Limnetica, 42(1): 85-99 (2023). DOI: 10.23818/limn.42.07
© Asociación Ibérica de Limnología, Madrid. Spain. ISSN: 0213-8409

Littoral areas of Amazonian floodplain lakes: a biological reserve to biodiversity loss

Donato-R, Jhon C.[1,*] and Santiago R. Duque[2]

[1] Departamento de Biología. Universidad Nacional de Colombia, Sede Bogotá. Av. (Cra.) 30 No. 45-03, Bogotá, Colombia.
[2] Laboratorio de Manejo y Gestión de Humedales. Instituto Amazónico de Investigaciones (Imani). Universidad Nacional de Colombia, Sede Amazonia.

[*] Corresponding author: jcdonator@unal.edu.co

Received: 22/04/21 Accepted: 16/03/22

ABSTRACT

Littoral areas of Amazonian floodplain lakes: a biological reserve to mitigate biodiversity loss

Carbon from aquatic plants and periphyton in littoral zones subsidize food webs. Field work was carried out in two different lake types in the Colombian Amazon: a *várzea* (Yahuarcaca) and an *igapó* (Pacatúa). Plants in the littoral zone of *várzea* Lake had higher photosynthetic biomass compared to the plants of the littoral zone of *igapó*, but differences in root biomass were not significant. The two littoral zones contained a relatively high species richness and diversity (Shannon-Wiener Index) of organisms associated with the roots, although no significant differences existed between the two lakes. Littoral areas may be important in relatively isolated and physically fragmented large terrestrial landscapes such as the Amazon basin.

Key words: aquatic plants, *várzea*, *igapó*, floodplains, Amazonia, Colombia

RESUMEN

Áreas litorales de los lagos de la llanura aluvial amazónica: una reserva biológica para mitigar la pérdida de biodiversidad

El carbono de las plantas acuáticas y el perifiton en las zonas litorales alimenta las redes tróficas. Se realizó un trabajo de campo en dos tipos diferentes de lagos en la Amazonía colombiana: una de várzea *(Yahuarcaca) y una de* igapó *(Pacatúa). Las plantas de la zona litoral del lago* várzea *presentaron mayor biomasa fotosintética en comparación con las plantas de la zona litoral de* igapó, *pero las diferencias en la biomasa radicular no fueron significativas. Las dos zonas litorales contenían una riqueza y diversidad de especies (índice de Shannon-Wiener) asociadas a las raíces, relativamente altas, aunque no existieron diferencias significativas en la diversidad entre los dos lagos. Las áreas litorales pueden ser importantes en grandes paisajes terrestres relativamente aislados y físicamente fragmentados, como la cuenca del Amazonas.*

Palabras clave: *plantas acuáticas,* várzea, igapó*, planos inundables, Amazonia, Colombia*

INTRODUCTION

The Amazon region is located between the Guiana and Brazilian shields, and with an area of 6.3 million km^2 includes the largest forest and longest river system on the planet (Wesselingh et al., 2010; Prieto, 2018). The Amazon rainforest, the largest remaining rainforest in the world, is home to a good part of the planet's species and is a priority region for conserving biodiversity.

In the Colombian Amazon research has been mainly focused on terrestrial environments rather than on aquatic ecosystems (Castello et al., 2013). However, freshwater ecosystems in the region suffer increasing impacts associated with deforestation (Armenteras et al., 2006; Arias et al., 2018), fire (Armenteras et al., 2017), chemical pollution (Val et al., 2017), dam construction (Latrubesse et al., 2017), overexploitation of plant and animal species (Castello et al., 2013), and climate change (Feng et al., 2020). These transformations result in habitat loss and changes in river flow dynamics that reduce both their diversity and complexity (Palmer, 2010; Rozo et al., 2014).

The Amazon basin is interconnected with countless small streams and numerous rivers. The surrounding areas to the main channels are characterized by periodical flood pulses (Junk et al., 1989) and direct rains or groundwater inputs. Shallow lakes are located in the floodable zones and are characterized by an exuberant growth of macrophytes and associated periphyton and biofilm communities (Montoya & Aguirre, 2009; Silva et al., 2010). These produce close to the 34 % of the primary production of the Amazon basin (300 Tg C a^{-1}) (Piedade et al., 1991; Melack et al., 2009; Silva et al., 2009) and contribute to the spatial heterogeneity of the floodplains and their biodiversity (Amoros & Bornette, 2002, Petry et al., 2003; Granado et al., 2007; Correa et al., 2008; Dias et al., 2010; Röpke et al., 2013).

Three water types in the Amazon (whitewater, blackwater, and clearwater) may be recognized in the Amazon (Sioli (1975) and Ríos-V et al. (2013). These are differentiated by geology, soils and organogenic processes. This classification in the Colombian Amazonia separates two further classes of whitewater and two of blackwater according to the suspended sediment load, pH, conductivity, and transparency of the water (Duque et al., 1997; Núñez-A & Duque, 2001).

The *várzea* (such as the Yahuarcaca Lake) are high primary productivity lakes. This accounted for the contributions of the Amazon River, which is subjected to flood pulses, making up high waters, falling waters, low waters and rising waters phases (Bohórquez, 2011, Salcedo-H et al., 2012; Torres-B et al., 2013). Other lakes, such as the Pacatúa Lake are associated with the blackwater rivers that have lower productivity and diversity than várzea lakes (Palma et al., 2014).

The Neotropical region has the highest diversity of macrophyte species on the planet, with about 1566 species, and aquatic macrophyte habitats often represent the most diversified, productive and heterogeneous portions of water bodies (Chambers et al., 2008). Macrophytes together with periphyton contribute organic carbon to other trophic levels, particularly in oligotrophic and shallow lakes (Petry et al., 2003; Kluijver et al., 2015).

Carbon subsidizes bacterioplankton and zooplankton, then cascading on the whole food web (Torres-B et al., 2014; Bozelli et al., 2015). Additionally, macrophytes contribute significantly to both floodplain carbon and high rates of primary production, those reach a total production between 2400 to 3500 gm^{-2} yr^{-1} with values above water between 650 and 1100 gm^{-2} yr^{-1}, and a production below water between 1700 and 2600 gm^{-2} yr^{-1} (Silva et al., 2010).

Aquatic plants in the littoral zone represent a large surface area that can be colonized by microflora (Andramunio-A et al., 2018, Andramunio-A & Caraballo, 2012). Additionally, they represent a reserve of associated organisms that enhance productivity in oligotrophic lakes (Bozelli et al., 2015).

The present study aims to establish the differences in the physical and chemical properties of the lakes, as well as estimates of the plant biomass in the littoral areas and of the great number of species they harbor. We propose that that despite the differences between types of water, the organisms diversity of the littoral zones demonstrates their value in conservation and management of the aquatic ecosystems of the Colombian Amazon.

