Physical-Biotic Structure in an Aquatic-Terrestrial Convergence Area in the San Francisco Marsh of the Ayapel Swamp System, Córdoba, Colombia

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ABSTRACT

This research analyzed the effect of border vegetation and pastures on the physical-biotic structure in a border sector of an aquatic-terrestrial convergence area, of the San Francisco Marsh of the Ayapel Swamp System (ASS), through organism groups, such as aquatic and terrestrial vegetation, aquatic macroinvertebrates and periphyton. In general, during the first phase of the flood pulse, a greater abundance of aquatic vegetation and periphyton algae was found (18 genera were determined in the forest and 16 in the pasture). Additionally, three families of aquatic macroinvertebrates were found in each study area. Good quality water was also found in the forest area, while moderately polluted water was found in the pasture. In the second phase of the flood pulse, the nutrients increased, the aquatic vegetation and periphyton algae densities decreased (seven genera were found in the forest and eight in the pasture), whereas the aquatic macroinvertebrates density increased, identifying six families in the forest and four in the pasture. Finally, both study areas had moderately polluted water. It is important to conserve and recover the native vegetation because it allows the presence of periphyton organisms, and aquatic macroinvertebrates, thereby making possible inorganic carbon fixation, nutrients recycling and organic matter availability. These contribute to the fish recovery, which is a fundamental economic resource in Ayapel and the surrounding areas.

Keywords: Border vegetation, flood pulse, aquatic macroinvertebrates, periphyton and transect lines.

RESUMEN

Esta investigación analizó el efecto de la vegetación de borde y de las pasturas, sobre la estructura físico-biótica en un sector de borde de una zona de convergencia acuático-terrestre, de la ciénaga San Francisco del sistema cenagoso de Ayapel-SCA, a través de grupos de organismos, como vegetación acuática y terrestre, macroinvertebrados acuáticos y las algas del perifiton. En general, en la primera fase del pulso de inundación, se encontró mayor abundancia de vegetación acuática y de algas pertenecientes al perifiton (se determinaron 18 géneros en el bosque y 16 en el pasto). Además, en cada una de las zonas de estudio se hallaron 3 familias de macroinvertebrados acuáticos. También se encontró agua de buena calidad en la zona de bosque, mientras que en el pasto hubo agua de moderada contaminación. En la segunda fase del pulso de inundación, aumentaron los nutrientes y disminuyeron las densidades de vegetación acuática y algas del perifiton (se hallaron 7 géneros en el bosque y 8 en el pasto), sin embargo, aumentó la densidad de macroinvertebrados acuáticos, determinándose 6 familias en el bosque y 4 en el pasto. Finalmente, ambas zonas de estudio tuvieron aguas en moderada contaminación. Es importante conservar y recuperar la vegetación nativa, debido a que permite la presencia de organismos del perifiton y los macroinvertebrados acuáticos, posibilitando así la fijación de carbono inorgánico, el reciclaje de nutrientes y la disponibilidad de materia orgánica. Estos favorecen a que se recupere la oferta de peces, siendo un recurso económico fundamental en Ayapel y las zonas aledañas.

Palabras clave: Vegetación de borde, pulso de inundación, macroinvertebrados acuáticos, perifiton y líneas transectas

INTRODUCTION

Floodplains are complex and dynamic wetland systems that oscillate periodically between the terrestrial and aquatic phases, flooded by lateral overflow of rivers or lakes, and by direct precipitation or groundwater. The resulting physical-chemical characteristics cause the biota to respond by adapting to their characteristics (Ramsar 2007; Rúa et al. 2014).

Wetlands are considered among the most productive environments in the world, they are strategic ecosystems ecologically and socially as they act as regulators of the hydrological cycle and are an important source of goods and services for the livelihood of surrounding populations (Ramsar 2016; Rúa et al. 2014). They are a source and sink of sediment, organic matter and nutrients, on which countless plant and animal species depend for subsistence. Making it a suitable habitat for the establishment of great biological diversity, such as species of birds, mammals, reptiles, amphibians, fish and invertebrates (Ramsar 2016; Rúa et al. 2014). The global area of natural wetlands is estimated to have decreased by 3.4 million km2, corresponding to a loss of approximately 21% (Fluet-Chouinard et al. 2023). The most significant impact factors are pollution (54%), use of biological resources (53%), modification of natural systems (53%), and agriculture and aquaculture (42%). More than half of wetlands are affected by three to four factors (Xu et al. 2019). Other causes associated with wetland deterioration are extreme climatic events (severe droughts and floods), eutrophication, sedimentation, erosion, mining, drainage, infrastructure development such as

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dams, dykes, channelization, mines and roads, and tourism and recreational activities (Gardner and Finlayson 2018; Mason et al. 2021; Patino and Estupinan-Suarez 2016; Kinimo et al. 2018). These activities cause deterioration of riparian vegetation, including arboreal vegetation, aquatic vegetation and pastures, which give stability to the ecosystem, provide ecological functions for the amphibians, reptiles, birds and mammals, and are a fundamental resource for fishes (Clavijo and López 2017).

In the Ayapel Swamp System (ASS), 70% of the aquatic plants are free-floating, whose roots provide shelter and food areas for small fishes along with spawning, nesting, and raising of larvae and juveniles. Fifty-two species of fish have been reported, including 15 migratory species. A common evergreen riparian tree, Symmeria paniculata is found in the swamp. It has the characteristics and ecological functions of the mangroves and serves as a niche for many species of birds, mammals, reptiles, and fishes (Marín 2012). The research question formulated in this project was: How is the physical-biotic structure in an aquatic-terrestrial convergence area with arboreal vegetation and pastures, in the San Francisco Marsh of the Ayapel Swamp System during two contrasting moments of the hydrologic cycle? Therefore, our hypothesis is that removing the semi-aquatic arboreal vegetation has a negative effect on the complexity and stability of the ecotone (Aquatic Terrestrial Transition Zone - ATTZ). The terrain becomes more unstable due to the grazing, thereby negatively impacting water quality and biodiversity among other environmental conditions and the negative impact it has on ecosystem services. This negative impact occurs because the riparian vegetation dampens flood pulses, prevents erosion, contributes organic matter to the wetland, functions as a filter improving water quality, controls the entry of pollutants, regulates temperature and the flow of matter and energy (Clavijo and López 2017; Greer et al. 2012; Möller 2011; Rodríguez et al. 2012), protecting the littoral zone from the natural and anthropic pressures to which the system is subjected, in addition to having decisive structural and operational functions for the species, since it is the site of their feeding and reproduction.

To analyze the effect of the presence of arboreal vegetation on the physical-biotic structure and the impact of its removal and replacing it with pasture, we conducted a baseline study examining a relatively undisturbed section of the San Francisco Marsh of the Ayapel Swamp System. This study would provide a reference condition for later assessing conditions in disturbed áreas that would then establish its effect on water quality and aquatic biodiversity.

