoring units in the study site.

SIMPER, and BEST/BIOENV tests, and PCORD 6 to run the MDS ordination.

RESULTS

We recorded a total of 30 species, 11 trees or tree-like species, 13 herbs, and 6 shrubs or sub-shrubs. Table 2 shows the list of these species and their habit. The seven species with the highest average RIV (±1 SE, $n = 19$ MUs), in order from highest to lowest, were: Antelope Grass (*Echinochloa pyramidalis*; 15.0 ± 4.88), White Mangrove (*Laguncularia racemosa*; 11.8 ± 4.42), Black Mangrove (*Avicennia germinans*; 11.2 ± 5.21), Red Mangrove (*Rhizophora mangle*; 10.8 ± 4.78), Mexican Palm (*Sabal mexicana*; 9.6 ± 4.02), Giant Sensitive Plant (*Mimosa pigra*; 6.4 ± 2.69), and Pond Apple (*Annona glabra*; 6.1 ± 3.42). According to the composition of species, the MUs cluster into five significant (SIMPROF test; $Pi = 5.73$, $p = 0.001$) groups (Figure 7). From left to right, Group I had a similarity of 35.2%, and includes the nine MUs from flooded grassland. In this group the contribution of *E. pyramidalis* was 64.76 % (SIMPER test), while *Mimosa pigra* contributed with 21.41%. This was the only group dominated by herbaceous vegetation. Group II had a similarity of 67.4%, and included two MUs from the freshwater swamp: 100% of the contribution of this group was *Annona glabra*, although there was also a presence of the palm *S. mexicana*. This group included the MU "FWS_01" that was monospecific *Annona glabra* (Figure 8). Group III had a similarity of 54.53%; it included two MUs from palm forest swamp. The species that contributed the most to the formation of this group were *S. mexicana* (32.75%) and Guayabillo (*Ginoria nudiflora*; 30.12%), but the terrestrial Bullhorn Acacia (*Acacia cornigera*) was also present and contributed with 20.91%. Group IV had a similarity of 70.4%, and includes the four MUs from mangrove swamp that had co-dominance of *R. mangle* (40.70%) and *L. racemosa* (40.57%). *A. germinans* also was present in the mangrove, but with low contribution to the group (18.73%). Group V included one MU from the freshwater swamp and one from the palm swamp. This group had a similarity of 65.66% and the vegetation was a mixture of *S. mexicana* with mangrove species (*L. racemosa* and Buttonwood - *Conocarpus erectus*) and other trees from freshwater swamp (e.g., Strangler Fig - *Ficus cotinifolia* and *Annona glabra*). *Sabal mexicana* contributed 32.75%, while *L. racemosa* and *C. erectus* accounted for 27.68% and 24.57%, respectively.

The 2-dimensional MDS ordination of 20 MUs and plant species (stress = 10.34 for two dimensions; final instability = 1.0×10^{-8} with 75 iterations) shows a gradient from high salinity and low water levels to low salinity and high water levels (Figure 9). Along Axis 1, the herbaceous

Table 2. List of species found in the different wetlands of this study.