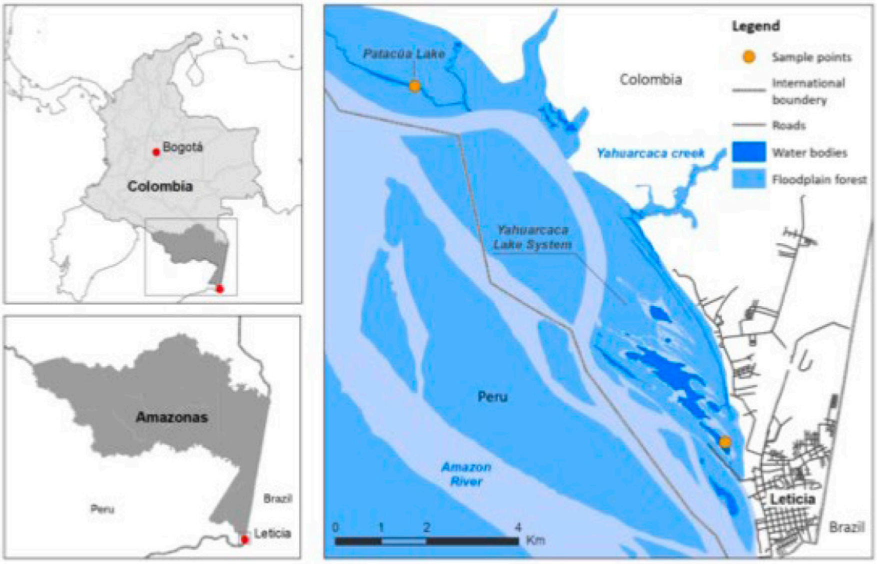

Figure 1. Geographical location of Pacatúa Lake and Yahuarcaca Lake (Leticia, Colombia). *Ubicación geográfica de los lagos Pacatúa y Yahuarcaca (Leticia, Colombia).*

METHODS

Study Area

The study area was located close to the Amazon River and included two classes of water according to the characteristics of the water such as sediment, pH, conductivity, and transparency. Whitewater *type I* is a product of the mountain contributions of Ecuador (Napo River) and Perú (Ucayali and Marañón Rivers). The mineralization of these waters is high (> 100 µS/cm) and the pH is neutral to basic. The cations (Na^+, K^+, Ca^{++} and Mg^{++}) are relatively high (1.37-1.48 meq/l^{-1}). The other class of water is type I blackwater that comes from the forest and owes its color to the partial decomposition of organic matter. This water type has lower mineralization and pH.

The Yahuarcaca Lake is a typical *várzea* system located at 4° 12' 00'' S and 69° 57' 5'' W, at an altitude of 89 m a.s.l. and 2 km upstream from the town of Leticia (Amazonas, Colombia), (Fig. 1). The lake receives water from both the Amazon River (white water *type I* of Andean origin) and black water *type I* from the Yahuarcaca stream (which originates in the forest), with an area of 1 km^2, it originates in a small depression within the floodplain landscape built by the fluvial dynamics of the Amazon River.

The Pacatúa Lake is located at 4° 7' 48'' S and 70° 0' 42'' W at a height of 90 m a.s.l. (Fig. 1). This *igapó* is basically fed by Patacua and Pichuna streams, both of which run through the forest. It receives white waters from the Amazon River at times of maximum flooding of the river (Duque, 1993).

Both types of lakes develop extensive littoral zone with numerous aquatic plants (*Azolla filiculoides*, *Salvinia auriculata*, *Eichhornia crassipes*, *Pistia stratiotes*, *Paspalum* spp, *Victoria amazonica*, and others), with specific bioforms (emergent rooted, floating-leaved rooted, free-floating, submerged) and different mechanisms of vegetative propagation (clone, resprouts, seeds).

Rainfall in the area varies between 3000-4500 mm with a single-mode regimen with higher rainfall from December to May and lower rainfall during the remaining months. The Amazon River shows rising and high waters between November and June with decreasing and low waters during the rest of the annual period (Torres-B et al., 2013), affecting the Yahuarcaca lake water level considerably, but only affecting Pacatúa Lake when high waters reach its maximum levels. This water regime as well as the contributions of organic matter, and the extensive annual floods mediate biotic adaptations up to hypoxic and even anoxic conditions at the bottom of the lakes (Salcedo-H et al., 2012).

Sampling Methods

We selected a sector of the littoral zone of each lake with successional phases of slightly transformed areas. Three linear transects were established from the limnetic zone to the littoral area in each littoral zone, and the aquatic plants were sampled in three 50 x 50 cm quadrants, spaced 2 m apart.

In each sampling date the physical and chemical variables of the water (pH [H^+], temperature (°C), conductivity (µS/cm), dissolved solids (mg/l) and concentration and percentage of dissolved oxygen (mg/l) were measured. The depth of each sampling point was established using a bathymetric probe. The sampling was carried out in low water, when the lakes were disconnected from the Amazon River. Once the environmental variables were measured, the vegetation and the associated organisms present in each quadrant was collected.

In the laboratory, aquatic plants in each quadrant were carefully washed, and the associated organisms (algae, zooplankton, macroinvertebrates, and others) were extracted by squeezing the roots. The algal samples were preserved with Transeau solution in a 1:1 ratio. Zooplankton was fixed with 38 % formaldehyde (4 % final concentration). The aquatic macroinvertebrates adhered to the roots were selected and preserved in 70 % ethanol. Both macroinvertebrates and planktonic organisms were identified to the family level using regional keys.

The photosynthetic part of each plant (*Azolla filiculoides*, *Salvinia auriculata*, *Limnobium laevigatum*, *Ceraptopteris pteridoides*, *Echinochloa polystachya*, *Hydrocotyle ranunculoides*, *Pistia stratiotes*, *Eichhornia crassipes*, *Paspalum* spp, and *Panicum dichotomiflorum*, principally) was separated from its root portion and their fresh weights were obtained. Subsequently and following the recommendations of Wetzel & Likens (2000), the dry weight (PS) of both the photosynthetic and the radical tissue was obtained. In addition, the ash free dry weight (PSLC) was estimated.

In each sample extracted, a 1 L aliquot was taken from the squeezing, and the organisms were counted until reaching 100 individuals of the most abundant taxa. Rare or less abundant species or categories (algae, zooplankton, macroinvertebrates) were also considered. The ranges of variation of the abundance were for algae ind/ml, zooplankton ind/l. and for the macroinvertebrates ind/m^2.

Data Analysis

To data analysis, statistical programs were used to identify general trends in the data. Figures of each of the physical and chemical variables *vs.* quadrants and transects were made for each lake to establish possible differences between the measurements of the quadrants (sites) and lakes. A principal component analysis (PCA) was run to identify the environmental variables that discriminated the differences between sites and lakes. With the biomass data (dry weight, fresh weight, ash-free dry weight -AFDW-) of each aquatic plant species, a matrix was elaborated, and figures of biomass (g.dry wt/m^2) of the photosynthetic tissue and roots were prepared for each lake. A one-way ANOVA was run to test if there were differences in plant biomass (g.dry wt/m^2) between the two lakes. differences in diversity and species richness between the lakes were verified using the relative abundances of the associated microorganisms in each category. Finally, we used one- way ANOVA and non-parametric tests (Kruskal-Wallis) to make comparisons and verify whether or not significant differences in the diversity [H´] values between the two lakes.

RESULTS

Physical and chemical characteristics of the lakes

Minor differences were observed in the physical and chemical variables of the two lakes (Fig. 2).

