



## Spatial and temporal variation of the macrophyte assemblage in Santo Tomás, a wetland in the Caribbean Colombian

Variação espacial e temporal da assembleia de macrófitas aquáticas em Santo Tomás, uma área alagável no Caribe Colombiano

María Isabel Pozo-García<sup>1</sup> , José Andrés Posada-García<sup>1</sup>  and Aracelly Caselles-Osorio<sup>1\*</sup> 

<sup>1</sup>Universidad del Atlántico, Carrera 30 No 8-49, Puerto Colombia, Colombia

\*e-mail: [aracellycaselles@mail.uniatlantico.edu.co](mailto:aracellycaselles@mail.uniatlantico.edu.co)

**Cite as:** Pozo-García, M.I., Posada-García, J.A. and Caselles-Osorio, A. Spatial and temporal variation of the macrophyte assemblage in Santo Tomás, a wetland in the Caribbean Colombian. *Acta Limnologica Brasiliensia*, 2022, vol. 34, e22.

**Abstract: Aim:** The associated flood events to floodplain of many rivers in the world affect the composition and structure of aquatic biota due the water levels variation can ensure ecological integrity of associated wetlands. This study describes the spatial and temporal variation in the macrophyte assemblage in the Santo Tomás wetland during seasonally flood-pulsed of the Magdalena River (North of Colombia). **Methods:** For eight months, between 2017 and 2018 samplings were carried out in three stations for composition and abundance of aquatic macrophytes. Spatio-temporal pattern of richness was estimated with Chao methodology and vegetation cover was calculated using Kruskal-Wallis and U Mann-Whitney tests. A range abundance curve was used for species dominance between samplings and stations. A non-metric multidimensional scaling (nMDS) was used to analyze the Spatio-temporal distribution, Canonical Correspondence Analysis (ACC) was performed to relate the physicochemical variables to the species composition. **Results:** A total of 24 species of aquatic plants distributed in 23 genera and 15 families were registered in the transects. The most abundant species (% of vegetation cover) were *Ipomoea aquatica* (19%), followed by *Ludwigia helminthorrhiza* (14%) and *Eichhornia azurea* (13%). The most frequent life form was free-floating, followed by the emergent one. The Spatio-temporal changes and the highest values of richness and vegetation cover in the Santo Tomás wetlands occurred during the filling and high waters period. *L. helminthorrhiza*, *E. azurea*, *Pistia stratiotes*, *Neptunia oleracea*, *I. aquatica*, *Salvinia auriculata*, and *Hymenachne amplexicaulis* were the most dominant species. The quality water of Santo Tomás Wetlands showed spatial and temporal variations during flooding pulse and some physicochemical variables such as organic matter (COD, BOD<sub>5</sub>), pH, depth, ammonia, and fecal coliforms were related to macrophyte community composition **Conclusions:** Spatial and temporal changes of aquatic plants in Santo Tomás wetlands were related to the flooding pulse of Magdalena River.

**Keywords:** physicochemical conditions; diversity; seasonal pulsing.

**Resumo: Objetivo:** Os eventos de inundação associados às planícies de inundação de muitos rios do mundo afetam a composição e estrutura da biota aquática, pois a variação do nível de água pode garantir a integridade ecológica das áreas úmidas associadas. O objetivo do presente é descrever a variação espacial e temporal na composição da assembleia de macrófitas aquáticas em uma área alagável em Santo Tomás durante um período de inundação no rio Magdalena (norte da Colômbia). **Métodos:** Nós avaliamos a composição e abundância da comunidade de macrófitas aquáticas em três estações de coleta no rio Magdalena mensalmente durante 8 meses entre 2017 e 2018. Nós estimamos a variação espaço-temporal da comunidade usando o método Chao e a cobertura vegetal usando os



testes de Kruskal-Wallis e U Mann-Whitney. Uma curva de abundância de classificação foi usada para a dominância das espécies entre os meses de amostragem e as estações. Uma escala não métrica multidimensional (nMDS) foi utilizada para analisar a distribuição espacial e temporal e a análise de correspondência canônica (CCA) foi realizada para estudar a relação entre a composição das espécies de macrófitas e as variáveis físico-químicas da água. **Resultados:** Nos transectos foi registrado um total de 24 espécies de plantas aquáticas distribuídas em 23 gêneros e 15 famílias. A espécie mais abundante (% de cobertura vegetal) foi *Ipomoea aquatica* (19%), seguida por *Ludwigia helminthorrhiza* (14%) e *Eichhornia azurea* (13%). Espécies flutuantes e emergentes foram observadas com mais frequência. As mudanças espaço-temporais e os maiores valores de riqueza e cobertura de macrófitas aquáticas nas zonas úmidas de Santo Tomás ocorreram durante a estação das chuvas. As espécies mais dominantes foram *L. helminthorrhiza*, *E. azurea*, *Pistia stratiotes*, *Neptunia oleracea*, *I. aquatica*, *Salvinia auriculata* e *Hymenachne amplexicaulis*. A qualidade da água apresentou variações espaciais e temporais durante o pulso de inundação, e algumas variáveis como matéria orgânica (DOQ, DBO<sub>5</sub>), pH, profundidade, amônia e coliformes fecais foram relacionados à composição da comunidade de macrófitas. **Conclusões:** Em suma nós concluímos que o pulso de inundação do rio Magdalena influenciou a composição das plantas aquáticas nas zonas úmidas de Santo Tomás.

**Palavras-chave:** condições físico-químicas; diversidade; pulsação sazonal.

## 1. Introduction

In tropical areas, the floodplains support a great diversity of aquatic organisms adapted to flooding and drought dynamics (Murray-Hudson et al., 2014). These areas are particularly vulnerable to hydrological changes and vary with climate, water quality, vegetation, and other factors including human disturbance (Rameshkumar et al., 2019). In Colombia, there is 30.781.149 ha of wetlands that are influenced by the water flow cycle and flood pulse of rivers. The low zone of the Magdalena River, in northern Colombia, includes swamps, channels, and lagoons that are influenced by river dynamics. Buffer zones, flow, and floods are linked to high productivity and diversity (Echevarría & Machado-Allison, 2014). These environments provide areas for reproduction, feeding, and growth of fish, bird invertebrates, and aquatic plants (Ferreira de Deus et al., 2020). The Santo Tomás Wetlands (STW) is in the floodplain of the Magdalena River and supports local commercial fishing. Water in STW is used for agricultural irrigation, cattle grazing, and treated domestic wastewater discharges the flood plains. Displaced migrants inhabit the flood plains without sewage treatment (ASOCAR & Universidad del Magdalena, 2011). Despite these problems, diversity of fish, birds, invertebrates, and aquatic macrophytes has been reported on the eastern slope of the Magdalena River in the Atlantic Department (Escolar, 2007); ASOCAR & Universidad del Magdalena, 2011). The aquatic macrophytes have an important role in this ecosystem due to their nutrient absorption, and biomass production and can be phytoremediation by accumulating heavy metals from contaminated water (Jiménez-Segura et al., 2010; Echevarría & Machado-Allison, 2014).

The composition of aquatic macrophytes has been widely studied around the world (Mormul et al., 2013; Ramos-Montaño et al., 2013) and in Colombia, some studies have been carried out on the subject (Cataño-Vergara et al., 2008; Rangel-Ch, 2010; Cortés-Castillo & Rangel-Ch, 2013; Madriñán et al., 2017). Several studies have shown that differences in plant composition are related to the river water regime (Murray-Hudson et al., 2014; Reid & Quinn, 2004). Aquatic macrophytes have reproductive strategies (clonal and sexual) and morphological characteristics that permit them to lead with water level variation (Delatorre et al., 2019; Eckert et al., 2016; Rameshkumar et al., 2019).

The environmental conditions in aquatic ecosystems regulate the life forms of macrophytes since emergent, rooted submerged, and free-floating use light, nutrients, and other resources in a specific way and also differed in their response to environmental changes (Schneider et al., 2018). According to Regmi et al. (2021) in sub-tropical floodplain wetlands of Nepal, excessive growth of floating macrophytes in particular invasive species such as *Eichhornia crassipes* and *Typha angustifolia* tend to increase biomass during high water levels periods, while with water level drawdown, species emergents like *Alternanthera* spp. and *Cyperus* spp increase and establishing. Additionally, several authors have been concluded that submerged aquatic vegetation (Example: *Ceratophyllum* sp., *Egeria* spp., *Lemna* spp, *Marsilea* spp) is an environment indicator it exists where there is a better water quality condition (Rameshkumar et al., 2019)

Tropical floodplains can show a progression from grasslands to emergent aquatic plants

depending on the depth and frequency of flooding (Murray-Hudson et al., 2014). Thus, floods can act as a homogenizing factor that promotes changes in aquatic macrophyte species, whether they increase or decrease during flood cycles (Catian et al., 2018; Delatorre et al., 2019). Consequently, this study aimed to examine macrophytes composition and their Spatial-temporal dynamic during different climatic periods in relationship with the water physicochemical variables in Santo Tomás wetland on flood plain Magdalena River (Colombian Caribbean).