METHODOLOGY

Study Area

The Ayapel Swamp System (ASS), part of the wetland and floodplain macro-ecosystem in the Momposina Depression, is a system of lakes on the alluvial plain of the San Jorge River, located in the Colombian Caribbean side in the Department of Córdoba (altitude of 20 m.a.s.l.) (Aguilera 2009). The hydrological cycle in Ayapel is monomodal, with a rainy season (between April and November) and a dry season (between December and March). As a result, the flood pulse presents a season of low water from December into March, high water in August and September, and the so-called rising and falling water transitions in the two

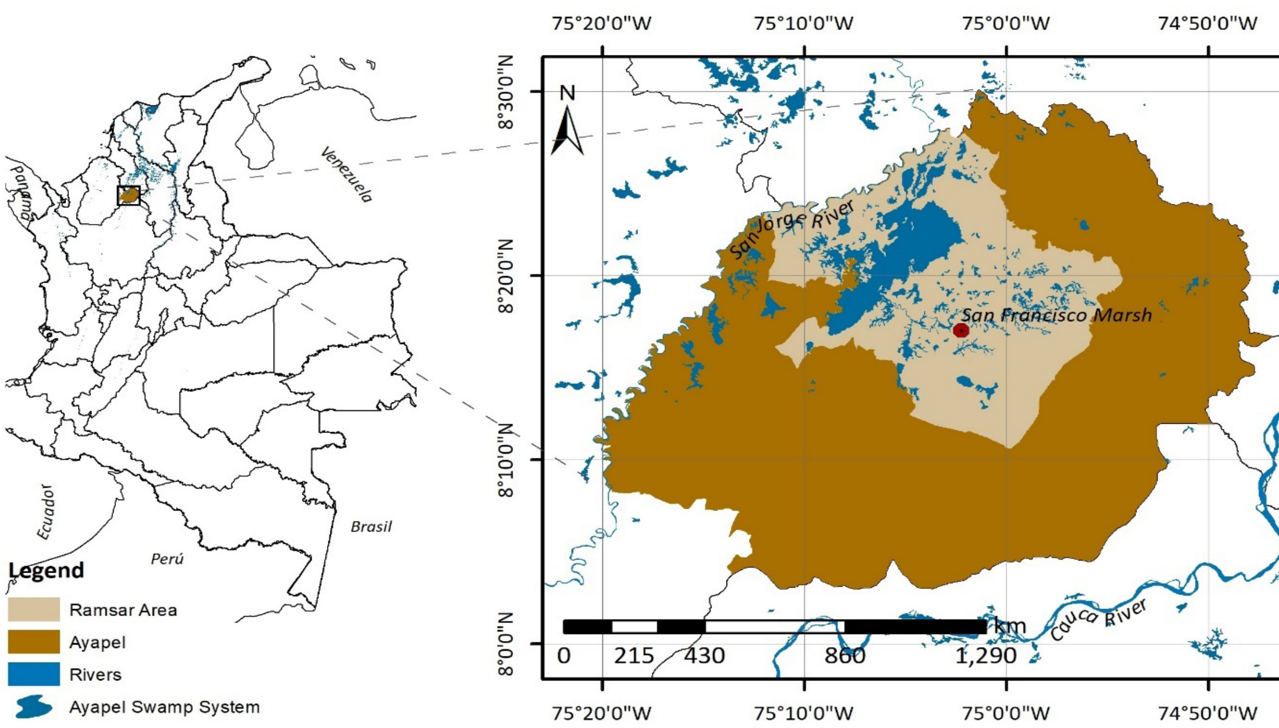

Figure 1. Ayapel Location, Córdoba; Ramsar polygon and sampling site (Prepared by Maria Díaz-Mesa).

Figure 2. Aerial view of the San Francisco Marsh (from Google Earth)

remaining intervals (Serna and Cañón 2020). Depth ranges can vary between 2 and 8 meters in the high water phase, and in dry seasons, between 1 and 3 meters; the area of the water mirror is 145 km2 in the high water season and in the dry season it can reach 40 km2 (Serna and Cañón 2020).

Field Visits

San Francisco Marsh was chosen as a sampling site. This site was selected because it is in relatively natural conditions with low anthropic influence. San Francisco is located in a fluvial environment, its geoforms originate from erosion processes of the water body currents and the accumulation or sedimentation of materials. It has a flat morphology and plain or gently inclined slopes. Areas of the marsh were chosen to have grasslands and zones of trees and shrubs where the main species cover was Symmeria paniculata. Two visits were made to the study area to collect the samples and the necessary information at two contrasting moments of the flood pulse, the first moment in rising waters (July/2018) (8°17'4.95"N, 75°2'26.04"W), and the second one in low waters (February/2019) (8°17'1.26"N, 75°2'16.85"W). The two observations were made in different sectors due to the fact that the first sector was completely dry at low water phase.

Vegetation Sampling, Identification, and Analysis

At the sampling sites, four 10 m transect lines were placed, located 5 m over the land area, and 5 m over the aquatic area. Two transect lines were in forest area (B1 y B2) and two transect lines were in pasture area (P1 y P2).In the terrestrial area, the taxonomic identification of the vegetation was carried out, of each individual along the rope was carried out. The vegetation taxonomy was identified at the sampling site, with the assistance of Prof. Dr. rer. nat. Néstor Aguirre. Contrasted with virtual collections: Colombian National Herbarium (COL, for its Spanish acronym) – GBIF (http://www.biovirtual.unal.edu.co/, and https://www.gbif.org/), The Tropicos Database (https://www.tropicos.org/home), and Global Plants JSTOR (https://plants.jstor.org/).

The surface soil samples were extracted through a shovel-width hole to a maximum depth of 20 cm. Moisture, density, and porosity were evaluated by the gravimetric method, which consisted of determining the masses of the wet and dry samples, and by difference, the moisture content was determined. Sediment density was calculated from the dry mass and the measured sample volume, a method described by Dadey, Janecek, and Klaus (1992). As for the granulometric analysis, it was performed by the hydrometer method according to the procedure described by the I.N.V.E--123-E-13 standard of 2007.

In the aquatic area, vegetation samples were collected using a 1 m² quadrant located over the water surface. In these samples, the aquatic macroinvertebrates and the periphyton associated with their roots were extracted, based on the methodology of Aguirre and Caicedo (2015). The vegetation taxonomy was identified at the sampling site, while those individuals for which this was not possible were preserved in alcohol, and were subsequently identified at the herbarium of the University of Antioquia (B2 - 411), with the assistance of Professor Francisco Javier Roldán Palacio.

For the identification of the aquatic macroinvertebrates, the stereoscope BST-606 (BOECO + Co - Hamburg, Germany) was used, as well as the taxonomic keys of Machado (1989), Linares et al. (2019), Arnett and Thomas (1999), Lancaster and Downes (2014), and Domínguez and Fernández (2009). After the identification, the abundance and richness were calculated based on the methodology of Aguirre and Caicedo (2015) and the Standard Methods (2013). For identification of the periphytic algae, 30 fields were observed with 40X in the Inverted Microscope BIB-100 (BOECO + Co - Hamburg, Germany). Periphyton identification was made with the keys of Streble and Krauter (1988), and Taylor et al. (2007), and consulting the Algaebase website (https://www.algaebase.org). The Past3 software (Øyvind Hammer, Natural History Museum, University of Oslo) was used to calculate the diversity indices (Shannon-Weaver (H) diversity index, Simpson (D) dominance index and Pielou (J) equity index).

