Connectivity of River Floodplains - The Case of Ibera Wetlands after 10,000 Years of Isolation from Parana River

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ABSTRACT

"Esteros del Ibera" is one of the most outstanding wetlands in South America, by its size (12,300 km^2) and biodiversity, the largest recorded at this latitude. Owing to this, it is recognized as a Ramsar Wetland of International Importance and as a National Park in Argentina. Esteros del Ibera is an "open-air laboratory" since its landscape was created by the lateral migration of the Parana River, leaving a vast paleo-alluvial fan from Argentina to Paraguay. Here, we compare the species richness in the landscapes of Ibera with that in the equivalent landscapes of the active course of Parana River in order to understand the causes of change in diversity patterns over the past 10,000 years. We found that the loss of connectivity with the pulse regime of Parana River led to an increase in specific complexity of Ibera biota. This likely resulted from the combination of a limited change in water quality, the belonging to the vast Amazon biogeographical domain, the natural niche amplitude of wetland species, and the self-designing capacity of the Ibera ecosystem.

INTRODUCTION

Understanding the spatial and temporal variability of wetlands at different time scales requires analyzing the underlying biogeochemical and ecological processes (Junk 1997; Tiner 2003; Neiff 2004; Dawidek and Ferencs 2016). There is consensus on the importance of connectivity between the river's course and the floodplain (Junk et al. 1989; Neiff 1990; Junk 1997; Melack and Forsberg 2001) as the variation in water level is responsible for a complex dynamic equilibrium in floodplain landscapes (Amoros and Bornette 2002; Thoms 2003; Bunn et al. 2006; Wiens 2009; Dawidek and Ferencs 2016). However, the effects of connectivity may be uneven for populations and communities (Neiff et al. 2009). Tockner et al. (1998) found that the connectivity of floodplain habitats to the river course showed diverging values for different organisms. While fish diversity was higher in the active Danube floodplain, amphibians showed greater diversity in floodplain habitats isolated from the river. Wiens (1989) pointed out that floodplain landscape should be observed from the perspective of organisms instead of from an anthropocentric viewpoint. Episodes of flooding change the proportion of aquatic and terrestrial landscapes, altering physico-chemical properties and biotic exchanges between water and land (Wiens 2002; McClain and Naiman 2008; Almeida and Melo 2009).

Current concepts apply according to the particular definition of connectivity adopted. According to the River Continuum Concept (Vannote et al. 1980), the idea of longitudinal connectivity prevails. The Serial Discontinuity Concept (Ward and Stanford 1995), used for single-channel rivers, states that the stability is varyingly influenced by terrestrial ecosystems. Wiens (2002) argued that connectivity has three dimensions, namely longitudinal, lateral and vertical. The vertical dimension of connectivity seems obvious, due to the turbulence of the flow. These three dimensions of connectivity as well as the pulse regime should be evaluated at different scales depending on the landscape interactions and the processes analyzed.

To the best of our knowledge, no previous study addressing the natural loss on connectivity of fluvial wetlands on the scale of thousands of years exists in the literature. We have an example from South America – for the Ibera wetland in northeastern Argentina, a former floodplain of the Parana River.

- While numerous studies addressed the limnological features of Parana River and Ibera wetland since the 1980s, basic questions remain:

- Was there a substitution of plant and animal species in Ibera as result of the isolation from the river's pulses?

- Has the complexity of the assemblages been modified at the level of species richness, or the spectrum of bioforms in the vegetation?

- Has the isolation of the Ibera wetland produced changes in resilience?

- Was the capture and accumulation of carbon in the Ibera wetland modified?

We believe that studies on a long-term scale (10,000 years) allow a better understanding of the resilience of biota, the functioning and organisation of the natural system. Here we provide a first attempt to address these issues based on available information. This knowledge is expected to prove useful for environmental management, biodiversity conservation, and for evaluating carbon sequestration and current problems of tropical wetlands. We propose that the collection of plant and animal species in Ibera, although it evolved in response to the new connectivity conditions (i.e., isolation from fluvial processes), preserved most of the species of the river domain.