Family	Species	Habit	Vegetation type*			
			FWS	PFS	FG	MS
Acanthaceae	*Avicennia germinans* (L.) L.	Tree		x		x
Amaryllidaceae	*Hymenocallis littoralis* (Jacq.) Salisb.	Herb			x	
Annonaceae	*Annona glabra* L.	Tree	x		x	
Arecaceae	*Sabal mexicana* Mart.	Rosette tree (palm)	x	x		
Asteraceae	*Eclipta prostrata* (L.) L	Herb			x	
Combretaceae	*Conocarpus erectus* L.	Tree	x	x		
Combretaceae	*Laguncularia racemosa* (L.) C.F. Gaertn.	Tree	x	x		x
Commelinaceae	*Commelina* sp.	Herb			x	
Convolvulaceae	*Ipomoea tiliacea* (Willd.) Choisy	Herb (vine)			x	
Cucurbitaceae	*Melothria pendula* L.	Herb (vine)			x	
Cyperaceae	*Eleocharis interstincta* (Vahl) Roem. & Schult.	Herb (sedge)			x	
Cyperaceae	*Eleocharis mutata* (L.) Roem. & Schult	Herb (sedge)			x	
Cyperaceae	*Fuirena simplex* Vahl	Herb (sedge)			x	
Fabaceae	*Acacia cornigera* (L.) Willd	Shrub		x		
Fabaceae	*Dalbergia brownei* (Jacq.) Schinz	Climbing shrub		x	x	
Fabaceae	*Mimosa pigra* L.	Shrub			x	
Fabaceae	*Pithecellobium dulce* (Roxb.) Benth	Tree		x		
Lythraceae	*Ginoria nudiflora* (Hemsl.) Koehne	Tree		x		
Moraceae	*Ficus cotinifolia* Kunth	Tree	x	x		
Onagraceae	*Ludwigia octovalvis* (Jacq.) P.H. Raven	Sub-shrub			x	
Poaceae	*Echinochloa pyramidalis* (Lam.) Hitchc. & Chase	Herb (grass)			x	
Poaceae	*Leersia hexandra* Sw.	Herb (grass			x	
Polygonaceae	*Coccoloba barbadensis* Jacq.	Tree		x		
Pontederiaceae	*Pontederia sagittata* C. Presl	Herb			x	
Pteridaceae	*Acrostichum aureum* L.	Herb (fern)	x			
Rhizophoraceae	*Rhizophora mangle* L	Tree		x		x
Verbenaceae	*Lippia nodiflora* (L.) Michx.	Herb			x	
Unknown	Unknown (Bush_sp1)	Shrub			x	
Unknown	Unknown (Bush_sp2)	Shrub			x	
Unknown	Unknown (Tree_sp1)	Tree			x	

* FWS = freshwater swamp, PFS = palm forest swamp, FG = flooded grassland, and MS = mangrove swamp.

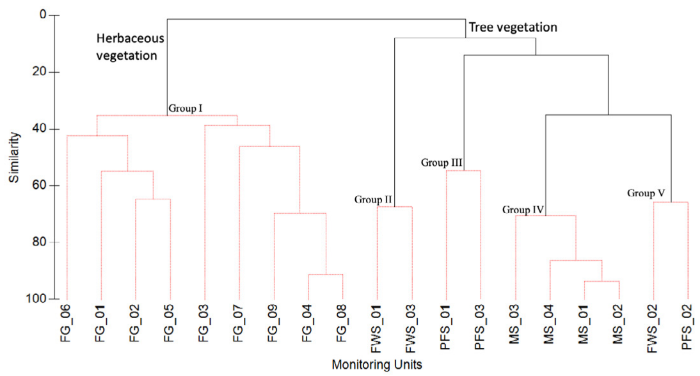

Figure 7. Dendrogram of the numeric classification of the 19 monitoring units. The red color indicates groups, significantly different (SIMPROF test, $p < 0.01$).

Figure 8. Monospecific formation of *Annona glabra*, as a type of freshwater swamp (MU FWS_01). (Photo by Hugo López Rosas)

vegetation (MUs from flooded grassland) is ordered to right side, where the water levels are higher and there are low salinity levels. The MUs of the palm forest swamp are ordered on the far right of the plot, where the water level values are the lowest and salinity values are high. On this side of the graph the MUs of the mangrove swamp are also located, but slightly more to the right of the MUs from the palm swamp grove - lower salinity and higher water level than the palm swamp. The MUs from the freshwater swamp and the palm forest swamp, with exception of FWS_01 and PFS_03, had a heterogeneous species composition, sometimes mixing with palm or mangrove species. These MUs are located in an intermediate space of the gradient, although the MU FWS_02 has more affinity with the MUs of the palm grove. With the BEST we obtained that the combination of salinity and water level had a high and significant correlation (0.574; BEST/BIOENV; *Rho* = 0.598, $p = 0.01$), indicating that both variables form the principal environmental gradient in the study site.