Water Quality Sampling and Analysis

For water quality, samples were taken in the subsurface part (at 20cm depth) of the water column in each area (pasture and forest). Dissolved oxygen, temperature, conductivity, and pH were measured in situ with the Multiparametric 3630 IDS (WTW - Bavaria, Germany). Turbidity was measured with the 2100Q turbidimeter (HACH - Iowa, USA), while the carbon dioxide content was measured by the colorimetric method. Phosphorus content was measured with the PF-12 photometer (Macherey-Nagel - Düren, Germany), using the Visocolor Kit reference 931-284 with measurement range of 0.20-5.00 $mg.L^{-1}$ PO_4^{-}-P (Macherey-Nagel - Düren, Germany). In the same way, the concentrations of nitrites, nitrates, and ammonium were measured using the Visocolor Kits reference 931-244 (measuring range 0.02-0.50 mg.L-1 NO2-), reference 931-241 (measuring range 1.00-120.00 mg.L-1 NO3‾), and reference 931-010 (measuring range 0.50-15.00 mg.L-1 NH4+), respectively (Macherey-Nagel - Düren, Germany). At the Laboratory of Environmental Studies (LEA, for its Spanish acronym) of the University of Antioquia, the total suspended solids, volatile suspended solids, and fixed suspended solids were calculated by the gravimetric method, following the Standard Methods for water and wastewater analysis (PHA 2013). Finally, the data were analyzed in the laboratory and the results interpreted, applying the diversity indices according to the methodology of Aguirre and Caicedo (2015) and Standard Methods (2013). The similarity between the sampling sites was also analyzed using the BioDiversity Pro 2.0 software (SAMS - Oban, United Kingdom) through the Bray - Curtis Cluster analysis.

RESULTS

Rising Water Phase

Forest Area. The terrestrial vegetation coverage was composed only of *Symmeria paniculata* (Approx. 3m tall), it is a common, evergreen tree species from the lowest part of the flooding gradient in inundation forests (Waldhoff, D.

Table 1. Comparison of soil type, physicochemical and biotic characteristics of the San Francisco Marsh.

	Variable	Units	Rising Water Phase				Low Water Phase			
			Pasture		Forest		Pasture		Forest	
			P1	P2	B1	B2	P1	P2	B1	B2
Soils	**Silt**	%	12.8		34.5		23.9		50.1	
	Clay	%	27.0		18.7		15.4		13.6	
	Fine sands	%	60.2		46.8		60.8		36.2	
	Moisture	%	89.0		53.7		94.4		54.4	
	Density	g/cm^3	1.6		1.9		2.1		1.0	
	Porosity	%	54.6		33.1		32.9		68.9	
Physicochemical characteristics	***Secchi depth***	m	0.70		1.05		0.11		0.19	
	T H_2O	°C	32.45		31.60		33.40		33.40	
	Turbidity	NTU	9.37		8.15		257.50		97.70	
	Conductivity	$\mu S.m^{-1}$	144.70		147.60		181.00		179.90	
	O_2	$mg.L^{-1}$ O_2	4.19		5.85		0.26		5.04	
	CO_2	$mg.L^{-1}$ CO_2	30.80		28.60		154.00		88.00	
	pH	-	7.46		7.41		7.94		7.34	
	TSS	$mg.L^{-1}$	85.00		50.00		61.50		80.50	
	FSS	$mg.L^{-1}$	50.00		10.00		48.50		65.00	
	VSS	$mg.L^{-1}$	35.00		40.00		13.00		15.50	
	Ammonium	$mg.L^{-1}$ NH_4^+	<0.50		<0.50		1.10		1.65	
	Nitrates	$mg.L^{-1}$ NO_3^-	<1.00		<1.00		12.00		21.50	
	Nitrites	$mg.L^{-1}$ NO_2^-	<0.02		<0.02		0.12		0.23	
	Phosphate	$mg.L^{-1}$ PO_4^--P	0.07		0.06		1.65		2.85	
Aquatic macroinvertebrates	**Abundance**	# families	3.00	2.00	3.00	1.00	4.00	3.00	6.00	2.00
Periphyton	**Abundance**	# genera	9.00	12.00	16.00	15.00	5.00	6.00	4.00	3.00
	H	-	2.33	2.61	3.07	3.09	1.63	1.97	1.35	1.64
	D	-	0.12	0.09	0.06	0.06	0.22	0.16	0.27	0.24
	J	-	0.91	0.90	0.90	0.88	0.91	0.95	0.98	0.84