## 2. Methods

### 2.1. Study area

Santo Tomás wetland (STW) is a lentic ecosystem located in the floodplain area of the Magdalena River (Arias, 1985). STW is in the Atlantic department between 10° 45' N and 74° 44' O in Santo Tomas municipality in the Caribbean Colombian. It is connected directly to the Magdalena River by a 2.12 km long canal entitled "El Canal" (The Channel) (Figure 1).

The total area of STW is 650 ha at 8 meters above sea level. Temperature ranges from 26 to 30°C with a relative humidity between 84 and 95% and a total annual precipitation of 1200 mm (Escolar, 2007). There are two dominant tropical seasons in the region. In the dry season (December-April), the surface water is significantly reduced (approximately 67 ha), with maximum depths of 1 m, while in the rainy season (May-October), the surface water can cover the total wetland

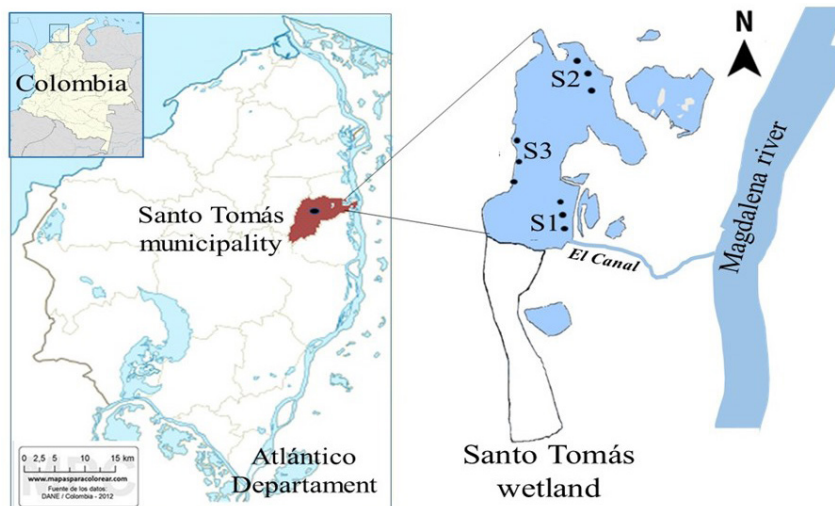
area, 650 ha surface and reach 3 m in depth. However, El Niño Southern Oscillation (ENSO) can modify drastically the season in the Caribbean region (USAID, 2016). In fact, in 2010 the STW suffered severe flooding (Alvarado, 2016), and in 2016 caused a drought reduced surface water area by 90% (direct observations). Additionally, STW is affected by discharges of treated wastewater from lagoon stabilization ponds.

### 2.2. Field sampling design

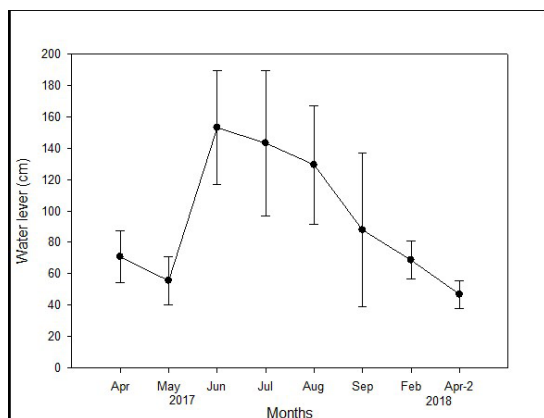
Field samplings were carried out, one by month, for eight months in the STW during the rainy and dry seasons. We sampled abiotic and biotic data from April to September 2017 (rainy season) and from February to April 2018 (dry season). Consequently, two hydrology periods were studied: rising water level (high water level) and decreasing water level (low water level) (Figure 2).

We established three permanent stations concerning impact degree: S1, The Canal's direct communication with the Magdalena River, S2 the area near the domestic wastewater discharge, and S3, Santo Tomás municipality population.

Three permanent stations registered with a GPS (Garmin Etrex 20) were established for monitoring. Site S1 was El Canal which communicates with the Magdalena River, site S2 was located in the area near the discharge of domestic wastewater of Santo Tomas municipality of Santo Tomás, and site S3 was located near the urban area. At each site, every 20 m, three transects of 10 m<sup>2</sup> each were established. These were located in parallel in the areas most exposed to aquatic vegetation.



**Figure 1.** Santo Tomás municipality in Colombia and Santo Tomás wetland showing the sample sites. The black points indicate the transects number by the station.



**Figure 2.** The average water level during 2017 and 2018 in Magdalena River (Colombia). Taken of IDEAM (2022).

### 2.3. Macrophyte community

We sampled all macrophytes we found inside the quadrats. Aquatic macrophyte taxa were identified according to Velásquez (1994); Posada & López, (2011), Cirujano et al. (2014) and Madriñán et al. (2017). When necessary, plants were compared in the herbarium reference: Armando Dugand Gnecco Herbarium from Universidad del Atlántico to confirm identification. We classified the macrophyte taxa into three life forms, based on Gyosheva et al. (2020) classification: free-floating (plants on the water surface), rooted-floating (rooted plants in sediment with floating leaves on the water surface), and emergent plants (the aboveground part of the plant emerges above the waterline).

The vegetation cover (%) was estimated in the climatic year according to the Magdalena River flood pulse, following the methodology by Ramos-Montaña et al. (2013). Through a small boat by direct observation and using a 1m<sup>2</sup> quadrant which one was moving to cover the total transect area (10m<sup>2</sup>). Three replicates at an interval of 20 m<sup>2</sup> in each transect by sampling site were reached. Once the data was obtained, was calculated as a sum of relative frequency and relative abundance of macrophytes and 100% of each transect was weighted. Statistical and diversity analyses by site and period were performed with these data.

To facilitate the estimation of the vegetation cover in the transects, a general recognition of the aquatic plant species of the STW was carried out. For this purpose, a reference collection was made and deposited in the Armando Dugand Gnecco Herbarium of the Universidad del Atlántico. For their identification, they were compared with herbarium collections and with the help of specialized

literature (Velásquez, 1994; Posada & López, 2011, Cirujano et al., 2014 and Madriñán et al., 2017). According to Gyosheva et al. (2020), they were classified into three life forms: floaters (plants on the water surface), rooted floaters (plants rooted in sediment with leaves floating on the water surface), and emergent plants (the aerial part of the plant emerges above the waterline).

### 2.4. Environmental data

Water physicochemical parameters such as pH, ORP (EH), and dissolved oxygen (DO) were measured in situ using a multiparameter probe (Hanna HI 9829), both at the beginning and at the end of each transect to calculate the average of each parameter. To minimize fluctuation in water quality parameters due to temperature, measurements were carried out between 9-11 am. Transparency was measured with a Secchi disk. Water samples were collected, stored at 4 °C, and transported to Laboratories of Universidad del Atlántico for organic matter, nutrients, and coliforms analysis following APHA-AWWA-WEF (APHA, 2012) methods.

### 2.5. Data analysis

Spatial and temporal species composition was evaluated with Chao et al. (2014) methodology. Hill numbers were used to measure species effectiveness using the EstimateS 9.2 program (Colwell, 2009). True Diversity, species richness (<sup>0</sup>D), Shannon Index exponential diversity (<sup>1</sup>D), and Simpson Index inverse (<sup>2</sup>D) were compared using the superposition of confidence intervals at 95% in R program version 3.1. Spatial and temporal variations were evaluated with the Kruskal-Wallis test, supported by the U Mann-Whitney paired comparisons test. To compare the dominance and uniformity of species between samplings and stations, range-abundance curves were used (Cultid-Medina et al., 2012).

A community Principal Component Analysis (PCA) was used to establish the dominant macrophyte species. Last, Canonical Correspondence Analysis (CCA) was used to investigate the relationship of abundant species spatially and temporally. Non-metric multidimensional scaling (nMDS) was performed to investigate the variations between periods and sampling months (Arellano et al., 2013). ANOSIM similarity analysis was used to detect differences in community composition. For the multivariate analysis, the dominant species were first determined using the Olmstead-Tukey

test (Sokal & Rohlf, 1995), considering the frequency of occurrence and abundance of each taxon. In addition, before the construction of the matrices for the analyses, the physicochemical variables whose values between the samplings and study sites were below the detection limit of the respective methods and those that were collinear or correlated with each other were excluded, performing a collinearity and Spearman's correlation analysis. Canonical Correspondence Analysis (CCA) was then selected to establish the spatial and temporal relationship between the dominant species with the set of physicochemical variables. These analyzes were realized using the Past 2.17 program (Hammer et al., 2001).