Hydroperiods show a similar pattern in herbaceous or arboreal wetlands (Figure 10), indicating hydrological connectivity. The wetlands have two flood peaks, one during the rainiest months (September-October), and one during the winter months when the sandy bar of the lagoon is closed and the water level rises gradually with the permanent entry of water from the river. The year 2019 presented a prolonged drought, and the water level of the wetlands did not recover until the end of the rainy season (Figure 10). The salinity and water level values of the different types of wetlands are presented in Table 3. In general, salinity values are low, even for the mangroves. According to the classification proposed by Montagna et al. (2017), the flooded grassland has oligohaline conditions and the freshwater swamp has oligohaline or slightly mesohaline conditions, while the mangrove swamp had mesohaline conditions. The palm forest swamp had a high variation, with a minimum value of 4.1 ppt (oligohaline) and a maximum of 13.6 ppt (mesohaline). The study area is a coastal plain in a tropical rainy region, receiving permanently subterranean flows from the mountain range close by and from the extensive dune system (Yetter 2004), as well as from the *Caño Gallegos* River. These sources supply freshwater to all the wetlands, thereby reducing salt stress. The water levels correspond to the beginning of the rainy season, with the variation in these levels due to the different topographic levels of the system (Flores-Verdugo et al. 2007) and the geomorphology of the landscape (Brinson 1993). The mangrove swamp and the flooded grassland are located in the floodplain, so they have the highest water levels, whereas the palm forest swamp and the freshwater swamp are in a topographic depression (dune slack) at the edge of the dune system, so they had low water level values.

DISCUSSION

The wetlands in this study are hydrologically connected and they respond to a salinity and water level gradient. The herbaceous vegetation is dominated by the African grass *Echinochloa pyramidalis*, and occurs in the areas with the highest flooding and lowest salinity levels. In the areas of higher salinity, the mangrove and the palm forest swamp are located, but the latter is found at higher elevations, with less flooding. In intermediate zones of the gradient is the freshwater swamp, which may support monospecific *Annona glabra* formations, but may also have a diverse mix of mangrove and palm elements.

Figure 11 presents a hypothetical model of the zonation of the different tropical coastal ecosystems in response to the combination of flood and salinity gradients (Moreno-Casasola 2016; Silva et al. 2017). Small salinity changes and flood levels result in a variety of wetlands with different species. The results of the present study confirm that these two variables are the main determinants of the distribution of vegetation in tropical coastal wetlands. Nonetheless, the actual delimitation between types of vegetation is complex because the species possess wide tolerances. In this study, it was possible to find mangrove species, such as *L. racemosa* and *R. mangle*, mixed in areas dominated by the palm *Sabal mexicana*. Also, although we observed areas dominated by *S. mexicana*, this species also mixes with species of flooded forest, such as *Ficus cotinifolia* or *Conocarpus erectus*. The higher species richness in the flooded grassland (16) is explained by the low salinity levels; while in the palm forest swamp its high richness (14) is due to its transitional location between oligohaline and mesohaline environments, and the low stress by inundation, sharing species with the freshwater swamp and the mangrove swamp, and with the presence of terrestrial plants. The MUs from the freshwater swamp only had six species due to the high dominance of *A. glabra*. This type of plant formation is rare in the coastal plain of Veracruz, and we have very little information about its natural history. The type of vegetation poorest in species (3) was the mangrove forest, because of saline stress. Rincón-Perez et al. (2020) found a similar pattern in relation to lower species richness associated with higher salinity in a gradient of coastal wetlands on the Mexican Pacific coast. In this study we did not obtain productivity data, but Infante-Mata et al. (2012) made the comparison of this variable in five freshwater coastal swamps of the Gulf of Mexico, including one in the study region, and they concluded that the litter production of this wetland type is similar to that of mangroves.

The area with the highest flooding and least saline influence was dominated by *E. pyramidalis*. This species had the highest RIV in this study. Despite being an herbaceous species with a maximum height of 2.0 m, this species had a higher RIV than the arboreal species due to its high coverage. This species has been reported as an invasive species of freshwater wetlands in this region of the country (López-Rosas et al. 2006). Due to the presence of isolated individuals of *Annona glabra* immersed in the grassland, we consider that this area was originally a swamp, but the historical management in the area caused the loss of

Vegetation type	Salinity (ppt)	Water level (cm)
Freshwater swamp (n=3)	5.9 ± 0.87	11.6 ± 1.18
Palm forest swamp (n=3)	8.0 ± 2.87	-36.3 ± 16.23
Flooded grassland (n=9)	1.2 ± 0.08	16.3 ± 1.42
Mangrove swamp (n=4)	11.6 ± 1.18	11.3 ± 1.18

Table 3. Salinity and water level by vegetation type.