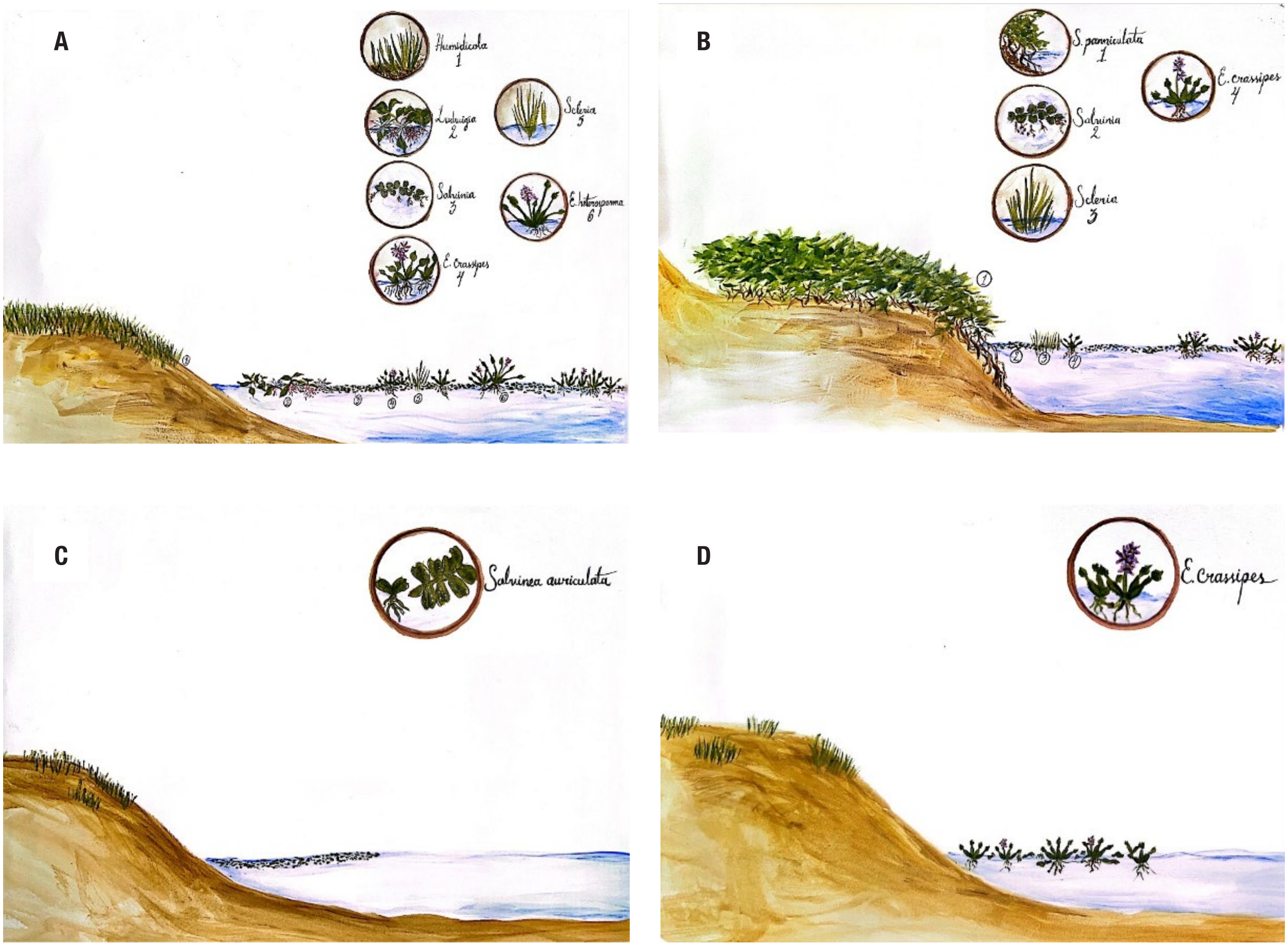

Figure 3. Topographic profiles, San Francisco Marsh of the ASS: a) pasture area, rising waters, b) forest area, rising waters, c) pasture area, low waters, and d) forest area, low waters. (Illustration by Sara Ramirez, 2019)

et al. 2002). The aquatic area contained *Salvinia minima*, *Eichhornia crassipes*, and *Scleria* sp. (Figure 3b). The soil found was fine-grained, classified as 34.5% silt, 18.7% clay and 46.8% fine sands. And its physical characteristics were 53.7% moisture, density 1.9 g/cm3 and porosity 33.1% (Table 1). The physicochemical characteristics, such as *Secchi depth*, turbidity, water temperature, and dissolved oxygen, were: 1.05 m, 8.15 NTU, 31.60 °C and 5.85 mg.L-1 O2, respectively; and the total suspended solids were 50.00 mg.L-1, with 40.00 mg.L-1 of volatile suspended solids and 10.00 mg.L-1 of fixed solids. During this season, the concentrations of nitrites and nitrates were below the detection limit of the measurement method, and the phosphorus concentration in the phosphates was 0.06 $mg.L^{-1}$ PO_4^{-}-P (Table 1).

Additionally, the biota associated with the aquatic vegetation roots in this area had aquatic macroinvertebrates from the families Ampullariidae, Hydrophilidae, and Planorbidae, with the latter being the most abundant, with 11 individuals in B1 and 13 in B2 (Table 2 and Figure 4).

There were 18 different genera of algae belonging to the periphyton, being Cymbella sp. (145 org.mL-1 in B1 and 170 org.mL-1 in B2) and Diatoma sp. (187 org.mL-1 in B1 and 119 org.mL-1) (Table 3 and Figure 5) being the most abundant. The Shannon-Weaver diversity calculated was 3.07, and 3.09 in B1 and B2, respectively. Simpson dominance with values of 0.06 for B1 and B2. And Pielou equity was 0.90, and 0.88, in B1 and B2, respectively (Table 1).

Pasture Area. The terrestrial vegetation coverage was composed of Humidicola grass. The aquatic area contained *Salvinia minima, Eichhornia crassipes, Scleria* sp., *Ludwigia* sp. and *Eichhornia heterosperma* (Figure 3a). The soil found was fine-grained, classified as 12.8% silt, 27% clay and 60.2% fine sands. And its physical characteristics were 89% moisture, density 1.6 g/cm3 and porosity 54.6% (Table 1). The physicochemical characteristics, such as Secchi depth, turbidity, water temperature, and dissolved oxygen, were: 0.70 m, 9.37 NTU, 32.45 °C, and 4.19 mg.L-1 O2, respectively, and total suspended solids were 85.00 mg.L-1, with 50.00 mg.L-1 of fixed suspended solids and 35.00 mg.L-1 of volatile suspended solids. The concentra-

Table 2. Abundance and relative abundance of aquatic macroinvertebrates per transect line, associated with the aquatic vegetation roots in the San Francisco Marsh.

		Abundance (#org)									Relative Abundance (%)							
		Rising Water Phase				Low Water Phase				Total	Rising Water Phase				Low Water Phase			
Order	Family	P1	P2	B1	B2	P1	P2	B1	B2		P1	P2	B1	B2	P1	P2	B1	B2
Mesogastropoda	Ampullariidae sp 1	0	2	1	0	0	0	0	0	**3**	0.00	14.29	7.69	0.00	0.00	0.00	0.00	0.00
	Ampullariidae sp 2	1	1	0	0	0	0	0	0	**2**	8.33	7.14	0.00	0.00	0.00	0.00	0.00	0.00
Coleoptera	Carabidae sp 1	0	0	0	0	0	0	3	0	**3**	0.00	0.00	0.00	0.00	0.00	0.00	4.48	0.00
	Dytiscidae sp 1	1	0	0	0	3	0	4	0	**8**	8.33	0.00	0.00	0.00	3.90	0.00	5.97	0.00
	Dytiscidae sp 2	0	0	0	0	0	7	0	0	**7**	0.00	0.00	0.00	0.00	0.00	11.67	0.00	0.00
	Hydrophilidae sp 1	0	1	1	0	17	3	5	6	**33**	0.00	7.14	7.69	0.00	22.08	5.00	7.46	13.64
	Hydrophilidae sp 2	3	2	0	0	0	0	2	0	**7**	25.00	14.29	0.00	0.00	0.00	0.00	2.99	0.00
	Hydrophilidae sp 3	2	7	0	0	0	2	8	3	**22**	16.67	50.00	0.00	0.00	0.00	3.33	11.94	6.82
	Hydrophilidae sp 4	3	0	0	0	2	4	1	4	**14**	25.00	0.00	0.00	0.00	2.60	6.67	1.49	9.09
	Hydrophilidae sp 5	2	1	0	0	2	3	0	2	**10**	16.67	7.14	0.00	0.00	2.60	5.00	0.00	4.55
	Hydrophilidae sp 6	0	0	0	0	2	3	2	2	**9**	0.00	0.00	0.00	0.00	2.60	5.00	2.99	4.55
	Hydrophilidae sp 7	0	0	0	0	0	0	1	0	**1**	0.00	0.00	0.00	0.00	0.00	0.00	1.49	0.00
	Hydrophilidae sp 8	0	0	0	0	0	0	2	1	**3**	0.00	0.00	0.00	0.00	0.00	0.00	2.99	2.27
	Noteridae sp 1	0	0	0	0	40	26	31	26	**123**	0.00	0.00	0.00	0.00	51.95	43.33	46.27	59.09
	Noteridae sp 2	0	0	0	0	10	12	6	0	**28**	0.00	0.00	0.00	0.00	12.99	20.00	8.96	0.00
Basommatophora	Planorbidae sp 1	0	0	5	5	0	0	0	0	**10**	0.00	0.00	38.46	38.46	0.00	0.00	0.00	0.00
	Planorbidae sp 2	0	0	6	5	0	0	1	0	**12**	0.00	0.00	46.15	38.46	0.00	0.00	1.49	0.00
	Planorbidae sp 3	0	0	0	3	0	0	0	0	**3**	0.00	0.00	0.00	23.08	0.00	0.00	0.00	0.00
Mesogastropoda	Thiaridae sp 1	0	0	0	0	1	0	1	0	**2**	0.00	0.00	0.00	0.00	1.30	0.00	1.49	0.00
Total		**12**	**14**	**13**	**13**	**77**	**60**	**67**	**44**	**300**	**100.00**	**100.00**	**100.00**	**100.00**	**100.00**	**100.00**	**100.00**	**100.00**