### 3. Results

#### 3.1. Water quality of the Santo Tomás Wetland (STW)

The variation ranges of the physicochemical parameters between the hydrological periods and between the sampling stations indicated slight transitions in most of the variables (Table 1). Electrical conductivity and COD values increased during low water levels while nitrates and total coliforms decreased under the same water level conditions. The concentrations of organic matter (COD, BOD<sub>5</sub>) and nutrients (Ammonium, Nitrate, and Orthophosphate) were relatively similar in rising and falling waters, as well as in each sampling station. High concentrations of nitrate were recorded concerning ammonium,

probably due to the effect of runoff from nearby agricultural areas. The transparency of the water was around 30 cm at low and high water levels. The pH was kept in neutral conditions and dissolved oxygen presented relatively low values throughout the study.

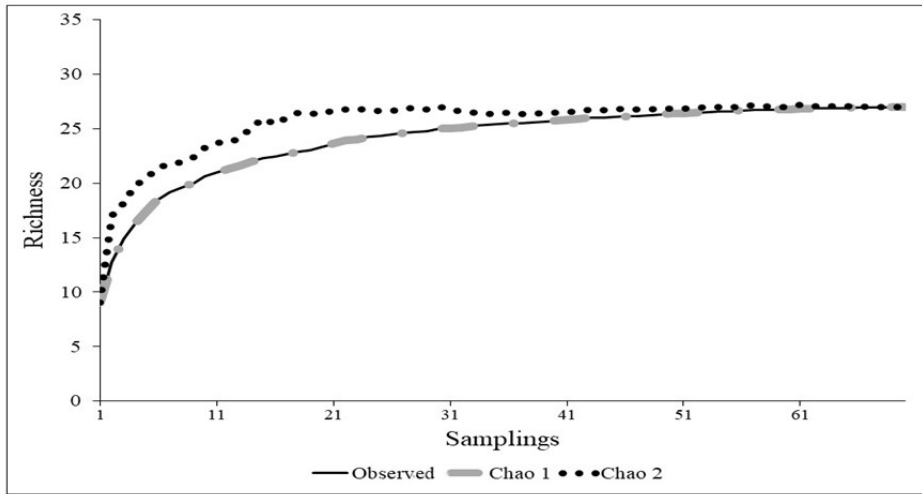
#### 3.2. Aquatic plant: composition and abundance

A total of 41 aquatic plant species were registered and distributed in 36 genera and 22 families (Figure 3 and Table 2). Transects registered 24 species being *Ipomoea aquatica* was the most abundant of the species with 19% of cover, followed by *Ludwigia helminthorrhiza* (14%) and *Eichhornia azurea* (14%).

Floating, followed by rooted floating were frequent life forms (Table 2). During April and May 2017 (water rise) *Eichhornia azurea* was the predominant species with more than 22% vegetation cover, while between February and April 2018 (waterfall) *Ipomoea aquatica* exceeded 37% vegetation cover (Table 2). Regarding sampling sites, *I. aquatica* presented the highest percentage of vegetation cover in S1 (38.20%), followed by *Eichhornia. azurea* in S2 (20.32%) and *Ludwigia helminthorrhiza* in S3 (19.92%) (Table 3). *Limnobium laevigatum*, *Najas arguta*, *Marsilea polycarpa*, *Enydra fluctuans*, *Phyllanthus fluitans*, *Utricularia foliosa*, *Spirodela polyrhiza*, *Thalia geniculata*, and *Wolffiella* sp., were recorded in at least two stations. *Nymphaea ampla* and *Utricularia gibba* were found only in S2 and *Wolffia* sp. only on S1.

**Table 1.** Variation ranges of physicochemical characteristics in high- and low-level water scenery and average values and standard deviation (in brackets) of the physicochemical characteristics of water in the sampling stations of the Santo Tomás wetlands.

Parameter	Rising and high water level	Falling and low water level	Sampling stations		
			S1	S2	S3
			El Canal	Wastewater discharge	Urban area
pH	6.8-7.2	6.7-7.3	7.0 (±0.1)	7.0 (±0.2)	7.0 (±0.4)
Electric Conductivity, $\mu\text{S}\cdot\text{cm}^{-1}$	148.0-566.0	240.0-934.0	443.1 (±351.0)	415.2 (±244.6)	428.1 (±2.7)
Dissolved Oxygen, $\text{mg}\cdot\text{L}^{-1}$	0.8-4.1	0.9-6.4	2.1 (±1.7)	3.3 (±2.5)	3.8 (±2.7)
Redox Potential, mV	-1.8-186.0	32.0-180.0	92.0 (±119.0)	25.0 (±208.0)	92.0 (±122.0)
Temperature, °C	28.9-31.8	28.1-30.6	29.8 (±1.7)	25.0 (±208.0)	30.9 (±1.5)
COD, $\text{mg}\cdot\text{L}^{-1}$	7.0-44.0	25.7-47.9	25.4 (±21.1)	30.3 (±17.3)	36.4 (±20.4)
BOD <sub>5</sub> , $\text{mg}\cdot\text{L}^{-1}$	9.4-27.1	8.3-19.5	17.9 (±9.4)	13.5 (±8.8)	14.5 (±11.3)
Ammonium, $\text{mg}\cdot\text{L}^{-1}$	0.2-1.0	0.1-0.7	0.4 (±0.4)	0.2 (±0.3)	0.4 (±0.6)
Nitrate, $\text{mg}\cdot\text{L}^{-1}$	1.1-10.0	0.6-2.5	4.3 (±5.2)	3.2 (±3.2)	5.4 (±6.1)
Orthophosphate, $\text{mg}\cdot\text{L}^{-1}$	0.5-3.2	0.4-0.6	1.4 (±1.8)	0.9 (±0.8)	0.6 (±0.5)
Total coliforms, CFU.100 mL <sup>-1</sup>	33.9-250.0	7.5-23.3	64.6 (±94.2)	70.5 (±93.2)	63.3 (±77.2)
Fecal coliforms, CFU.100 mL <sup>-1</sup>	0.0-0.9	0.0-0.8	0.8 (±1.2)	0.3 (±0.3)	0.5 (±0.8)
Transparency, cm	31.8-28.9	28.1-30.6	31.3 (±14.4)	70.2 (±51.2)	47.6 (±24.2)
Deep, cm	51.2-143.3	46.9-117.7	90.4 (±36.8)	110.6 (±57.5)	61.8 (±31.0)



**Figure 3.** Accumulation of aquatic plant curve using Chao 1 and Chao 2 methodology in Santo Tomás wetlands during the study.

**Table 2.** Aquatic macrophytes species registered in the Santo Tomás Wetlands, their life forms, and total vegetation cover during the study period.

Species	Total vegetation cover (%)
<b>Free-floating</b>	
<i>Ludwigia helminthorrhiza</i> (Mart.) H. Hara	14.32
<i>Pistia stratiotes</i> L.	10.75
<i>Neptunia oleracea</i> Lour.	10.52
<i>Eichhornia crassipes</i> (Mart.) Solms	6.64
<i>Salvinia auriculata</i> Aubl.	6.33
<i>Lemna aequinoctialis</i> Welw.	1.52
<i>Limnobium laevigatum</i> (Humb. & Bonpl. ex Willd.) Heine	1.48
<i>Wolffiella</i> sp.	1.22
<i>Azolla filiculoides</i> Lam.	0.60
<i>Wolffia</i> sp.	0.34
<i>Ceratopteris pteridoides</i> (Hook.) Hieron	0.30
<i>Spirodela polyrhiza</i> (L.) Schleid.	0.22
<i>Phyllanthus fluitans</i> Benth. ex Müll. Arg.	0.10
<b>Rooted- floating</b>	
<i>Ipomoea aquatica</i> Forssk.	18.75
<i>Eichhornia azurea</i> (Sw.) Kunth.	13.58
<i>Marsilea polycarpa</i> Hook. & Grev.	2.92
<i>Aeschynomene cf. indica</i> L.	0.23
<i>Nymphaea ampla</i> (Salisb.) D.C.	0.06
<b>Emergent</b>	
<i>Hymenachne amplexicaulis</i> (Rudge) Ness	2.99
<i>Luziola subintegra</i> Swallen	2.46
<i>Oxycaryum cubense</i> (Poepp. & Kunth.) Palla	1.68
<i>Enydra fluctuans</i> D.C.	0.06
<i>Mimosa pigra</i> L.	0.05
<i>Thalia geniculata</i> L.	0.01

**Table 3.** Richness and abundance variation in coverage percentage of the aquatic plants by stations (S) sampling in Santo Tomás wetlands.