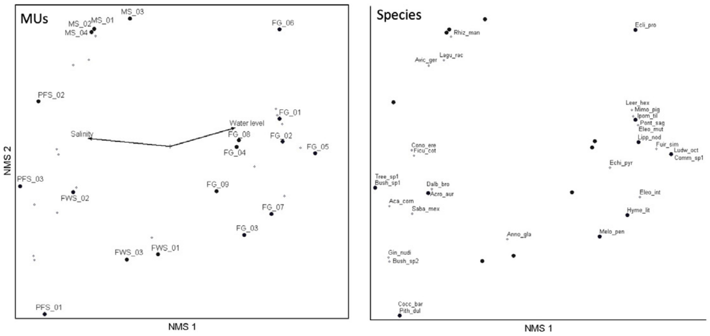

Figure 9. MDS ordination of 19 monitoring units (MUs) and wetland species. Ordination based on relative importance values of species data. Abiotic data are represented by vectors. The angle and length of vectors indicates the direction and strength of the relationships between abiotic factors and ordination scores.

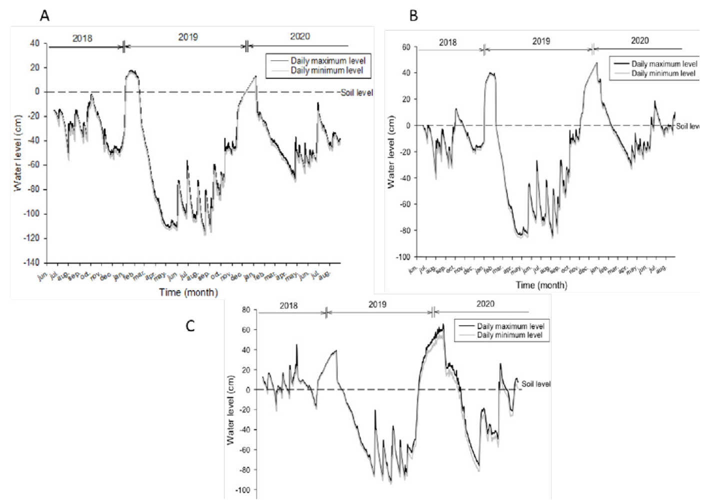

Figure 10. Hydroperiods for three type of wetlands in the study area from June 2018 to August 2020. The dashed line is ground level and the solid lines indicate the daily maximum (black) and minimum (gray) levels of the hydroperiods: A - freshwater swamp dominated by *Annona glabra* (MU FWS_01), B - freshwater swamp mixed with palm and mangrove species (MU FWS_03), and C - flooded grassland dominated by *Echinochloa pyramidalis* (MU FG_01).

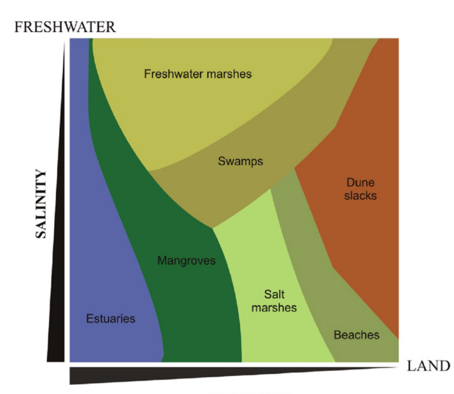

Figure 11. Schematic representation of the zonation of coastal ecosystems in a combined salinity and flood gradient. (Modified from Moreno-Casasola 2010 and Moreno-Casasola 2016)

the vegetation cover and its transformation into a flooded grassland. In this region of Mexico, freshwater wetlands are replaced by grasslands for extensive livestock farming. In mangroves this practice is not successful due to salt stress, which does not allow the survival of pasture grasses.

Ecological studies of tropical coastal wetlands show a strong bias towards only one type of wetland: mangroves. However, the results of the present study, as well as those of other authors (López-Rosas et al. 2021; Rincón Pérez et al. 2020), indicate that it is necessary to recognize and understand the patterns and processes of other types of coastal wetlands, that may be connected with mangroves. The bias in the research has prevented finding those relationships that are imperative for the generation of management and conservation proposals and obscure differences in ecosystem functioning such as productivity.

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