tions of nitrites and nitrates were below the detection limit of the measurement method, and the phosphorus concentration in the phosphates was 0.07 mg.L^{-1} PO_4^--P (Table 1). The biota associated with the aquatic vegetation roots were aquatic macroinvertebrates from the families Ampullariidae, Dytiscidae, and Hydrophilidae, the latter being the most abundant (10 organisms at P1 and 11 at P2) (Table 2 and Figure 4). There were a total of 16 different genera of algae belonging to the periphyton, with Diatoma sp. (68 org.mL-1 at P1 and 94 org.mL-1 at P2) and Fragilaria sp. (60 org.mL-1 at P1 and 17 org.mL-1 at P2) being the most abundant (Table 3 and Figure 5). The Shannon-Weaver diversity were 2.33, and 2.61 for P1 and P2, respectively. Simpson dominance with values of 0.12 and 0.09 for P1 and P2, respectively. And the Pielou equity were 0.91 and 0.90, in P1, P2, respectively (Table 1).

Low Water Phase

Forest Area. The terrestrial part in forest and pasture areas showed Humidicola grass. The reason why grass was found in both areas, although one of them was forest (as shown in Figure 2), was because in this season the water surface contracts, exposing areas that in previous seasons were covered by a water column, and the vegetation that germinates first are grasses, as explained by Junk in the flood pulse theory (1989). *Eichhornia crassipes* was found in the aquatic area (Figure 3d). The soil found was fine-grained, classified as 50.1% silt, 13.6% clay and 36.2% fine sands. And its physical characteristics were 54.4% moisture, density 1.0 g/cm3 and porosity 68.9% (Table 1). The Secchi depth, turbidity, water temperature and dissolved oxygen were: 0.19 m, 97.70 NTU, 33.40 °C, and 5.04 mg.L^{-1} O2, respectively (Table 1). The total suspended solids were 80.50 mg.L^{-1}, containing 65.00 mg.L^{-1} of fixed suspended solids and 15.50 mg.L^{-1} of volatile suspended solids. During that time, the nutrient levels increased; the nitrites, nitrates, and the orthophosphates phosphorus were 0.23 mg.L^{-1}NO_2^-, 21.50 mg.L-1 NO_3^-, and 2.85 mg.L-1PO_4^--P, respectively (Table 1). The biota associated with the aquatic vegetation roots in this area showed aquatic macroinvertebrates of the families Carabidae, Dytiscidae, Hydrophilidae, Noteridae, Planorbidae, and Thiaridae, being Noteridae the most abundant: 37 individuals in B1 and 26 in B2 (Table 2 and Figure 4). A total of 7 different genera of algae belonging to the periphyton were presented, with *Pinnularia* sp. being the most abundant in B2 with 68 org.mL-1, and Navicula sp. in B1 with 17 org.mL-1 (Table 3 and Figure 5). Shannon-Weaver diversity was values were 1.35 and 1.64, for B1 and B2, respectively. Simpson dominance were 0.27 and 0.24 for B1 and B2. And Pielou equity, the values were 0.98 and 0.84, in B1 and B2, respectively (Table 1).

Pasture Area. Salvinia auriculata was found in the aquatic area of the pasture (Figure 3c). The soil found was fine-grained, classified as 23.9% silt, 15.4% clay and 60.8% fine sands. And its physical characteristics were 94.4% moisture, density 2.1 g/cm3 and porosity 32.9% (Table 1).The physicochemical characteristics, such as Secchi depth, turbidity, water temperature, and dissolved oxygen, associated with the forest area were: 0.11 m, 257.50 NTU, 33.40 °C, and 0.26 mg.L-1 O_2, respectively. The total suspended solids were 61.50 mg.L-1, divided into fixed suspended solids (48.50 mg.L-1) and volatile suspended solids (13.00 mg.L-1) (Table 1). The nutrient concentrations