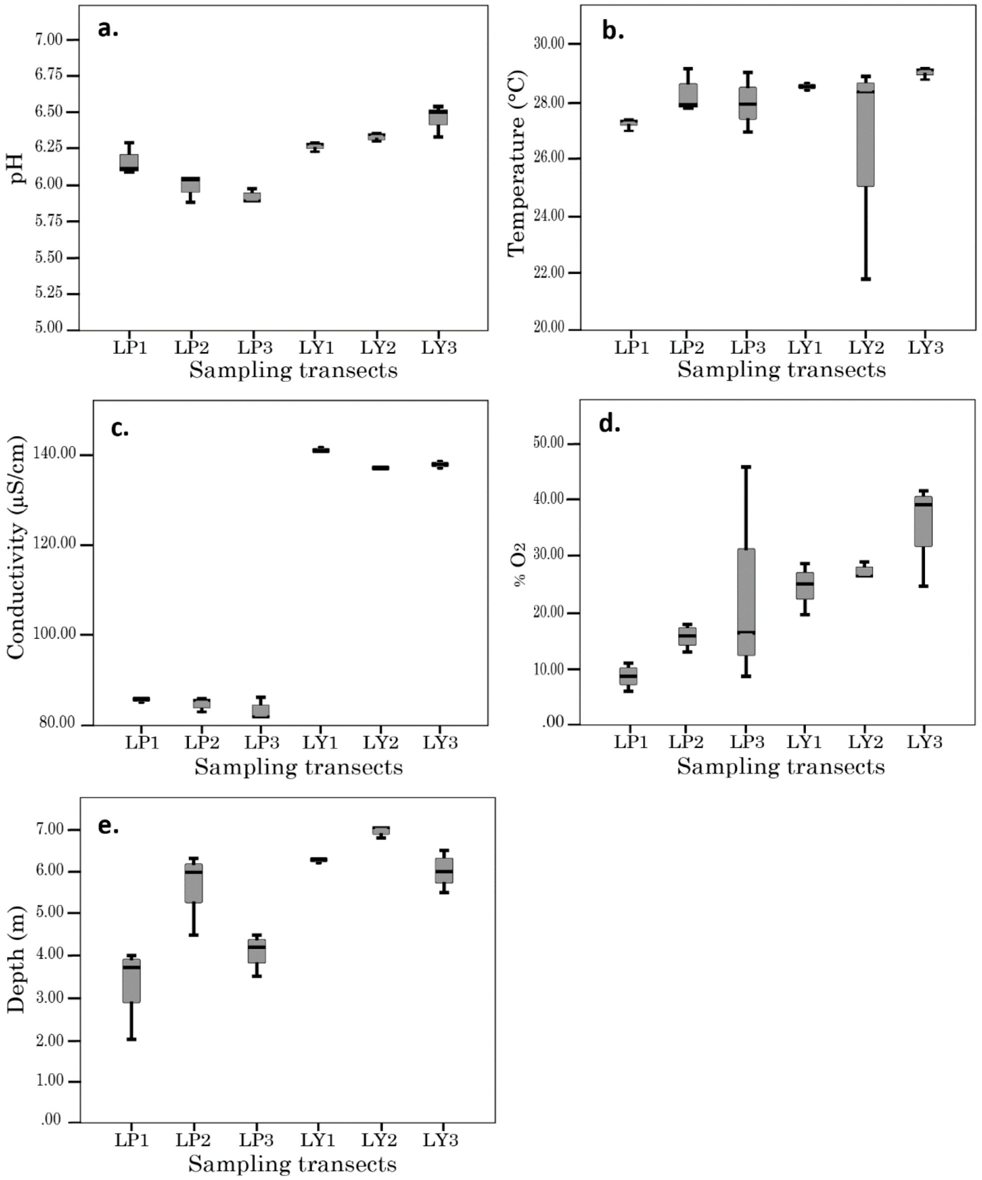

Figure 2. Comparison of physical and chemical variables (LP= Pacatúa Lake; LY = Yahuarcaca Lake). a) pH; b) Temperature; c) Conductivity; d) dissolved oxygen; e) Depth. *Comparación de las variables físicas y químicas entre los lagos (LP= Lago Pacatúa; LY = Lago Yahuarcaca) a) pH; b) Temperatura; c) Conductividad; d) Oxígeno disuelto; e) Profundidad.*

An exception was the conductivity, which ranged 82 and 86 µS/cm in Pacatúa Lake and 137-142 µS/cm in Yahuarcaca Lake (F = 32.8, N = 18, $p = 0.0003$). Also, the dissolved solids showed (LP = 52 mg/l; LY = 84 mg/l) significant differences between the lakes (F = 23.75, N = 18, $p = 0.0002$). The pH was closer to neutrality in the Yahuarcaca and acidic in Pacatúa (Fig. 2). Differences in conductivity and dissolved oxygen mainly segregated Yahuarcaca Lake from Pacatúa lake. By ordering the physical and chemical variables (94.9 % of the variance of the data in the first two axes), the first axis was associated with dissolved oxygen (considering percentage of saturation) and the second axis was associated with variables related to the mineralization of the water (water conductivity and dissolved solids) (Fig. 3).

Composition and comparison of macrophytes in the two lakes

The two macrophyte communities represented lake-type associations. The macrophytes covered ca. 30 % of the water surface in both lakes, and successional phases included individuals from the pleustophytes, then the rhizophytes, to the phase of grass (Gramineae) bordering the forest. The dominant species were *Azolla filiculoides*, *A. caroliniana*, *Salvinia auriculata*, *S. minima*, *Limnobium laevigatum*, *Ceraptopteris pteridoides*, *Echinochloa polystachya*, Hydrocotyle ranunculoides, *Pistia stratiotes*, *Eichhornia crassipes*, *Pontederia rotundifolia*, *Paspalum repetula*, *P. orbandicratum*, *Panicum dichotomiflorum*, and *Victoria amazonica*.

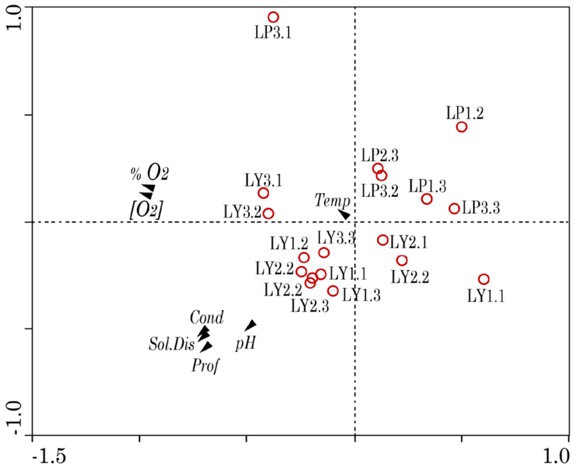

Figure 3. Principal Component Analysis (PCA) based on physical and chemical variables of the lakes. *Análisis de componentes principales (PCA) basado en las variables físicas y químicas de los lagos.*

In Yahuarcaca Lake, species with the highest biomass (g. dry wt/m^2) were *P. stratiotes*, *E. crassipes* (pleustophytes), *Paspalum repens* and *Paspalum* sp. (rhizophyte). In Pacatúa Lake, *Salvinia auriculata* (pleustophyte), *E. crassipes* (pleustophyte) and *Bidens* sp., (rhizophyte) had the highest biomass values. The average root and photosynthetic biomass (g.dry wt/m^2) were higher in Yahuarcaca Lake than in Pacatúa Lake (Fig. 4 and Fig. 5a, b).

Figure 5 shows how in Yahuarcaca Lake there is a high density of roots of *Pistia stratiotes* and *Eichhornia crassipes* while in Pacatúa Lake *Salvinia* sp. and *Eichhornia crassipes* had higher root density. In the littoral zone of Yahuarcaca Lake macrophytes had a higher average root biomass than those of Pacatúa Lake. *Pistia stratiotes* had a higher photosynthetic and root biomass in

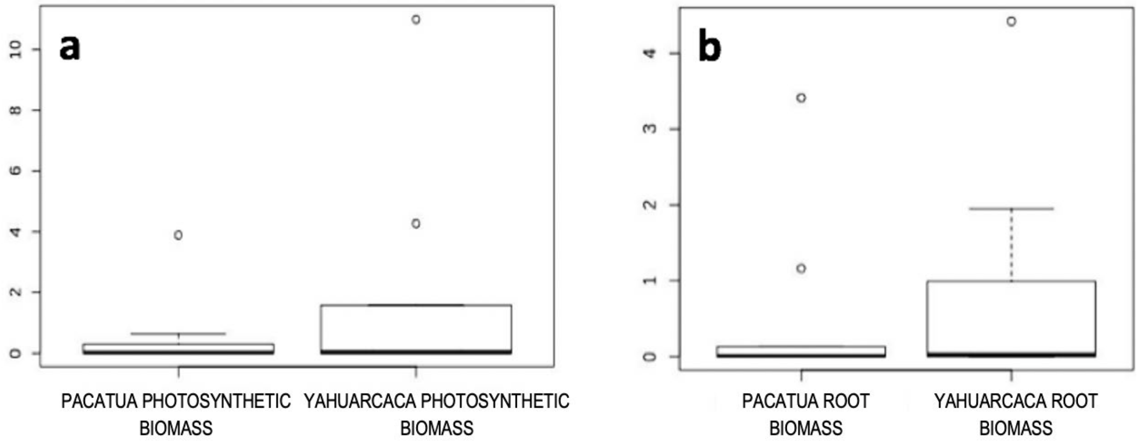

Figure 4. Average photosynthetic biomass (g.dry. wt/m2) (a) and root biomass in lakes (g.dry. wt/m2) (b). *Promedio de la biomasa fotosintética (gPs/m2) (a) y biomasa de raíz (gPs/m2) (b) en los lagos.*