Species	Stations sampling		
	S1	S2	S3
<i>Aeschynomene cf. indica</i>	0.05	0.32	0.35
<i>Azolla filiculoides</i>	0.64	0.76	0.39
<i>Ceratopteris pteridoides</i>	0.33	0.01	0.56
<i>Eichhornia azurea</i>	10.47	20.32	10.65
<i>Eichhornia crassipes</i>	3.33	5.17	12.13
<i>Enydra fluctuans</i>	0.13	0.00	0.03
<i>Hymenachne amplexicaulis</i>	5.55	1.89	0.98
<i>Ipomoea aquatica</i>	38.20	12.63	1.19
<i>Lemna aequinoctialis</i>	0.28	1.34	3.22
<i>Limnobium laevigatum</i>	0.00	3.33	1.43
<i>Ludwigia helminthorrhiza</i>	8.88	15.33	19.92
<i>Luziola subintegra</i>	4.00	1.89	1.15
<i>Marsilea polycarpa</i>	7.68	0.04	0.00
<i>Mimosa pigra</i>	0.01	0.04	0.10
<i>Najas arguta</i>	0.00	0.03	8.91
<i>Neptunia oleracea</i>	5.94	9.83	16.78
<i>Nymphaea ampla</i>	0.00	0.21	0.00
<i>Oxycaryum cubense</i>	2.25	0.18	2.48
<i>Phyllanthus fluitans</i>	0.26	0.00	0.01
<i>Pistia stratiotes</i>	1.93	18.14	14.10
<i>Salvinia auriculata</i>	9.82	5.41	3.00
<i>Spirodela polyrhiza</i>	0.01	0.71	0.00
<i>Thalia geniculata</i>	0.00	0.02	0.01
<i>Utricularia foliosa</i>	0.13	0.01	0.00
<i>Utricularia gibba</i>	0.10	0.00	0.00
<i>Wolffia</i> sp.	0.00	1.10	0.00
<i>Wolffiella</i> sp.	0.00	1.29	2.63

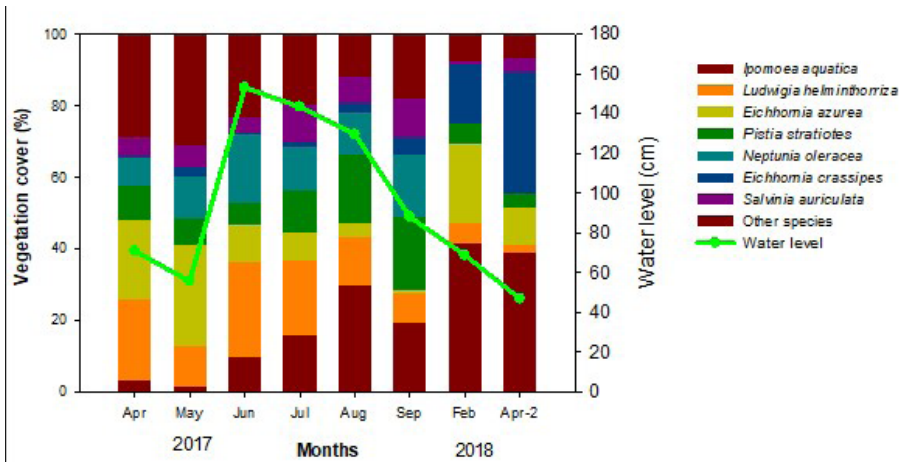


Figure 4. Vegetation cover during sampling months in the Santo Tomás wetland and water level variation.

Figure 4 shows the highest vegetation cover by month and their relation to the water level. In 2017 when the level of river water was around 60 cm, *Eichhornia azurea*, and *Ludwigia helminthoriza* were dominants, while in 2018, and low-level water, *Ipomoea aquatica* was dominant. High-level water favors the aquatic macrophytes' diversity.

*Ipomoea aquatica*, *Ludwigia helminthoriza*, and *Eichhornia azurea* showed the highest vegetation cover in both stations 1 and 2 (Figure 5). These species were also present at station 3 but to a lesser extent.

3.3. Aquatic macrophyte richness: spatial and temporal variation

The greatest species richness occurred in April-May 2017 (raising water), while the lowest values occurred in February-April 2018 (falling water). During the high-water months (Apr-May-Jul/17), species richness ( $^0D$ ), common ( $^1D$ ), and abundant species ( $^2D$ ) were high with values of 24, 10, and 8 respectively, compared to the recorded in the low water months (Feb-Apr/18) with values of 15, 5 and 4 respectively (Figure 6). The S2 and S3 stations were statically different from S1 and showed values of 24, 10, and 8 richness, common and abundant species, respectively. S1 presented lower values of 21, 8, and 5 for species richness, common species, and abundant species, respectively. Similarly, aquatic plant coverage percentage (Figure 4) was higher in April and May 2017 (13 and 14%, respectively) and significantly different ( $P < 0.05$ ), in February and April 2018 (11 and 9%, respectively).

Spatially, vegetation cover was higher and significantly different in S1 (38%) compared to S2, where the lowest value was recorded (31%).

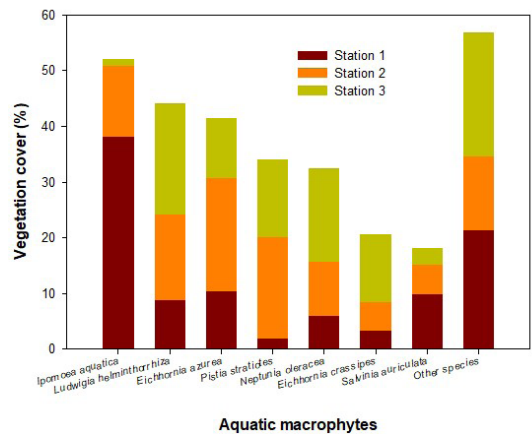
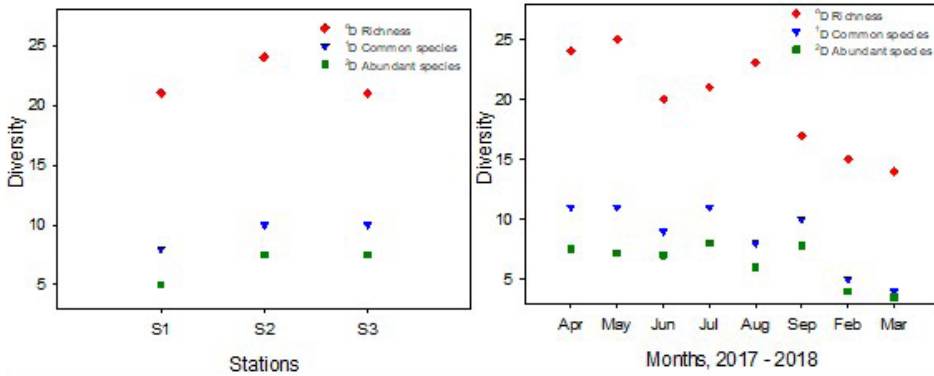


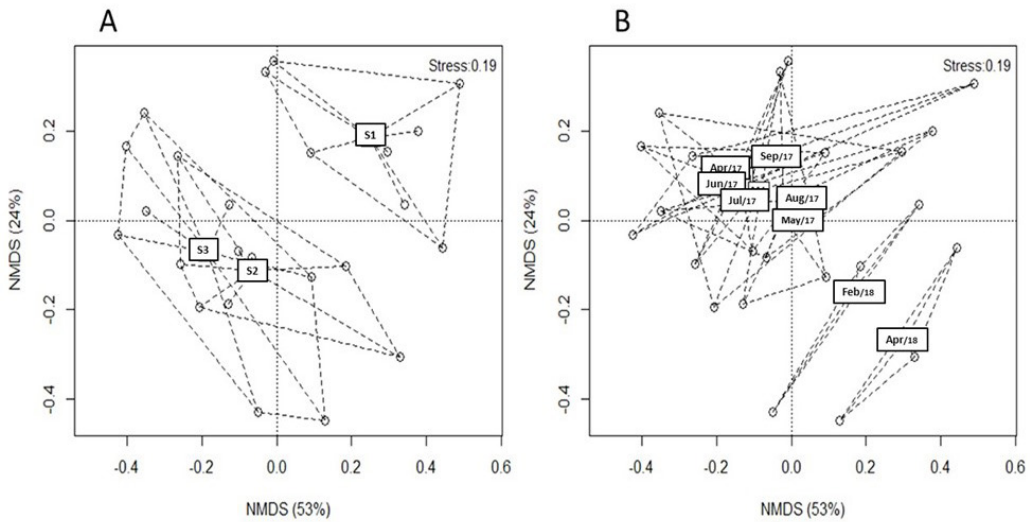
Figure 5. Vegetation cover variation of principal aquatic macrophytes by station sampling in Santo Tomás wetlands during the study period.