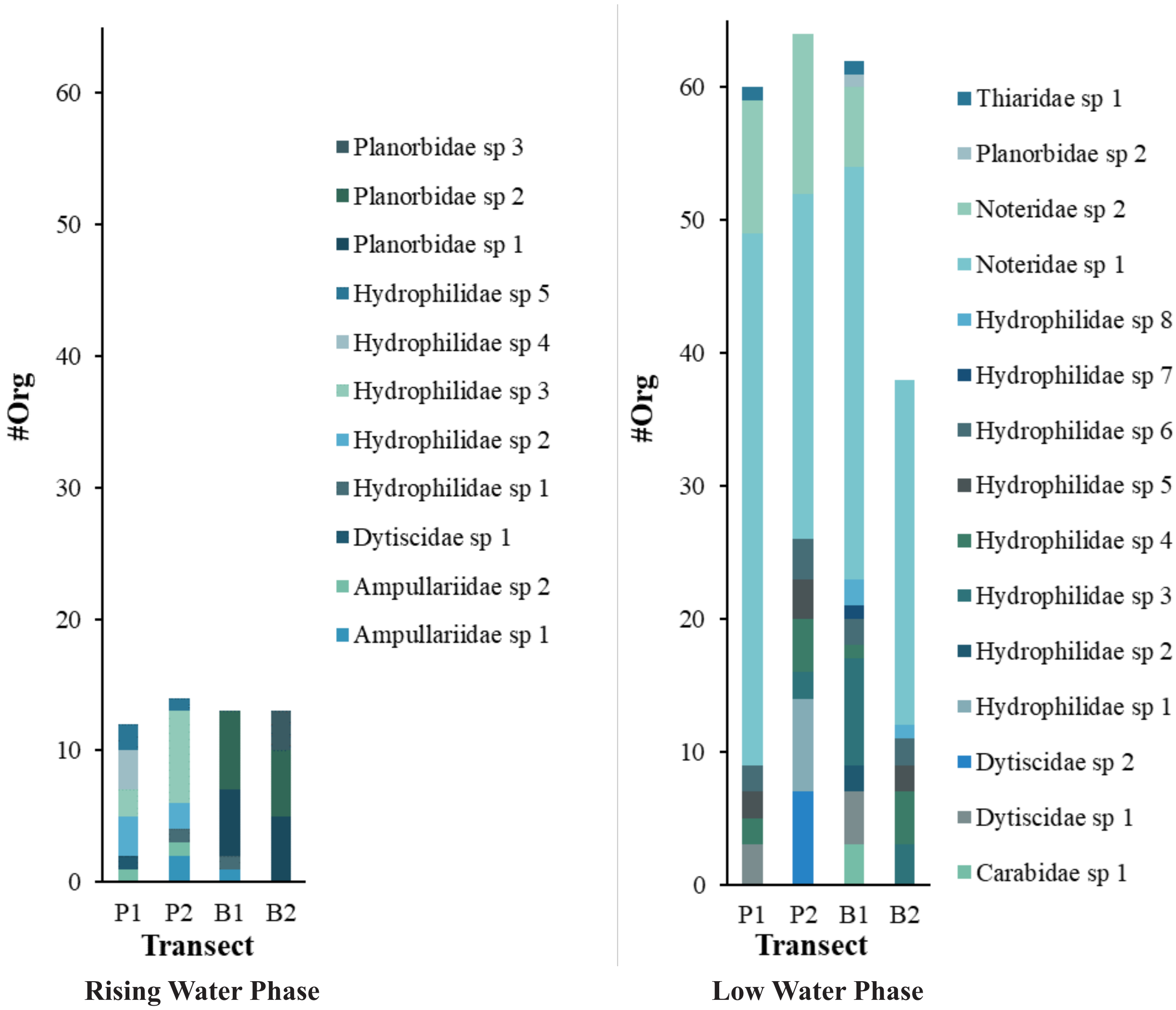

Figure 4. Abundance of aquatic macroinvertebrates associated with the aquatic plant roots, in the San Francisco Marsh during rising and low water phases.

increased compared to the previous season. The nitrates, nitrites, and the phosphorus in the orthophosphates were 12.00 mg.L-1 NO_3^-, 0.12 mg.L-1 NO_2^-, and 1.65 mg.L-1 PO_4^--P, respectively (Table 1). The biota associated with the aquatic vegetation roots of this transect presented aquatic macroinvertebrates of the families Dytiscidae, Hydrophilidae, Noteridae, and Thiaridae, where the families with greater abundance were Hydrophilidae (23 organisms at P1 and 15 at P2), and Noteridae (50 individuals at P1 and 38 at P2) (Table 2 and Figure 4). There were 8 different genera of algae belonging to the periphyton, being the *Surirella* sp. the most abundant with 51 org.mL-1 at P1, and 34 org. mL-1 at P2 (Table 3 and Figure 5). The Shannon-Weaver diversity with values of 1.63 and 1.97 for P1 and P2, respectively. Simpson dominance were 0.22 and 0.16 for P1 and P2. And the Pielou equity, the values were 0.91 and 0.95, in P1 and P2 (Table 1).

DISCUSSION

The results showed that the flood pulse determines the dynamics of the marsh, i.e., the high level of the water column generates a greater aquatic plant diversity and a lower nutrient concentration, since aquatic plants absorb nutrients and incorporate them into their metabolic processes (Ávalos and Pérez 2009; Montoya et al. 2011; Junk et al. 1989; Mackay et al. 2012). In contrast, the shallower the depth, the more homogeneous the vegetation becomes. Aquatic plants die and accumulate on the riverbanks, therefore, the nutrient concentration increases in the water column and dissolved oxygen decreases, since this is used in the oxidation of nutrients and organic matter coming from the decomposing vegetation (Montoya et al. 2011; Junk et al. 1989; Mackay et al. 2012; Rúa et al. 2014). Besides, riparian vegetation in the forest area such as S. paniculata facilitates nutrient and sediment retention, so the water has less turbidity and less concentration of suspended solids, thereby increasing the Secchi depth (Marín et al. 2012; Rodríguez et al. 2012). This last factor possibly allows the productive area of the marsh to be deeper, favoring the presence of autotrophic organisms (Brinson et al. 1981; Miller and Fujii 2010). In comparison, the pasture vegetation favors nutrient presence due to the pesticides used to

Table 3. Peripheral algae density associated with aquatic plants in the San Francisco Marsh.

	Density (#org.mL⁻¹)							
	Rising waters phase				Low waters phase			
	P1	P2	B1	B2	P1	P2	B1	B2
Amphora sp 1	0	17	26	9	0	0	0	0
Amphora cf2	0	0	34	43	0	0	0	0
Aulacoseira sp 1	0	43	68	0	0	0	0	0
Aulacoseira cf2	0	26	51	9	0	0	0	0
Chroococcus sp 1	0	0	0	0	0	0	0	9
Crucigenia sp 1	0	0	0	34	0	0	0	0
Cyclotella sp 1	0	0	26	9	0	0	0	0
Cymbella sp 1	26	26	119	145	0	0	0	0
Cymbella cf2	0	9	0	17	0	0	0	0
Cymbella sp 3	0	0	26	9	0	0	0	0
Diatoma sp 1	17	26	85	43	17	9	0	0
Diatoma sp 2	51	68	102	77	0	0	0	0
Elakatothrix sp 1	9	0	0	0	0	0	0	0
Eunotia cf1	17	43	77	17	0	9	0	0
Eunotia cf2	0	0	17	26	0	0	0	0
Eunotia cf3	0	0	26	9	0	0	0	0
Eunotia cf4	0	0	9	43	0	0	0	0
Eunotia cf5	0	0	0	0	0	0	0	0
Fragilaria cf 1	9	0	17	0	0	0	17	0
Fragilaria sp 2	51	9	68	68	0	0	0	0
Fragilaria sp 3	0	9	0	9	0	0	0	0
Fragilaria cf4	0	0	34	9	0	0	0	0
Frustulia sp 1	9	0	17	0	0	0	0	0
Gomphonema cf1	0	0	0	0	0	0	17	0
Gomphonema cf2	26	0	9	17	0	0	0	0
Gomphonema cf3	9	0	0	9	0	0	0	0
Gomphonema sp 4	0	0	0	17	0	0	0	0
Gomphonema cf5	0	0	0	9	0	0	0	0
Melosira sp 1	0	9	0	0	0	0	0	0
Navicula sp 1	0	0	0	0	9	0	0	0
Navicula sp 2	0	0	9	0	0	9	0	0
Navicula sp 3	0	0	17	34	0	9	0	0
Navicula sp 4	9	9	0	0	0	0	17	0
Navicula sp 5	9	9	119	51	0	0	0	0
Navicula sp 6	0	0	0	17	0	0	0	0
Nitzschia sp 1	0	9	26	17	17	0	0	0
Nitzschia sp 2	0	0	17	0	0	0	0	0
Nitzschia sp 3	0	0	0	26	0	0	0	0
Nitzschia sp 4	0	0	0	9	0	0	0	0
Nitzschia cf5	0	0	0	9	0	0	0	0
Oedogonium sp 1	0	9	60	9	0	0	0	0
Pinnularia sp 1	0	17	17	77	0	0	0	43
Pinnularia sp 2	0	0	9	9	0	9	0	0
Pinnularia sp 3	0	0	0	0	0	0	0	9
Pinnularia sp 4	0	0	0	0	0	0	0	9
Pinnularia sp 5	0	9	9	0	0	0	0	9
Pleurotaenium cf1	0	9	0	0	26	0	0	0
Rhoicosphenia sp 1	17	0	0	0	0	0	0	0
Stauroneis cf1	0	0	0	9	0	0	9	0
Surirella sp 1	0	0	0	0	43	26	0	43
Surirella sp 2	0	0	0	0	9	9	0	9
Tabellaria sp 1	0	0	43	0	0	0	0	0
Trachelomonas sp 1	0	0	9	17	0	0	0	0
Trachelomonas sp 2	0	0	0	0	0	9	0	0
Ulothrix cf1	0	0	9	0	0	0	0	0