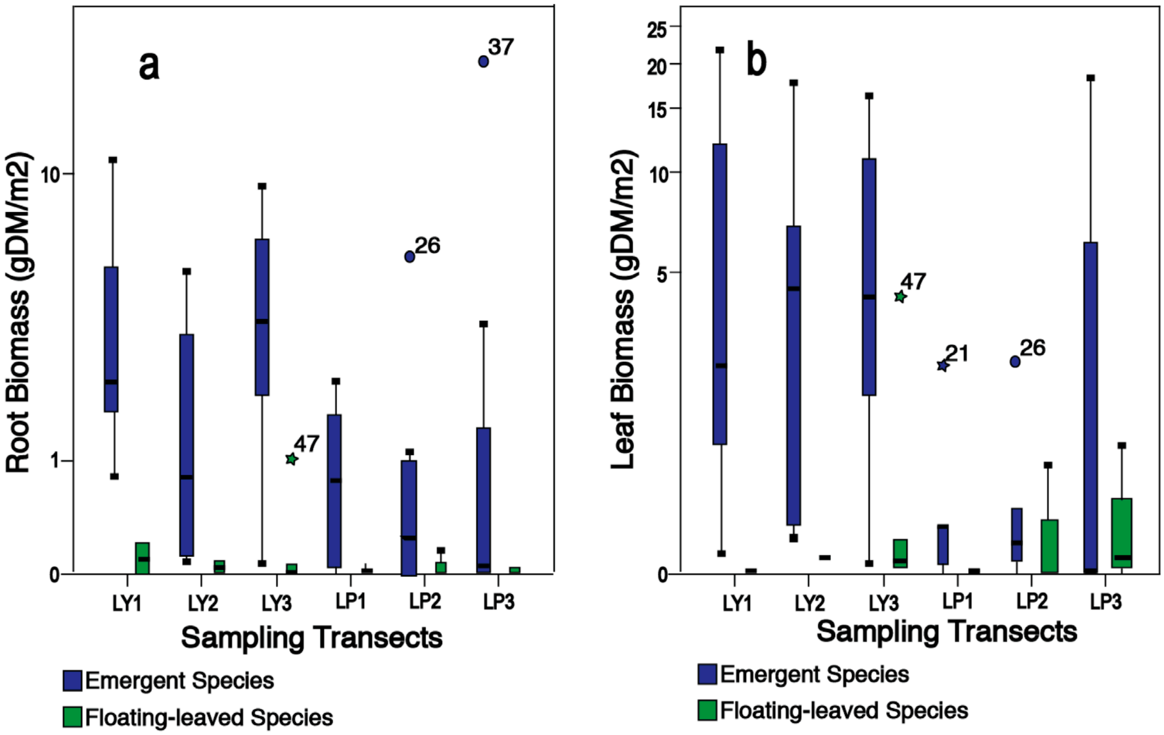

Figure 5. Comparison of root (a) and photosynthetic (b) biomass (g.dry. wt/m2) of emerging and floating species of aquatic plants. (LP= Pacatúa Lake; LY = Yahuarcaca Lake). *Comparación de la biomasa de raíz y fotosintética, en plantas emergentes y flotantes. (LP= Lago Pacatúa; LY = Lago Yahuarcaca).*

the Yahuarcaca Lake. In the Pacatúa Lake the presence of *Salvinia auriculata* was dominant. The photosynthetic biomass was higher than the root biomass in both lakes, but always with higher values in Yahuarcaca Lake.

There were no differences in the root biomass between the two lakes ($F = 1.122$, $N = 60$, $p = 0.294$), but significant differences were found for the photosynthetic biomass ($F = 5.171$, $N = 60$, $p = 0.027$). These were determined by the biomass of *Pistia stratiotes*, *Salvinia auriculata* and *Paspalum* spp.

Composition, species richness and diversity of organisms associated with the littoral zone

A lower number of organisms was recorded in Pacatúa compared to Yahuarcaca. The latter had 48 taxa of algae, macroinvertebrates, and zooplankton), while in Pacatúa there were 28 taxonomic groups (Table 1).

Ticoplankton algae was the most abundant category in both lakes, composed mainly of diatoms (*Eunotia*, *Pinnularia*, *Navicula*), Chlorococcales (*Pediastrum simplex*) and Euglenales (*Euglena*, *Phacus*, *Trachelomonas*). In Yahuarcaca Lake, protozoa, rotifers, coleopterans and dipteran larvae (Simulidae and Chironomidae) were dominant, and bivalve, Ephemeroptera, Thysanoptera, Trichoptera, Plecoptera and Hirudinea were only recorded there. In Pacatúa Lake, some groups were more common than in Yahuarcaca (Arachnida, Nematoda and Hydracarina).

Diversity values [H´] varied between 0.7 to 1.5 bits in Yahuarcaca, while in Pacatúa were slightly higher (1.0 to 1.7 bits) (Fig. 7). However, based on the variance and Kruskal-Wallis analyses, no significant differences were found in the diversity values of the littoral areas between lakes ($F = 0.31$; $N = 54$, $p = 0.94$).

Table 1. Littoral organisms of Yahuarcaca and Pacatúa lakes. Reports from this study and from, Duque (1995); Duque & Nuñez- A (1997); Nuñez & Duque (1998;2000); Duarte & Capador (2006); Andrade et al., 2011; Aranguren (2013). *Organismos del litoral de los lagos Yahuarcaca y Pacatúa. Reportes a partir de este estudio y de Duque (1995); Duque & Nuñez- A (1997); Nuñez & Duque (1998;2000); Duarte & Capador (2006); Andrade et al., 2011; Aranguren (2013).*

	Species	Yahuarcaca	Pacatúa
Copépoda	*Mesocyclops longisetus longisetus*	*	
	Mesocyclops meridianus	*	
	Microcyclops anceps anceps	*	
	Thermocyclops crassus	*	
	Thermocyclops tenuis	*	
Cladócera	*Moina micrura*	*	
	Moina minuta	*	
Rotífera	*Epiphanes clavulata*	*	
	Anuraeopsis fissa	*	
	Brachionus amazonicus	*	
	Keratella americana	*	
	Plationus palatus	*	
	Euchalis dilatata	*	
	Myrtilina ventralis	*	
	Trichotria tetractis	*	
	Eosphora anthadis	*	
	Dicranophoroides claviger	*	
	Lecane elegans	*	
	Colurella obtusa	*	
	Polyarthra vulgaris	*	
	Trichocerca braziliensis	*	
	Asplanchna sieboldii	*	
	Heaxarthra intermedia brasiliensis	*	
	Pompholyx complanata	*	
	Filinia limnetica	*	
Hydracarina			*
Araneae			*
Nematoda			*
Protozoa		*	*
Bivalve		*	
Hirudinea		*	
Díptera	*Probezzia sp*	*	
	Mansonia sp	*	
Coleóptera	*Endalus*	*	
	Elodes	*	
	Tropistemus	*	
	Hidrophilus	*	
	Erythemis	*	
Odonata	*Dythemis*	*	
	Coryphaeshna	*	
	Limnogous	*	
	Pelocoris	*	
Hemíptera	*Belostoma*	*	
	Hidrometra	*	
	Ranatra	*	
	Gonatozygon pilosum		*
	Mesotaenium endlicherianum		*
	Closterium closteroides		*
	Cosmarium commissurale		*
Zygophyceae	*Euastrum ansatum*		*
	Staurodesmus brevispina		*
	Staurodesmus dejectus		*
	Staurastrum quadrangulare		*
	Xanthidium trilobum		*
	Micrasterias radians	*	
	M. abrupta	*	
	Leponcinclis ovum globula		*
	L paxilliformis		*
	L texta richiana		*
	Phacus ephippion		*
	P. lefevrei		*
Euglenophyceae	*P. longicauda insecta*		*
	P. orbicularis		*
	Euglena acus		*
	E. oxyuris		*
	Trachelomonas superba superba		*
	Stombomonas fluviatilis		*
	S. verrucosa zmiewika		*
Chlorophyceae	*Pediastrum simplex simplex*	*	
Bacillariophyta	*Eunotia*	*	*
	Pinnularia	*	*
	Navicula	*	*