*I. aquatica*, *E. azurea*, and *L. helminthorhiza*, were more abundant in S1, S2, and S3 (Figure 5). *P. stratiotes*, *N. oleracea*, *E. crassipes*, *S. auricular* *I. aquatica*, *L. helminthorhiza*, and *E. azurea* were observed in all months of sampling. During April, May, and Jun 2017 during the high water period, *E. azurea*, *L. helminthorhiza*, and *N. oleracea* were the dominant species. In August and September 2017, when the water level was at their highest *P. stratiotes* and *S. auriculata* were abundant, and February-March 2018 when l water levels were at their lowest, *I. aquatica* and *E. crassipes*, were mainly dominants.

According to nMDS analysis, the species composition during the sampling period did not vary considerably and there were no statistical differences ( $P=0.181$ ) between plant groups shown in the level water variations periods (Figure 7B). nMDS analysis shows a weak relationship between



**Figure 6.** Diversity (richness <sup>0</sup>D, common <sup>1</sup>D, and abundant species <sup>2</sup>D) analysis for station and month sampling in Santo Tomás wetlands.



**Figure 7.** Non-metric multidimensional scaling (nMDS) analysis of species composition in Santo Tomás wetland by stations (A) and months sampling (B).

species composition and sampling periods, contrary to ANOSIM similarity results (Table 4) showed that spatially a plant group of S1 station is separated from S2 and S3 stations with statistical differences ( $P < 0.001$ ).

### 3.4. Environmental variables and aquatic macrophyte composition

Differences between water variables, hydrological periods, station sampling, and its relation with macrophytes composition were registered in Canonical Correspondence Analysis (CCA). CCA results show 62.31% of the variation of the data (Figure 8) in the first two axes with statistical significance ( $p < 0.02$ ). *I. aquatica* and *L. subintegra* showed the highest vegetation cover in the S1 station (36.38% of the variance). Particularly, *I.*

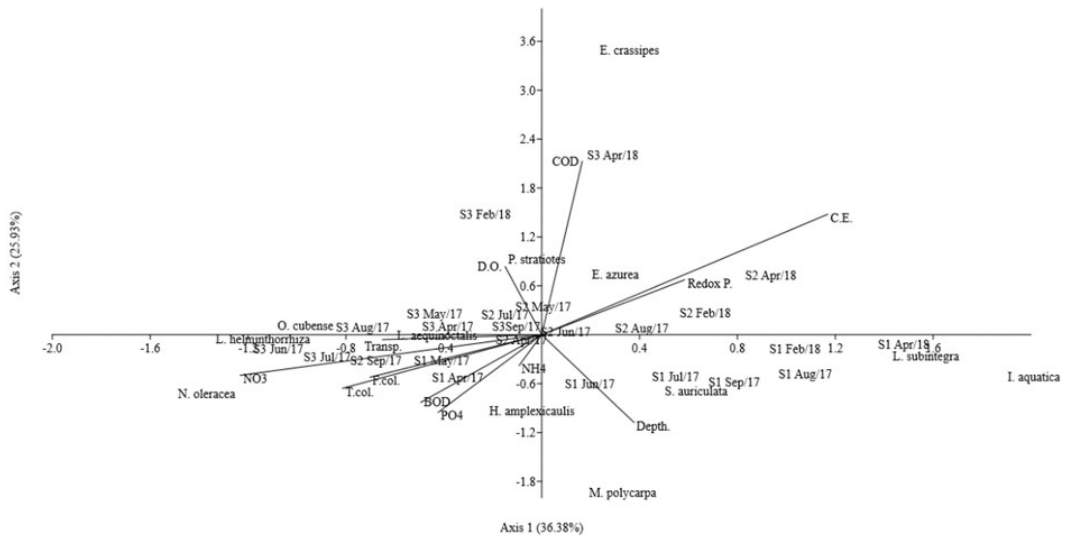
**Table 4.** Station sampling comparisons with ANOSIM similarity test.

Comparisons	R	P
S1 and S2	0.496	0.003
S1 and S3	0.594	0.001
S2 and S3	0.152	0.060

The variations in plant composition by stations could indicate that Station 1 is statically different from the 2 and 3 stations. R = Coefficient of determination; P = Probability.

*aquatica* showed a significant increase in vegetation cover during the dry period (Aug/17 and Apr/18), and then appear spatial-temporally differentiated. *N. oleracea*, *O. cubense*, and *L. helminthorrhiza* were associated with the negative quadrant of the first axis. This was related to nitrate concentrations,





**Figure 8.** Relations between physicochemical variables (COD, DBO, DO, NH<sub>4</sub>, NO<sub>3</sub>, PO<sub>4</sub>, Depth, F col, T col, Transp) of water and macrophyte composition in Santo Tomás wetlands. Canonical Correspondence Analysis diagram.

coliform bacteria, and water transparency. This association was evident in the first three months of sampling (Aug.-Sep.-Oct. 2017), corresponding to rising waters (Figure 2). A clear separation of the samplings carried out in S1 (negative quadrant of the second axis) is evidenced, mainly in the function of depth, (BOD, orthophosphates (PO<sub>4</sub><sup>-3</sup>), and ammonium (NH<sub>4</sub>)). *M. polycarpa*, *H. amplexicaulis*, and *S. auriculata* species showed high vegetation cover percentages in all sampling periods. *M. polycarpa* had a distribution restricted to the S1 station in samples Jun, Aug, Feb, and Apr.

## 4. Discussion

### 4.1. Composition and abundance of aquatic macrophytes

The composition of aquatic macrophytes in Santo Tomás Wetland (STW) was related to the water level in the floodplain of the Magdalena River. During the falling and high-water period, the highest values of richness and total vegetation cover occurred. *L. helminthorrhiza*, *E. azurea*, *P. stratiotes*, *N. oleracea*, *I. aquatica*, *S. auriculata*, and *H. amplexicaulis* were the most dominant species. The highest richness and diversity were recorded in the first two months of sampling when rising water occurred. Similar behavior was registered by (Agostinho et al., 2004) in flood pulse Paraná river (Brazil). During rising water levels, depth influences richness since macrophytes is commonly distributed along with the water mirror and the littoral zones of lowland wetlands (Santos & Thomaz, 2007).

The increase in the water level creates biotic gradients (Vieira et al., 2019). Richness can be explained from the littoral zone until the habitat is off with greater depth.

More than 170 aquatic plant species have been reported in 34 shallow freshwater wetlands in the Colombian Caribbean region (Cortés-Castillo, 2017). Several studies affirm that the cosmopolitan nature of many species of aquatic plants confers a similar composition (Álvarez-León et al., 2004; Rangel-Ch, 2010; Cataño-Vergara et al., 2008). However, some species in this study were not included in those studies, indicating that diverse factors can affect species composition (Rial, 2006). *E. azurea* and *E. crassipes* species, typical in tropical wetlands, spread on the surface of the water and persist throughout the flood cycle (Cortés-Castillo & Rangel-Ch, 2013). Regularly, dominant at the end of the rainy period and the beginning of the dry period (Cortés-Castillo & Rangel-Ch, 2013). *E. azurea* formed scattered abundant patches in the water body and on the banks of the STW (S2 and S3 stations). This behavior has also been observed in *L. helminthorrhiza*, especially on the banks and in shallow water sectors. Both *E. azurea* and *L. helminthoriza* species present rapid growth, high reproductive potential, latency, and adaptability that facilitate high and rapid proliferation (Cortés-Castillo & Rangel-Ch, 2013). During the dry period, *I. aquatica* presented greater vegetation cover, mainly on the shores of the STW. In America, this species is considered an invasive aquatic weed with high reproductive efficiencies (more than

200 seeds per plant) and a high colonizer potential of calm and shallow water (Staples, 1996).

Shallower areas are dominated by emerging species rooted while deeper zone, favor the development of floating, epiphytic, or submerged aquatic plants. According to (Santos & Thomaz, 2007), the depth dynamic in flood pulse causes the coexistence of various forms of life due to replacing species and consequently, increasing richness. Similarly, the light incidence in the water column also influences the structure of macrophyte communities, especially for submerged species. Low radiation can seed germination restricted, and avoid the establishment of propagules (Kettenring et al., 2006; Roldán & Ramírez, 2008). The highest richness values recorded at the S2 station, likely coincided, with the highest depth and transparency recorded at that station.