control crop pests as well as the cattle feces. Subsequently, these nutrients are transported to the water allowing the appearance of aquatic plants and their proliferation, generating eutrophication problems which prevent the passage of sunlight to the water, increase the turbidity, and decrease the dissolved oxygen (Chará et al. 2010; Rodríguez et al. 2012). Because of the above, in the first season, the aquatic vegetation density was higher. The growth of the periphyton assemblage growth was stimulated, since it uses the aquatic vegetation as a substrate; hence, nutrients in the water are consumed, which are accumulated there during the dry phase.

Because of the periphyton abundance, the aquatic macroinvertebrate density was lower (Junk et al. 1989; Montoya and Aguirre 2009b; Montoya and Aguirre 2009a; Montoya et al. 2011; Piedade et al. 2010). Nevertheless, this dynamic changed during the second season, since the aquatic vegetation and the periphyton densities decreased, allowing a greater nutrient concentration and an increase in the aquatic macroinvertebrate density (Junk et al. 1989; Montoya and Aguirre 2009b; Montoya and Aguirre 2009a; Montoya et al. 2011; Piedade et al. 2010). In this order of ideas, during the rising waters, there was lower aquatic macroinvertebrate density per transect line, and differences were found in the group to which the pasture and the forest organisms belong. In the former, the organisms are part of the Coleoptera, while in the latter they belong to the molluscs. On the other hand, during the low water season, both in the forest and in the pasture, the found organisms belong to the coleoptera (Arnett and Thomas 1999; Domínguez and Fernández, 2009; Lancaster and Downes 2014; Linares et al. 2019; Machado 1989). As claimed by some authors, the structure and spatial distribution of the macroinvertebrates in the swamps are associated with water volume alteration, which in turn affects habitat availability and heterogeneity, physical characteristics, trophic state, sediment conditions, dissolved oxygen, pH, temperature, organic matter, among other factors (Rivera et al. 2013; Mosquera 2018). In general terms, this research found greater richness in the forest area, which, in turn, had better water quality in terms of its physicochemical characteristics.

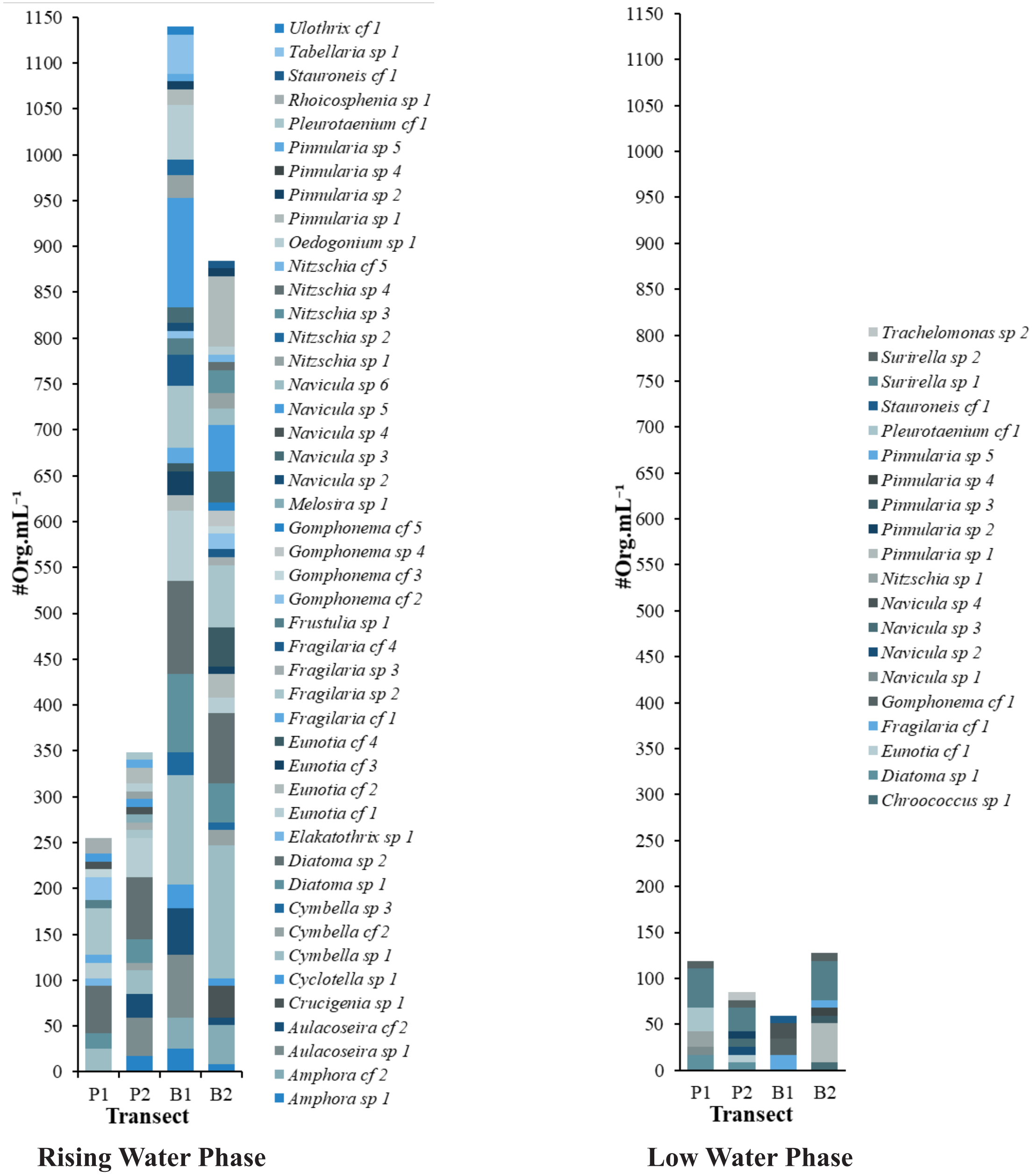

Figure 5. Periphyton density associated with aquatic plant roots in the San Francisco Marsh during rising wáter and low water phases.