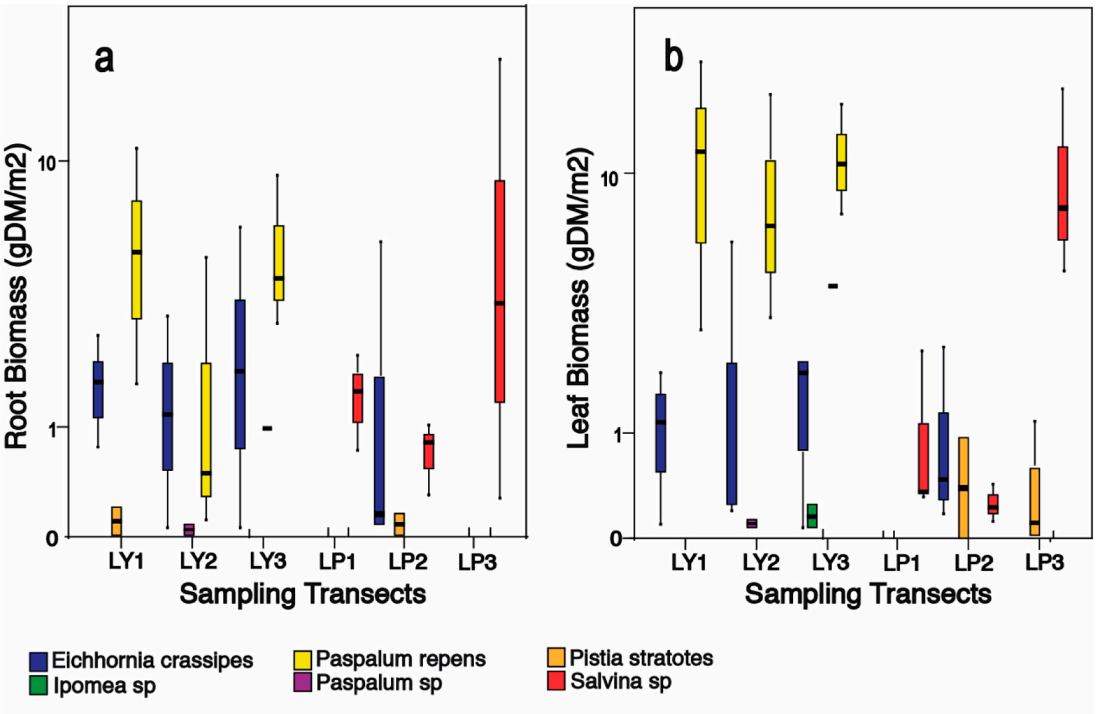

Figure 6. Root (a) and photosynthetic (b) biomass of the dominant aquatic plant species in lakes. (LP= Pacatúa Lake; LY = Yahuarcaca Lake). *Biomasa de raíz (a) y fotosintética (b) de las especies dominantes de plantas acuáticas en los lagos. (LP= Lago Pacatúa; LY = Lago Yahuarcaca).*

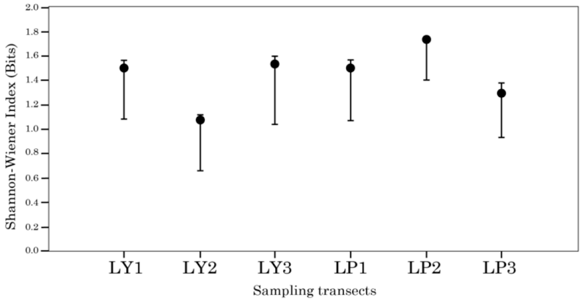

Figure 7. Diversity values (Shannon-Wiener Index) in the lakes. (LP= Pacatúa Lake; LY = Yahuarcaca Lake). *Valores de diversidad (Índice de Shannon-Wiener) en los lagos (LP= Lago Pacatúa; LY = Lago Yahuarcaca).*

DISCUSSION

Differences based on primary productivity subdivide floodplain areas into two categories: whitewater várzeas and blackwater igapos (Fittkau et al., 1975; Duque et al., 1997; Junk et al., 1984). Comparing our results with other environments associated to the Amazon River and the Colombian Amazon, we found values that differ in physical and chemical variables, such as water mineralization. The Colombian region of the Amazon River is an area of higher mineralization and productivity (Wissmar et al., 1981). Comparing Yahuarcaca Lake with Pacatúa Lake, the annual variation in conductivity generates differences in mineralization and pH, caused by the influence of the rivers (Amazon and Pacatúa) that may affect the lakes.

Ecological role of macrophytes in the lakes

In the flooded lakes of the Amazon River, macrophytes are one of the most important components of productivity (Junk & Howard-W, 1984). The littoral areas are characterized by a high variety, close to 387 species of herbaceous elements with 60 species of grass types in areas close to Manaus in Brazil (Junk & Piedade, 1994; Piedade et al., 2010). In Colombia, 27 species are recorded from several lakes (Duque, 1993), including the study area. The most common species reported for studies in Brazilian Amazon are *Oryza* spp., *Luziola spruceana*, *Echinochloa polystachya*, *Hymenachne amplexicaulis*, *Paspalum repens* and *Paspalum fasciculatum* (Junk & Howard-W, 1984), several of these are also reported for Pacatúa and Yahuarcaca Lakes (Ordóñez, 2002). Macrophytes adapt to changes in the flood pulse (Junk et al., 1989), likewise, but some species appear during ascending and high waters and disappear during the periods of minimum lake level, while others (grasses) live during the entire annual cycle (Fittkau et al., 1975). These macrophytes are type C4, which means that their productivity is very high (Piedade et al., 1991; Morrison et al., 2000). Silva et al. (2009) defines the productivity order associated to aquatic plants in the central Amazon to be related to *Echinochloa polystachya*, *Paspalum fasciculatum*, *Paspalum repens*, *Hymenachne amplexicaulis* and *Oryza perennis*. Piedade et al. (2010) indicate *Echinochloa polystachya* and *Paspalum fasciculatum* as being more important. C4 macrophytes have the highest productivity and work as "engineering species" (Jones et al., 1994), what makes them fundamental for Amazon lakes (Piedade et al., 2010). High productivity of littoral areas undoubtedly benefits the organisms associated with the macrophytes in the lakes.

The composition observed in the two lakes showed a first indication of the preference of certain plants to the particularities of each lake. In the case of the Yahuarcaca whitewater lake, the presence of the species *Salvinia* sp. or *Bidens* sp. was not observed, in Pacatúa Lake neither *Polygonium* sp. nor *Limnobium* sp. were observed.

In the Yahuarcaca Lake there is a dominance of *Pistia stratiotes* and *Eichhornia crassipes*, species characterized by rapid growth, related to their capacity to assimilate nutrients (Gao et al., 2016; Degaga, 2018). This characteristic explains the higher root biomass compared with same macrophytes species in Pacatúa Lake. It is worth noting that *P. stratiotes* takes advantage of highly nutritious and low-acid ecosystems (Dray & Center, 1989), conditions that occur in Yahuarcaca Lake. In contrast, *Salvinia* grows in favorable conditions and acidic waters (Owens et al., 2004; Wolff et al., 2012; Chapman et al., 2017).