Wallsten & Forsgren (1989) and Gordon (1998) state that in shallow tropical wetlands the abundance increases during the flood period but richness has a relative decrease. In STW, this situation was presented during April-Jun/2017, in rising and high water, when the highest abundance and decreased richness were recorded. Rial (2006) reported that the diversity and abundance of aquatic plants change with water level variation. Periodic fluctuations in the water level allow the establishment of plant communities with changes in the dominance of certain species (Delatorre et al., 2019). During the dry period, when the water level decreases, some species establish taking advantage of the supply of nutrients from the decomposition of other plants (Pérez-Vásquez et al., 2015). Functional diversity also varies according to the flood cycle, due to macrophytes with life forms predominant defining the community characteristics (Catian et al., 2018).

Therefore, exclusively aquatic plants such as *E. azurea*, *L. helminthorrhiza*, *N. oleracea*, *P. stratiotes*, and *S. auriculata*, dominated in rising period water (April-May-Jun/17). Emergent, amphibians or rooted plants such as *I. aquatica*, *E. crassipes*, and *H. amplexicaulis*, were more abundant in the low water level (February - April/18). *L. helminthorrhiza*, *N. oleracea*, *P. stratiotes*, and *S. auriculata*, (free-floating) present stems or leaves with aerenchyma and rhizomes for propagation. At a high water level, these forms of life have a competitive advantage over other species and are environmentally selected (Catian et al., 2018; van der Valk, 1981). During the descent water period, the decomposition of the plants that were submerged in the flood phase occurs. This condition provides nutrients

to the water, electrical conductivity increases, and floating and amphibian species optimize the nutrients available (Almeida & Melo, 2009). In this environment species such as *I. aquatica* and *H. amplexicaulis*, may have high growth due to not depending completely on the water to survive, making the best use of nutrients available, and the electrical conductivity of water conditions.

The aquatic plant's diversity responds to the evolutionary process and adaptations in land-water transition (Sculthorpe, 1967). Progressive adaptations to aquatic life suggested different reactions to fluctuations in the water level (Thomaz & Bini, 2003). Consequently, the heterogeneous environment imposes selection pressure on aquatic macrophytes that results in considerable Spatio-temporal diversity of life forms (Eckert et al., 2016). The clear temporal differentiation of macrophytes in the STW could be determined by the flood pulse and connectivity with the Magdalena River. The aquatic plant groupings correspond with water levels were contrasting. The cover, richness, and diversity changed throughout the study period as a response to the depth and extent of water body changes. This behavior has been reported in similar wetlands in the Colombian Caribbean (Cortés-Castillo & Rangel-Ch, 2013).

Extensive communities of *L. helminthorrhiza*, *N. oleracea*, and *P. repens*, increase the richness of species because, regularly during the rainy period, come accompanied by other species (Cortés-Castillo & Rangel-Ch, 2013; Gordon, 2000; Rangel-Ch, 2010). During the flood period, free-floating macrophytes proliferate in favorable conditions of nutrients, currents, and wind action (Vieira et al., 2019). Contrary, during the dry period, numerous species lose aerial tissues and die, decreasing the richness of species (Mereles et al., 2004). *L. aequinoctialis* and *U. gibba* (free-floating) and *Aeschynomene* cf. *indica* (aquatic-rooted), disappeared completely during the dry period. These variations in the composition and vegetation cover during the hydroclimatic regime have also been reported in Venezuela wetlands (Rial, 2006).

Regarding spatial similarity, the nMDS analysis showed that S1 stations were separate from S2 and S3 stations. Direct connection with the Magdalena River through the Channel caused a different dynamic. Probably, the current flow prevented the permanent establishment of some free-standing plants. However, during the water lowering period, the sediment accumulation favored slopes or small islands formation where species *I.*

*aquatica* was particularly abundant. This aquatic plant and *M. polycarpa* occupied a big extension from the litoral zone until the open water zone, similar to those reported in the Zapotosa wetland (Cesar, department) by Cortés-Castillo & Rangel-Ch, (2013). *M. polycarpa* is usually associated with shallow water and muddy substrates, while *I. aquatica* is related to shallow flooded sand soils (Cortés-Castillo & Rangel-Ch, 2013). S2 and S3 stations, areas far from the Magdalena River channel, allowed species establishments like *N. arguta*, a floating submerged macrophyte that grows in the most stable habitat and less current disturbance (Delatorre et al., 2019). In these stations, aquatic plant community composition was homogenous, likely the result of ecological functioning in the floodplain (Cortés-Castillo & Rangel-Ch, 2013).

#### 4.2. Environmental variables vs composition and structure of aquatic plants

A direct relationship between organic matter and nutrient concentrations and macrophyte species development has been reported by several authors (Endut et al., 2016; Gezie et al., 2018; Ondiba et al., 2018; Rameshkumar et al., 2019). For example, *E. crassipes* have high phenotypic plasticity and tolerance to level water variations (Gezie et al., 2018). This plant can fast grow in low contaminate waters or hypertrophic wetlands, even in wastewater with high contents of heavy metals (Rameshkumar et al., 2019). In the rainy period, floating associations of *L. helminthorrhiza*, *E. crassipes*, and *N. oleracea*, have been reported in Zapotosa wetlands and Ciénaga Grande de Santa Marta in the Colombian Caribbean (Cataño-Vergara et al., 2008; Cortés-Castillo & Rangel-Ch, 2013; Rivera-Díaz et al., 2013). In STW these associations were present in April-May/17 (rainy period) and coincided with high transparency and nitrate concentrations. Probably, the fertilization by flood pulse influence during the rainy period favors the fast growth and assemblage diversity of aquatic plants (Gómez-Rodríguez et al., 2017). Floating macrophytes such as *N. oleracea*, *L. helminthorrhiza*, *E. crassipes*, *E. azurea*, and *P. stratiotes*, intervene directly in water turbidity decrease and transparency increase (Martelo & Borrero, 2012; Meerhoff & Mazzeo, 2004).

On the other hand, aquatic plant velocity growth is affected by temperature. *N. arguta* was positively related to temperature during April and May/17, while, *L. subintegra*, and *I. aquatica* were

negatively related to depth. Probably, low water level exposes areas susceptible to being rapidly colonized, by floating and emerging rooted species (Rangel-Ch., 2010) and according to the results obtained in the ACC, it could be indicated that *M. polycarpa*, *H. amplexicaulis*, and *S. auriculata* proved to be tolerant to low oxygen concentrations or can certainly grow in eutrophic wetlands.

## 5. Conclusions

Spatial and temporal variations in the macrophytes assemblage were related to the hydrological period. During rising and high-level water periods the richness, vegetation cover, and diversity were increased. In the dry period, richness and abundance were lower due to the water low level. Water quality and physicochemical variables such as depth, temperature, organic matter, and nutrients were related to the greater abundance of *E. azurea*, *L. helminthorrhiza*, *N. oleracea*, *P. stratiotes*, *I. aquatica*, *L. subintegra*, and *E. crassipes* species. Some species of the aquatic plant reached high cover percentage, such *I. aquatica* (19%) or *E. azurea* (14%) principally in S1 station (Channel with the Magdalena River) and S2 stations. The presence of opportunistic species such as *I. aquatica* and *E. azurea* covered almost the entire area of these stations.

## Acknowledgements

The authors thank the Research office of the Universidad del Atlántico for the funding to carry out this project. To the Herbarium and to the Laboratory of Physicochemical Analysis of the Centro de Estudios de Agua of the Universidad del Atlántico for facilitating their spaces for the analysis of macrophytes and water quality, respectively. To the Fishermen's Association of the Santo Tomás wetland for supporting fieldwork. At Juan de La Hoz, biology student for your support in taking physicochemical water variables and biologist MSc Jaime Cerro for supporting map edition.