According to results of the biodiversity indices: the Simpson (D) dominance, the Shannon-Weaver (H) diversity, and the Pielou (J) equity, when the water level dropped, the pasture showed lower dominance and greater diversity. At this time, the previously mentioned system is more heterogeneous than the forest, which is supported by the Pielou equity, since its values were greater in the pasture area (Aguirre and Caicedo 2015; Pla 2006). However, when the water level increased, the forest area showed lower dominance, and greater diversity, which means this is a system with greater entropy, in other words, it is more heterogeneous (Aguirre and Caicedo 2015; Moreno et al. 2011; Pla 2006). In this system, the native coverage allows for a greater richness of species belonging to the periphyton, and there is greater dissolved oxygen content given the water quality, as shown in Figure 5 and Table 1. It is worth noting that according to the classification made by Wilhm and Dorris (1968) for the Shannon-Weaver diversity, in the transition season, the pasture area had values between 1.00 and 3.00, which classifies it as: "moderately polluted water"; meanwhile the forest area showed results above 3.00, meaning: "good quality water". Nevertheless, in the second season, the four sampling points had values between 1.00 and 3.00, in other words: "moderately polluted waters" (Aguirre and Caicedo 2015; Staub et al. 2015). The results found in the variables H, D and J indicate that the natural conditions of the marsh allow the presence of more specialized organisms, which need more specific characteristics to make their existence and reproduction possible. The hydrological seasonality determines the water resource availability, the composition of the vegetation coverage, the nutrient and dissolved oxygen availability, and all these

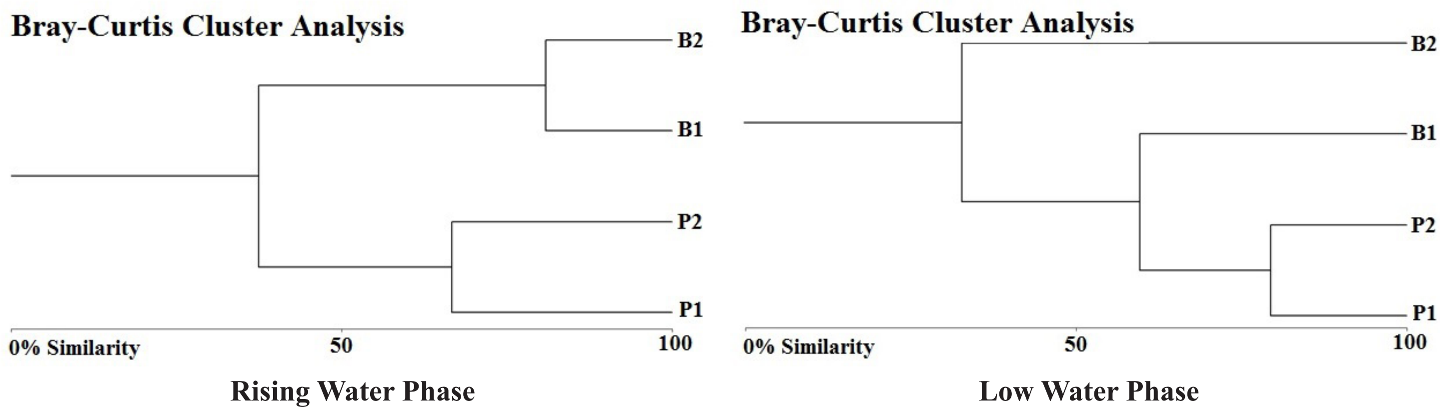

Figure 6. Bray-Curtis Cluster analysis of the sampling points in the San Francisco Marsh during the rising water phase (on left) and low water phase (on right).

characteristics determine which organisms of the periphyton and aquatic macroinvertebrates will be present in each season (Junk et al. 1989; Talley et al. 2010).

Figure 6 (left) shows the association between the sampling points of the rising water campaign, in which a similarity of 67% between P1 and P2, and 81% between B1 and B2 was found. Since the similarities are greater than 50%, both areas were related; nevertheless, the transects located in the forest had more resemblance than those in the pasture. In the same way, Figure 6 (right) shows the association between the sampling points of the low water campaign, in which a similarity of 79% between P1 and P2, and of 29% between B1 and B2 was found, which means that in the pasture area the similarity was above 50%, while in the forest it was lower, being the first zone the most related of them. In turn, the pasture and the forest were related in 60%. The decrease in diversity is due to the reduction in the biomass quantity when the water level drops, since the flood pulse determines the biota establishment in the ecosystem (Montoya and Aguirre 2010; Mitsch et al. 2015). However, when the native vegetation is replaced and the physicochemical and biological characteristics change, a greater aquatic vegetation density is generated, which acts as a biofilter that retains the sediments and contaminants from reaching the water body. Even so, when the aquatic vegetation grows in an uncontrolled manner, because of the nutrient abundance in the water, this vegetation prevents the sunlight from entering the water body, deteriorating its quality and decreasing its diversity (Quirós et al. 2006; Rejas et al. 2012). Less specialized organisms appear, which can live in both high and low waters, and whose most relevant impact is not allowing fish populations to exist. It cannot be forgotten that human communities are part of these ecosystems. Deforestation, mining, fishing, agriculture, and cattle raising are economic activities carried out in the region (Aguilera 2009; Marín et al. 2012; Puerta et al. 2016a; 2016b). To conserve ecosystems, people also must be considered. In summary, it is essential to find a balance between the conditions provided by the forest and the pasture. Finally, by declaring the Ayapel Swamp System as a Ramsar site, it becomes necessary to investigate, formulate, propose, and implement mechanisms to conserve and recover the natural characteristics (Ramsar 2007; 2014). Protecting the riverbanks is one of the strategies which can be carried out, in a way that improves the water quality of the marsh and ensures that the entire trophic chain functions properly, thus guaranteeing both native and endemic species can continue to coexist (González et al. 1995; Ramsar 2016).

CONCLUSION

This research was carried out in an area with low anthropic intervention. When the water level was high, the native vegetation coverage protected the marsh bank, the aquatic vegetation was heterogeneous and abundant during this flood pulse phase. Meanwhile, when the water level dropped and the floodplain was exposed, only grass was found in the terrestrial area, and the aquatic vegetation density decreased. The variations and differences given between the pasture and forest areas, are influenced not only by anthropic activities, which change the native coverage to pastures dedicated to activities such as cattle raising or agriculture, but also by the effect of the natural dynamics of the system. During the rising water season, the marsh shows differences in water quality, aquatic biota density, and richness between the forest and pasture areas; however, during the low water phase, the characteristics between the sampling sites tend to homogenize. In summary, native coverage favors the diversity of organisms belonging to the periphyton; this was reflected in the diversity indices. In the pasture area, moderately polluted waters were found, while in the forest, the water quality was good, resulting in a greater ecosystem diversity. Nonetheless, in low water conditions, all the indices acquire similar values, and the water quality deteriorates, classifying it as moderately polluted water. It is fundamental to conserve and recover the native vegetation because it allows for the presence of periphyton organisms and aquatic macroinvertebrates, thus enabling inorganic carbon fixation, nutrient recycling, and organic matter availability. These organisms are the base of the trophic chain, their presence contributes to the fish recovery, being these a fundamental economic resource in the region and the country.

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