Overall, the average biomass of root tissue was higher in the *varzea*-type than in the *igapó*-type lakes. This can be explained by the influence exerted by the Amazon River on varzea lakes. The main channel of the Amazon River is richer in nutrients water, and these supplied to the Yahuarcaca Lake. These nutrients can be used by macrophyte species generating a greater quantity of root biomass. However, blackwater igapós are nutrient poor.

Lake edges as a reservoir of diversity in these lakes

Amazonian lakes fed by the great rivers like the Amazon, contribute with the important development of floating mats of plants that generally have high productivity. Additionally, the annual hydrological dynamics with rises in the water level (expansion) and decreases (contraction) are an important evolutionary and productive engine. These attributes favor the growth of algae (Nuñez-A & Duque, 2001; Echenique et al., 2013), benthic algae (Castillo, 2000; Gantiva, 2000), bacteria and protozoa (Andramunio-A et al., 2018), macroinvertebrates (Bolivar, 2001), rotifers (Andrade et al., 2011) and fishes (Jiménez, 1995; Junk et al., 2007).

In synthesis, both the environmental factors, the habitat, as well as the taxonomic and functional properties of aquatic plants (de Menezes-B et al., 2014; Delatorre et al., 2019), contribute to the attributes of the ecological communities in the two lakes. Despite the differences in the conductivity and pH of the lakes, the diversity of the different groups of organisms did not vary substantially likely emphasizing the permanent role played by the littoral environments of the Amazonian lakes.

Conservation Implications

Threats to the aquatic ecosystems of the Amazon (climate change, drought, mining, eutrophication, and urbanization), may reduce the diversity of aquatic macrophytes in the future. Consequently, the conservation of littoral lake of Amazonian is fundamental to the ecology and the functioning of lakes.

On the other hand, aquatic plants are key organisms for the purpose of management and conservation, because they respond to local variations (Jones et al., 1994; Chappuis et al., 2014). Enhancing the knowledge of the composition and distribution of associated organisms is the first step for the preservation of aquatic flora and fauna and especially for the formulation of management plans and the design of protected areas (Valle-F, 2000) with the purpose of maintaining regional biodiversity.

As Castello et al. (2013) emphasize, it is imperative to change the conservation paradigm in the Amazon that focuses just on forests, for a broader vision focused on freshwater ecosystems that are irreplaceable components of the current and future functioning of the Amazon basin.

CONCLUSIONS

In the littoral zone of Yahuarcaca Lake, *Pistia stratiotes*, *Eichhornia crassipes* and *Paspalum repens* are dominant species, while *Salvinia auriculata* and *Eichhornia crassipes* are dominant in Pacatúa lake. In the two lakes the average photosynthetic biomass was higher than the root biomass. Both the photosynthetic and root biomass of Yahuarcaca were higher than in Pacatúa. Significant differences in macrophyte biomass were found between the lakes. The species with the highest biomass were floating species (pleustophytes) and those with the lowest biomass were the species rooted in the sediment (Helophytes). Although there is high species richness in the lakes, no significant differences were found in the diversity values of the organisms associated with aquatic plants.

ACKNOWLEDGMENTS

The authors thank to National University of Colombia (Bogotá and Amazonia campus) for the financial support for the project “Environmental and social appropriation of the urban and suburban wetlands of Leticia” (HERMES No. 47320). The authors would like to thank the two anonymous reviewers for their helpful commentaries and to Sergi Sabater C. (ICRA) and Thomas Defler for correcting and greatly improving the English text.

REFERENCES

Amoros, C & Bornette G (2002). Connectivity and biocomplexity in waterbodies of riverine floodplains. *Freshwater Biology*, 47(4), 761–776. DOI: 10.1046/j.1365-2427.2002.00905.x

Andrade-S, C., García-F, M., Rodríguez-M, C. A., Duque-E, S. R. & Realpe, E. (2011). Efectos de la fluctuación del nivel del agua sobre la estructura del ensamblaje de rotíferos en el lago largo (sistema Yahuarcaca - llanura de inundación del río Amazonas - Colombia). *Caldasia*, 33(2),519-537.

Andramunio-A, C. & Caraballo- G, P. (2012). Análisis de las relaciones tróficas en un lago de inundación de la Amazonia Colombiana. *Revista Colombiana de Ciencia Animal*, 4(1),102-120.

Andramunio-A, C. P., Caraballo-G, P., Duque-E, S. R., Solari, L. C. (2018). Cambios en la estructura de la comunidad perifítica en el sistema de lagos de Yahuarcaca, Amazonía colombiana. *Actualidades Biológicas*, 40 (109),139-161.

Aranguren, N. (2013). Diversidad ecológica de crustáceos planctónicos en sistemas lénticos colombianos. (Tesis doctoral. Universidad Nacional de Colombia. Bogotá, Colombia. 131 p.

Arias, M. E., Lee, E., Farinosi, F., Pereira, F. F., & Moorcroft, P. R. (2018). Decoupling the effects of deforestation and climate variability in the Tapajós river basin in the Brazilian Amazon. *Hidrological Processes*, 32(11), 1648-1663. DOI: 10.1002/hyp.11517

Armenteras, D., Rudas, G., Rodríguez, N., Sua, S., & Romero, M. (2007). Patterns and causes of deforestation in the Colombian Amazon. *Ecological Indicators*, 6, 353–368. DOI: 10.1016/j.ecolind.2005.03.014

Armenteras, D., Barreto, J. S., Tabor K., Molowny-H, R., & Retana, J. (2017). Changing patterns of fire occurrence in proximity to forest edges, roads and rivers between NW Amazonian countries. *Biogeosciences*, 14, 2755–2765. DOI: 10.5194/bg-14-2755-2017

Bohórquez, E. (2011). Métodos para la medición de flujos de dióxido de carbono y metano en zonas húmedas tropicales y variación de los volúmenes de agua en estos sistemas: Caso del lago Yahuarcaca, Amazonia colombiana. (Tesis de Pregrado. Universidad Nacional de Colombia, Sede Palmira. Colombia).

Bolívar, A. (2001). Estudio del aporte de biomasa de los macroinvertebrados asociados a macrófitos en sistemas fluviolacustres amazónicos (Leticia, Amazonas). (Tesis de pregrado. Universidad Javeriana. Bogotá. Colombia).

Bozelli, R. L., Thomaz, S. M., Padial, A. A., Lopes, P. M. & Bini, L. M. (2015). Floods decrease zooplankton beta diversity and environmental heterogeneity in an Amazonian floodplain system. *Hydrobiologia*, 753(1), 233-241. DOI: 10.1007/s10750-015-2209-1

Castello, L., McGrath, D. G., Hess, L. L., Coe, M. T., Lefebvre, P. A., Petry, P., Macedo, M. N., Reno, V. F. & Arantes, C. C. (2013). The vulnerability of Amazon freshwater ecosystems. *Conservation Letters*, 6(4), 217–229. DOI: 10.1111/conl.12008

Castillo, T. (2000). Productividad primaria de la comunidad fitoperifítica que coloniza sustratos artificiales en dos lagos de la Amazonia colombiana. (Tesis de maestría. Universidad Nacional de Colombia - Sede Bogotá. Colombia).