## References

- Agostinho, A.A., Gomez, L., Thomaz, S.M., & Hahn, N.S., 2004. The upper Paraná river and its floodplain: Main characteristics and perspectives for management and conservation. In: Thomaz, S.M., Agostinho, A.A., & Hahn, N.S., eds. The Upper Paraná River and its Floodplain. Leiden: Backhuys Publishers, 381-393.
- Almeida, F.F., & Melo, S., 2009. Considerações limnológicas sobre um lago da planície de inundação

- amazónica (lago Catalão – Estado do Amazonas, Brasil). *Scientiarum. Biol. Sci.* 31(4), 387-395. <https://doi.org/10.4025/actascibiolsci.v31i4.4641>.
- Alvarado, M., 2016. Sur del Atlántico, una nueva oportunidad (Online). Barranquilla: Funadación Promigas. Retrieved in 2021, November 25, from <http://hdl.handle.net/20.500.11762/20493>
- Álvarez-León, R., Carbonó-De la Hoz, E., Troncoso-Olivo, W.A., Casas-Monroy, O., & Reyes Forero, P., 2004. La vegetación terrestre, eurihalina y dulceacuícola de la ecorregión Ciénaga Grande de Santa Marta. In: Garay Tinoco, J., ed. Los manglares de la ecorregión Ciénaga Grande de Santa Marta: pasado, presente y futuro. Bogotá: INVEMAR, 77-96.
- American Public Health Association – APHA. American Water Works Association – AWWA. Water Environment Federation – WEF, 2012. Standard methods for the examination of water and wastewater (22nd ed.). Washington D.C.: APHA-AWWA-WEF.
- Arellano, L., León-Cortés, J.L., Halffter, G., & Montero, J., 2013. *Acacia woodlots*, cattle and dung beetles (Coleoptera: Scarabaeinae) in a Mexican silvopastoral landscape. *Rev. Mex. Biodivers.* 84(2), 650-660. <http://dx.doi.org/10.7550/rmb.32911>.
- Arias, P., 1985. Las ciénagas en Colombia. *INDERENA*. 22, 39-70.
- ASOCAR & Universidad del Magdalena, 2011. Ajuste del plan de ordenación y manejo del complejo de humedales de la vertiente occidental del Río Magdalena en el departamento del Atlántico y determinación de la ronda hídrica de los humedales de Sabanagrande, Santo Tomas y Palmar de Várela. Convenio de Asociación 01 de 2011 (Online). Santa Marta, Colombia. Retrieved in 2021, November 18, from <https://www.corpamag.gov.co/archivos/PMA/PlanManejoRBRamsar.pdf>
- Cataño-Vergara, Y., Quirós-Rodríguez, J., Ríos, J.A., Pastrana, J.N., & López, F.G., 2008. Estudio de la vegetación acuática en un área de inundación de la Ciénaga Grande del Bajo Sinú, sector Purísima, Departamento de Córdoba, Colombia. *Rev. Asoc. Col. Cienc. Biol.* (Online), 20, 34-47. Retrieved in 2021, November 25, from <https://revistaaccb.org/tr/index.php/accb/article/view/58>
- Catian, G., Muniz, D., Suárez, Y.R., & Scremin-Dias, E., 2018. Effects of flood pulse dynamics on functional diversity of macrophyte communities in the Pantanal Wetland. *Wetlands* 38(5), 975-991. <http://dx.doi.org/10.1007/s13157-018-1050-5>.
- Chao, A., Gotelli, N.J., Hsieh, T.C., Sander, E.L., Ma, K.H., Colwell, R.K., & Ellison, A.M., 2014. Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. *Ecol. Monogr.* 84(1), 45-67. <http://dx.doi.org/10.1890/13-0133.1>.
- Cirujano, B., Meco, A., & García, P., 2014. Flora acuática Española: hidrofitos vasculares (Online). Madrid: Real Jardín Botánico. Retrieved in 2021, October 20, from <https://bibdigital.rjb.csic.es/idurl/1/16128>
- Colwell, R., 2009. EstimateS 8.2: Statistical estimation of species richness and shared species from samples. (Online). Retrieved in 2021, November 25, from <http://viceroy.eeb.uconn.edu/EstimateS/>
- Cortés-Castillo, D., & Rangel-Ch, J.O., 2013. Vegetación acuática y de pantano de las ciénagas del departamento del Cesar (Colombia). In: Rangel-Ch., J.O., ed. Colombia diversidad biótica XIII: complejo cenagoso Zapatoza y ciénagas del sur del Cesar. Bogotá D.C.: Instituto de Ciencias Naturales, Universidad Nacional de Colombia, 301-329.
- Cortés-Castillo, D.V., 2017. Vegetación estuarina y vegetación acuática en complejos cenagosos del Caribe colombiano [PhD Thesis]. Bogotá: Universidad Nacional de Colombia. Retrieved in 2021, October 15, from <https://repositorio.unal.edu.co/bitstream/handle/unal/59487/DenisseV.Cort%c3%a9s-Castillo.2017.pdf?sequence=1&isAllowed=y>
- Cultid-Medina, C., Medina, C., Martínez, B., Escobar, A., Constantino, L., & Betancur, N. 2012. Escarabajos coprófagos (Scarabaeinae) del eje cafetero: guía para el estudio ecológico (Field Guide) (1. ed.). Villa Maria, Caldas: Cenicafé, Federación Nacional de Cafeteros de Colombia and Wild life Conservation Society. <https://doi.org/10.13140/RG.2.1.1013.9049>.
- Delatorre, M., Leme, N., & Rodrigues, R.B., 2019. Trait-environment relationship of aquatic vegetation in a tropical pond complex system. *Wetlands* 40, 299-310. <https://doi.org/10.1007/s13157-019-01189-0>.
- Echevarría, G., & Machado-Allison, A., 2014. Comunidades de peces en planicies de inundación de ríos tropicales: factores que intervienen en su estructura. *Bol. Acad. C. Fís. Mater. Nat* 74(1), 35-67.
- Eckert, C.G., Dorken, M.E., & Barrett, S.C.H., 2016. Ecological and evolutionary consequences of sexual and clonal reproduction in aquatic plants. *Aquat. Bot.* 135, 46-61. <http://dx.doi.org/10.1016/j.aquabot.2016.03.006>.
- Endut, A., Lananan, F., Hajar, S., Jusoh, A., & Wan, N., 2016. Balancing of nutrient uptake by water spinach (*Ipomoea aquatica*) and mustard green (*Brassica juncea*) with nutrient production by African catfish (*Clarias gariepinus*) in scaling aquaponic recirculation system. *Desalination Water Treat.* 57(60), 29531-29540. <http://dx.doi.org/10.1080/19443994.2016.1184593>.
- Escolar, A., 2007. Ecosistemas acuáticos del departamento del Atlántico (Online). Corporación Autónoma Regional del Atlántico. Retrieved in 2020, June 24, from <https://es.scribd.com/document/240606004/Ecosistemas-Acuaticos-Del-Dpto-Del-Atlantico>