Chambers P. A, Lacoul P, Murphy K. J, Thomaz S. M. (2008). Global diversity of aquatic macrophytes in freshwater. *Hydrobiologia*, 595,9–26. DOI: 10.1007/s10750-007-9154-6

Chapman, D., Coetzee, J., Hussner, A., Netherlands, M., Newman, J., Pescott, O., Stiers, I., van Valkenburg, J., & Tanner, R. (2017). *Salvinia molesta* D.S. Mitch. Bulletin OEPP/EPPO Bulletin, 47, 1-6. DOI: 10.1111/epp.12428

Chappuis, E., Gacia, E., Ballesteros, E., (2014). Environmental factors explaining the distribution and diversity of vascular aquatic macrophytes in a highly heterogeneous Mediterranean region. *Aquatic Botany*, 113, 72–82. DOI: 10.1016/j.aquabot.2013.11.007

Correa S. B., Crampton, W. G. R., Chapman, L. J., & Albert J. S. (2008). A comparison of flooded forest and floating meadow fish assemblages in an upper Amazon floodplain. *Journal of Fish Biology*, 72(3), 629-644. DOI: 10.1111/j.1095-8649.2007.01752.x

Da Silva, S. C. A., & Padial, A. A. (2021). Macrophyte functional composition is stable across a strong environmental gradient of a Neotropical floodplain. *Acta Botanica Brasilica*, 35(1), 62-69. DOI: 10.1590/0102-33062020abb0348

Degaga, A. H. (2018). Water Hyacinth (*Eichhornia crassipes*): Biology and its Impacts on Ecosystem, Biodiversity, Economy and Human Well-being.

Delatorre, M., da Cuhna, M. L., Batista-B, R., Damasceno-J, G. A., & Ferreira, V. (2019). Trait-Environment Relationship of Aquatic Vegetation in a Tropical Pond Complex System. *Wetlands*. DOI: 10.1007/s13157-019-01189-0

De Menezes- B, C. M., Gómez, L. C., & Takeda, A. M (2014). Taxonomic and numeric structure of Chironomidae (Diptera) in different habitats of a Neotropical floodplain. Iheringia, *Série Zoologia*, Porto Alegre, 104(3),314-322. DOI: 10.1590/1678-476620141043314322

Dias, M. S., de Toledo, J. J., Jardim, M. M., de Figueiredo, F. O. G., de Oliveira, C. L., Gomes, A. C. S., & Zuanon, J. (2010). Congruence between fish and plant assemblages in drifting macrophyte rafts in Central Amazonia. *Hydrobiologia*, 661(1), 457-461. DOI: 10.1007/s10750-010-0529-8

Dray Jr, F. A & Center, T. D. (1989). Seed production by *Pistia stratiotes* L. (water lettuce) in the United States. *Aquatic Botany*, 33(1-2), 155-160. DOI: 10.1016/0304-3770(89)90029-6

Duarte, J. J. & Capador, R. (2006). Entomofauna acuática asociada a *Paspalum repens* (Poaceae) en los lagos I y IV del sistema lagunar Yahuarcaca (Leticia, Amazonas). (Tesis de grado. Universidad Pedagógica Nacional. Bogotá. Colombia). 94 p.

Duque, S. R. (1993). Inventario, caracterización y lineamentos para la conservación de los humedales en el Departamento del Amazonas. Universidad Nacional de Colombia – INDERENA, Leticia.

Duque, S. R. (1995). Euglenofitas pigmentadas de la Amazonia colombiana. *Revista Colombi-*

ana de Ciencias Exactas Físicas y Naturales, 19 (75),651-659.

Duque, S. R & Nuñez-A, M. (1997). Ficoflora de algunos ambientes acuáticos de la amazonia colombiana. *Caldasia*, 19(1-2), 279-264.

Duque, S. R., Ruiz, J. E., Gómez, J. & Roessler, E. (1997). Tipificación ecológica de ambientes acuáticos en el área del eje Apaporis - Tabatinga, Amazonia Colombiana. En: IGAC (ed.). Zonificación ambiental para el plan modelo colombo – brasilero (eje Apaporis - Tabatinga: PAT) (pag: 69-126). Editorial Linotipia. Santafé de Bogotá.

Echenique, R. O., Nuñez-A, M. & Duque S. R. (2013). Chlorococcales de la Amazonia Colombiana. II. *Boletín Sociedad Argentina de Botánica*, 48(3-4), 407-420.

Feng, D., Raoufi, R., Beighley, E., Melack, J., Goulding, M., Barthem, R. B., Venticinque, E., Cañas, C., Forsberg, B. & Sorribas, M. V. (2020). Future climate impacts on the hydrology of headwater streams in the Amazon River Basin: Implications for migratory goliath catfishes. *Hidrological Processes*, 34 (26),5402-5416. DOI: 10.1002/hyp.13952

Fittkau, E. J., Irmler, U., Junk, W. J., Reiss, F., & Schmidt, G. W. (1975). Productivity, Biomass, and Population Dynamics in Amazonian Water Bodies. *Ecological Studies*, 289-311.

Fu, H., Zhong, J., Yuan, G., Xie, P., Guo, L., Zhang, X., Xu, J., Li, Z., Zhang, M., Cao, T & Ni, L. (2014). Trait-based community assembly of aquatic macrophytes along a water depth gradient in a freshwater lake. *Freshwater Biology*, 59, 2462–2471. DOI: 10.1111/fwb.12443

Gantiva, J. (2000). Composición y estructura del fitoperifiton en el lago Yahuarcaca (Amazonia colombiana), durante dos períodos hidrológicos. (Tesis pregrado. Universidad Nacional de Colombia - Sede Bogotá. Colombia).

Gao, L., Li, B., & Jin, L. (2016). Can water hyacinth (*Eichhornia crassipes*) be controlled by reducing nitrogen and phosphorus pollution of water bodies? *Applied Ecology and Environmental Research*, 14(3), 77-91. DOI: 10.15666/aeer/1403_077091

Granado-L, C., Lobón-C, J. L. & Lima -C, R. M. A. (2007). Floodplain lake fish assemblages in the Amazon River: directions in conservation biology. *Biodiversity and Conservation*, 16(3), 679-692. DOI: 10.1007/s10531-005-3742-4

Jiménez, L. F. (1995). Estructura de la comunidad íctica en gramalotes del Trapecio Amazónico colombiano. (Tesis Universidad Nacional de Colombia. Santafé de Bogotá. Colombia).

Jones, C. G., Lawton, J. H. & Shachak, M. (1994). Organisms as ecosystem engineers. *Oikos*, 69, 373-386.

Junk, W. J. & Howard-Williams, C. (1984). Ecology of aquatic macrophytes in Amazonia. In: Sioli H. (ed.): *The Amazon: limnology and landscape ecology of a mighty tropical river and its basin*. (pag 269- 293), Dr. W. Junk Publishers, Dordrecht, Boston, Lancaster.

Junk, W. J., Bayley, P. B. & Sparks, R. E. (1989). The flood pulse concept in river-floodplain systems. *Canadian Special Publication of Fisheries and Aquatic Sciences*, 106, 110–127.

Junk, W. J. & Piedade, M. T. F. (1994). Species diversity and distribution of herbaceous plants in the floodplain of the middle Amazon. *Verhandlungen des Internationalen Verein Limnologie*, 25(3),1862-1865.

Junk, W. J., Mota -S, M. G. & Bayley, P. B. (2007). Freshwater fishes of the Amazon River basin: their biodiversity, fisheries, and habitats, *Aquatic Ecosystem Health & Management*, 10(2), 153-173. DOI: 10.1080/14634980701351023

Kluijver, A., Ning, J. L., Zhengwen, A., Jeppesen, E., Gulati, R. & Middelburg, J. (2015). Macrophytes and periphyton carbon subsidies to bacterioplankton and zooplankton in a shallow eutrophic lake in tropical China. *Limnology and Oceanography*, 60, 375-385. DOI: 10.1002/lno.10040

Latrubesse, E. M., Arima, E. Y., Dunne, T., Park, E., Baker V. R., d'Horta, F. M., Wight, Ch., Wittmann, F., Zuanon, J., Baker, P. A., Ribas, C. C., Norgaard, R. V., Filizola, N., Ansar, A., Flyvbjerg, B. & Stevaux, JC. (2017). Damming the rivers of the Amazon basin. *Nature*, 546,213-369. DOI: 10.1038/nature22333

Melack, J. M., Novo, E. M., Forsberg, B. R., Piedade, M. T., & Maurice, L. (2009). Floodplain ecosystem processes. *Amazonia & Global Change*, 525-541. DOI: 10.1029/2008GM000721

Montoya-M, Y & Aguirre-R, N. (2009). Estado del arte de la limnología de lagos de planos inundables. *Revista Gestión y Ambiente*, 12(3), 85-106.

Morison, J. I. L., Piedade, M.T. F., Müller, E., Long, S. P., Junk, W. J. & Jones, M. B. (2000). Very high productivity of the C4 aquatic grass Echinochloa polystachya in the Amazon floodplain confirmed by net ecosystem CO_2 flux measurements. *Oecologia*, 125,400-411. DOI: 10.1007/s004420000464

Núñez-A, M. & Duque, S. R. (1998). Chlorococcales (Algae: Chlorophyceae) found in aquatic environments of the Colombian Amazon basin. *Caldasia*, 20(1), 5-11.

Núñez-A, M. & Duque, S. R. (2001). Fitoplancton en algunos ríos y lagos de la Amazonia Colombiana. En Franky, C & Zárate C. (eds.). *Imani Mundo: Estudios en la Amazonia colombiana*. (pág. 305-335.) Unibiblos Bogotá.

Ordóñez, Y. (2002). Estructura de la comunidad de algas epífitas en dos macrófitas Paspalum repens y Polygonum densiflorum en los lagos de Yahuarcaca, Amazonas - Colombia. (Tesis de maestría. Universidad de los Andes, Bogotá. Colombia).

Owens, C. S., Smart, R. M. & Stewart, R. M. (2004). Low temperature limits of giant Salvinia. *Journal of Aquatic Plant Management*, 42, 91–94.

Palma, L., Núñez, M. & Duque, S. (2014). Efecto de la conectividad del río Amazonas sobre la física y química de las aguas en ambientes de la planicie aluvial de Colombia. *Revista Colombia Amazónica*, 7,129-148.

Palmer, M. (2010). Beyond infraestructure. Nature, 467, 533-535. DOI: 10.1038/467534a

Petry, P., Bayley, P. B., & Markle, D. F. (2003). Relationships between fish assemblages, macrophytes and environmental gradients in the Amazon River floodplain. *Journal of Fish Biology*, 63(3), 547-579. DOI: 10.1046/j.1095-8649.2003.00169.x

Piedade, M. T. F., Junk, W. J. & Long, S. P. (1991). The Productivity of the C4 Grass Echinochloa Polystachya on the Amazon Floodplain. *Ecology*, 72(4), 1456-1463. DOI: 10.2307/1941118

Piedade, M. T. F., Ferreira, C. S., & Franco, A. C. (2010). Estrategias reproductivas de la vegetación y sus respuestas al pulso de la inundación en las zonas inundables de la Amazonía Central. *Ecosistemas*, 19(1), 52-66. Recuperado a partir de https://www.revistaecosistemas.net/index.php/ecosistemas/article/view/55

Prieto, P, E. F. (2018). Ecología trófica de un lago de Varzea (Amazonas, Colombia) (PhD thesis, Universidad de Murcia. España).

Ríos-V, E. A., Piedade, M.T. F., Da Costa, J. G., Adeney, J. M., & Junk W. J. (2013). Chemistry of different Amazonian water types for river classification: a preliminary review. *Water & Society*, 2(178), 17-28. DOI: 10.2495/13WS 0021

Röpke, C. P., Ferreira, E. & Zuanon, J. (2013). Seasonal changes in the use of feeding resources by fish in stands of aquatic macrophytes in an Amazonian floodplain, Brazil. *Environmental Biology of Fishes*, 97(4), 401-414. DOI: 10.1007/s10641-013-0160-4

Rozo, M. G., Nogueira, C. R. A. & Soto-C, C. (2014). Remote sensing-based analysis of the planform changes in the Upper Amazon River over the period 1986-2006. *Journal of South American Earth Sciences*, 51, 28-44. DOI: 10.1016/j.jsames.2013.12.004

Salcedo-H, M. J., Duque, S. R., Palma, L., Torres-B, A., Montenegro, D., Bahamón, N., Lagos, L., Alvarado, L. F., Gómez, M., & Alba, A. P. (2012). Ecología del fitoplancton y dinámica hidrológica del sistema lagunar de Yahuarcaca, Amazonas, Colombia: análisis integrado de 16 años de estudio. *Mundo Amazónico*, 3,17-42.

Sioli, H. (1975). Tropical rivers as expressions of their terrestrial environments. In: Goley, F. & E. Medina (Eds.). *Tropical ecological system. Trend in terrestrial and aquatic research*. (Pag 275-288). Springer-Verlag. New York Inc.

Silva, T. S. F., Costa M. P. F., & Melack, J. M. (2009). Annual net primary production of macrophytes in the eastern Amazon floodplain. *Wetlands*, 29(2), 747-758. DOI: 10.1672/08-107.1

Silva, T. S., Costa, M. & Melack, J. M. (2010). Spatial and temporal variability of macrophyte cover and productivity in the eastern Amazon floodplain: A remote sensing approach. *Remote Sensing of Environment*, 114(9), 1998-2010. DOI: 10.1016/j.rse.2010.04.007.

Torres-Bejarano, A. M., Duque, S. R., & Caraballo-G, P. (2013). Heterogeneidad temporal y espacial de dos lagos de inundación en la Amazonia colombiana. *Actualidades Biológicas*, 35(98), 63-76.

Torres-Bejarano, A. M., Duque S. R. & Caraballo- G, P. (2014). Papel trófico del zooplancton a través del análisis de isótopos estables en un lago de inundación en la Amazonia Colombiana. *Caldasia*, 36(2), 331-344.

Val, A., de Almeida-Val., Vera, M., Fearnside, P. M., dos Santos, G. M., Piedade, M.T. F., Junk, W., Nozawa, S. R., da Silva, S. T., Dantas, F. A. (2017). Amazonia: Water Resources and Sustainability. In: C.E.D. Bicudo., J. G.Tundisi & Scheuenstuhl, M. C. B. Waters of Brazil. *Strategic Analisys*. 73-88 p.

Valle-F, L. (2000). Effects of flooding duration on species richness, floristic composition, and forest structure in river margin habitat in Amazonian blackwater floodplain forests: implications for future design of protected areas. *Biodiversity and Conservation*, 9, 1–14. DOI: 10.1023/A:1018385529531

Wesselingh, F. P, Hoorn, C., Kroonenberg, S. B., Antonelli, A., Lundberg, J.G., Vonhof, H. B & Hooghiemstra, H. (2010). On the origin of Amazonian landscapes and biodiversity: a synthesis. In: C. Hoorn, F. P. Wesselingh. *Amazonia: Landscape and Species Evolution: A Look into the Past*. Blackwell Publishing Ltd.

Wissmar, R. C., Richey, J. E., Stallard, R. F., & Edmond, J. M. (1981). Plankton metabolism and carbon processes in the Amazon River, its Tributaries, and floodplain waters, Peru-Brazil, May-June 1977. *Ecology*, 62(6), 1622-1633. DOI: 10.2307/1941517

Wetzel, R. G. & Likens, G. E. (2000). *Limnological Analyses*. 3rd. ed. Springer-Verlag, N. Y. inc.

Wolff, G., Pereira, G. C., Castro, E. M., Louzada, J., & Coelho, F. F. (2012). The use of *Salvinia auriculata* as a bioindicator in aquatic ecosystems: Biomass and structure dependent on the cadmium concentration. *Brazilian Journal of Biology*, 72, 71–77. DOI: 10.1590/S1519-69842012000100009