- Ferreira de Deus, F., Schuchmann, K., Arieira, J., Silvia, A., Tissiani, D.O., & Marques, M.I., 2020. Avian Beta Diversity in a Neotropical Wetland: the effects of flooding and vegetation structure. *Wetlands* 40(5), 1513-1527. <http://dx.doi.org/10.1007/s13157-019-01240-0>.
- Gezie, A., Worie, W., Belachew, A., Wassie, G., Eshete, D., & Seis, M., 2018. Potential impacts of water hyacinth invasion and management on water quality and human health in Lake Tana watershed, northwest Ethiopia. *Biol. Invasions* 20(9), 2517-2534. <http://dx.doi.org/10.1007/s10530-018-1717-0>.
- Gómez-Rodríguez, A.M., Valderrama Valderrama, L.T., & Rivera-Rondón, C.A., 2017. Comunidades de macrófitas en ríos andinos: composición y relación con factores ambientales. *Acta Biol. Colomb.* 22(1), 45-58. <http://dx.doi.org/10.15446/abc.v22n1.58478>.
- Gordon, E., 1998. Seed characteristics of plant species from riverine wetlands in Venezuela. *Aquat. Bot.* 60(4), 417-431. [http://dx.doi.org/10.1016/S0304-3770\(97\)00057-0](http://dx.doi.org/10.1016/S0304-3770(97)00057-0).
- Gordon, E., 2000. Dinámica de la vegetación y del banco de semillas en un humedal herbáceo lacustrino (Venezuela). *Rev. Biol. Trop.* 48(1), 25-42.
- Gyosheva, B., Kalchev, R., Beshkova, M., & Valchev, V., 2020. Relationships between macrophyte species, their life forms and environmental factors in floodplain water bodies from the Bulgarian Danube River Basin. *Ecohydrol. Hydrobiol.* 20(1), 123-133. <http://dx.doi.org/10.1016/j.ecohyd.2019.06.003>.
- Hammer, Ø., Harper, D.A.T., & Ryan, P.D., 2001. Past: paleontological statistics software package for education and data analysis. *Palaeontol. Electronica* (Online), 4(1), 4-9. Retrieved in 2021, June 24, from [http://palaeo-electronica.org/2001\\_1/past/issue1\\_01.htm](http://palaeo-electronica.org/2001_1/past/issue1_01.htm)
- Instituto de Hidrología, Meteorología y Estudios Ambientales – IDEAM (Online), 2022. Bogotá D.C. Retrieved in 2022, August 18, from [www.ideam.gov.co](http://www.ideam.gov.co)
- Jiménez-Segura, L.F., Palacio, J., & Leite, R., 2010. River flooding and reproduction of migratory fish species in the Magdalena River basin, Colombia. *Ecol. Freshwat. Fish* 19(2), 178-186. <http://dx.doi.org/10.1111/j.1600-0633.2009.00402.x>.
- Kettenring, K., Gardner, G., & Galatowitsch, S., 2006. Effect of light on seed germination of eight wetland *Carex* species. *Ann. Bot.* 98(4), 869-874. PMID:16905568. <http://dx.doi.org/10.1093/aob/mcl170>.
- Madriñán, S., Rial, A., Bedoya, A.M., & Fernandez, L., 2017. Plantas acuáticas de la Orinoquía colombiana. Bogotá: Universidad de los Andes.
- Martelo, J., & Borrero, J.A.L., 2012. Macrófitas flotantes en el tratamiento de aguas residuales; una revisión del estado. *Ing. Cienc.* 8(15), 221-243. <http://dx.doi.org/10.17230/ingciencia.8.15.11>.
- Meerhoff, M., & Mazzeo, N., 2004. Importancia de las plantas flotantes libres de gran porte en la conservación y rehabilitación de lagos someros de Sudamérica. *Ecosistemas. Rev. Cient. Tec. Ecol. Medio Ambiente* 13(2), 13-22. <https://doi.org/10.7818/re.2014.13-2.00>.
- Mereles, H.M.F., Martín, C.L., De Egea, J., & Céspedes, G., 2004. Aportes al conocimiento de la vegetación del norte del Chaco boreal, Paraguay. *Rojasiana* 6(1), 126-128.
- Mormul, R.P., Thomaz, S.M., & Soares Vieira, L.J., 2013. Richness and composition of macrophyte assemblages in four Amazonian lakes. *Acta Scientiarum* 35(3), 343-350. <https://doi.org/10.4025/actasciabiolsci.v35i3.11602>.
- Murray-Hudson, M., Wolski, P., Murray-Hudson, F., Brown, M.T., & Kashe, K., 2014. Disaggregating hydroperiod: components of the seasonal flood pulse as drivers of plant species distribution in floodplains of a tropical wetland. *Wetlands* 34(5), 927-942. <http://dx.doi.org/10.1007/s13157-014-0554-x>.
- Ondiba, R., Omondi, R., Nyakeya, K., Abwao, J., & Oyoo-okoth, E., 2018. Environmental constraints on macrophyte distribution and diversity in a tropical endorheic freshwater lake (Lake Baringo, Kenya). *Int. J. Fish. Aquat. Stud.* 6(3), 251-259.
- Pérez-Vásquez, N. S., Arias-Ríos, J., & Quirós-Rodríguez, J.A., 2015. Variación Espacio-Temporal de plantas vasculares acuáticas en el complejo cenagoso del Bajo Sinú, Córdoba, Colombia. *Acta Biol. Colomb.* 20(3), 155-165. <http://dx.doi.org/10.15446/abc.v20n3.45380>.
- Posada, J.A., & López, M.T., 2011. Plantas Acuáticas del Altiplano del oriente antioqueño. Rionegro: Grupo de Limnología y Recursos Hídricos, Universidad Católica de Oriente, 121 p.
- Rameshkumar, S., Radhakrishnan, K., Rajaram, S., & Aanand, R., 2019. Influence of physicochemical water quality on aquatic macrophyte diversity in seasonal wetlands. *Appl. Water Sci.* 9(12), 1-8. <http://dx.doi.org/10.1007/s13201-018-0888-2>.
- Ramos-Montaña, C., Cárdenas-Avella, N.M., & Herrera Martínez, Y., 2013. Caracterización de la comunidad de macrófitas acuáticas en lagunas del Páramo de La Rusia (Boyacá-Colombia). *Cienc. Desarro. (Online)*, 4(2), 73-82. Retrieved in 2022, August 18, from [http://www.scielo.org.co/scielo.php?script=sci\\_arttext&pid=S0121-74882013000200009&lng=en&tlng=es](http://www.scielo.org.co/scielo.php?script=sci_arttext&pid=S0121-74882013000200009&lng=en&tlng=es)
- Rangel-Ch, J.O., 2010. Colombia diversidad biótica IX. Ciénagas de Córdoba: biodiversidad-ecología y manejo ambiental. Bogotá D.C.: Universidad Nacional de Colombia, Corporación Autónoma Regional de los valles del Sinú y del San Jorge (CVS).

- Regmi, T., Shah, D.N., Doody, T.M., Cuddy, S., & Tachamo, R.D., 2021. Hydrological alteration induced changes on macrophyte community composition in sub-tropical floodplain wetlands of Nepal. *Aquat. Bot.* 173, 103413. <http://dx.doi.org/10.1016/j.aquabot.2021.103413>.
- Reid, M.A., & Quinn, G.P., 2004. Hydrologic regime and macrophyte assemblages in temporary floodplain wetlands: implications for detecting responses to environmental water allocations. *Wetlands* 24(3), 586-599. [http://dx.doi.org/10.1672/0277-5212\(2004\)024\[0586:HRAMAI\]2.0.CO;2](http://dx.doi.org/10.1672/0277-5212(2004)024[0586:HRAMAI]2.0.CO;2).
- Rial, B.A., 2006. Variabilidad espacio-temporal en un humedal de los Llanos de Venezuela. *Rev. Biol. Trop.* 54(2), 403-413. PMID:18494311. <http://dx.doi.org/10.15517/rbt.v54i2.13882>.
- Rivera-Díaz, O., Rangel-Ch, J.O., Avella, A., García, J.D., & Castro-R, S.Y., 2013. Las plantas con flores del complejo cenagoso Zapatosa: incluye localidades de Mata de Palma y La Pachita. In: Rangel-Ch., J.O., ed. Colombia diversidad biótica XIII: complejo cenagoso Zapatosa y ciénagas del sur del Cesar. Bogotá D.C.: Instituto de Ciencias Naturales, Universidad Nacional de Colombia, 203-242.
- Roldán, G., & Ramírez, J.J., 2008. Fundamentos de Limnología Neotropical (2ª ed.). Medellín: Universidad de Antioquia, 421 p.
- Santos, A., & Thomaz, S.M., 2007. Aquatic macrophytes diversity in lagoons of a tropical floodplain: the role of connectivity and water level. *Austral Ecol.* 32(2), 177-190. <http://dx.doi.org/10.1111/j.1442-9993.2007.01665.x>.
- Schneider, B., Cunha, E.R., Marchese, M., & Thomaz, S.M., 2018. Associations between macrophyte life forms and environmental and morphometric factors in a large sub-tropical floodplain. *Front. Plant Sci.* 9, 195. PMID:29515608. <http://dx.doi.org/10.3389/fpls.2018.00195>.
- Sculthorpe, C.D., 1967. The biology of aquatic vascular plants. London: Edward Arnold, 610 p.
- Sokal, R.R., & Rohlf, F.J., 1995. Biometry: the principles and practice of Statistics in Biological Research (3rd ed.). New York: W.H. Freeman and Co.
- Staples, G.W., 1996. The identity of *Ipomea staphylina* (Convolvulaceae) in Asia. *Taiwania* 41(3), 185-196.
- Thomaz, S.M. & Bini, L.M. 2003. Ecologia e manejo de macrófitas aquáticas. Maringá: Universidade Estadual de Maringá.
- United States Agency for International Development – USAID, 2016. El Niño southern oscillation (ENSO) 2015-16 Latin American and Caribbean Region (Vol. 4). Florida, USA.
- van der Valk, A.G., 1981. Succession in wetlands: a gleasonian approach succession. *Ecology* 62(3), 688-696. <http://dx.doi.org/10.2307/1937737>.
- Velásquez, J., 1994. Plantas acuáticas vasculares de Venezuela. Caracas, Venezuela: Universidad Central de Venezuela, Consejo de Desarrollo Científico y Humanístico.
- Vieira, E.N., Moreira, B.M., & Mayer, P.F., 2019. Distribution of aquatic macrophytes along depth gradients in Lajeado Reservoir, Tocantins river, Brazil. *Acta Limnol. Bras.* 31, e6. <http://dx.doi.org/10.1590/s2179-975x9317>.
- Wallsten, M., & Forsgren, P.O., 1989. The effects of increased water level on aquatic macrophytes. *J. Aquat. Plant Manage.* 27, 32-37.

Received: 23 February 2021

Accepted: 18 August 2022

**Associate Editor:** Gustavo Henrique Gonzaga da Silva.