FIGURE 1. Parana River and Esteros del Ibera (adapted from Poi et al. 2017). The blue line delimits the Esteros de Ibera.
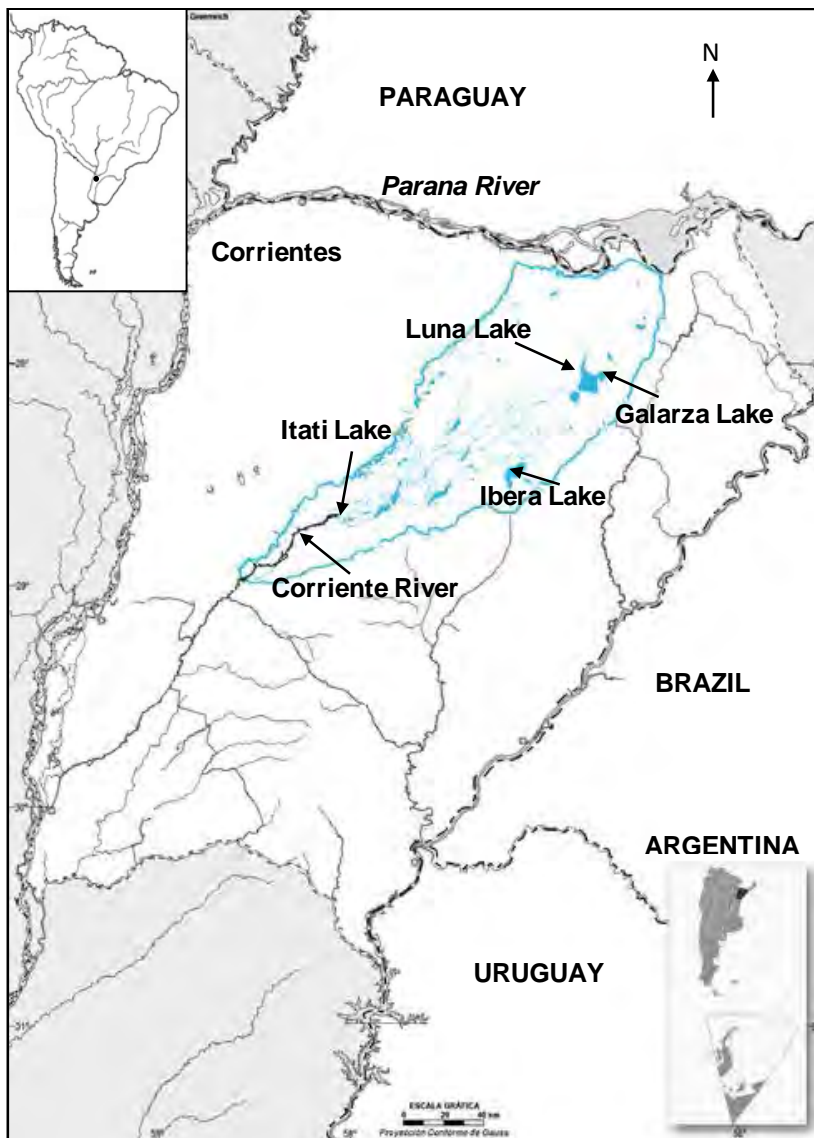
STUDY AREA

Our study area includes a portion of the Parana River in northeastern Argentina, its active floodplain and its former floodplain - the Ibera wetland (Figure 1). Parana River is anastomosed in this section and runs with a slope of 0.6-0.8 m/km on a bed of basalts covered by poorly sorted sands and clay that form bars and islands originating from the Pleistocene to the Holocene (Orfeo and Stevaux 2002). The hydrologic regime of Parana River is quite irregular. It includes a period of high waters in summer, with maximum levels in February-March, and a period of low waters, with minimum values between August and the beginning of September. The mean discharge is around of 18.000 m^3/s and peak flow around 65.000 m^3/s. In extraordinary floods, the entire floodplain is covered by a continuous mass of water, exposing only the treetops of the gallery forest on the floodplain.

Water of Parana River is, generally, neutral (pH 6.5-7.3), with low salinity (E.C. 40-90 μS.cm^{-1}), little calcium, abundant silica, and high turbidity and color during floods, due to loads of suspended solids reaching 100 mg L^{-1} (Bonetto 1986a).

During the Pliocene (5.3 to 2.5 million years ago), Ibera wetland was part of the extensive active floodplain of the Parana paleo-river. River water in Ibera flowed through braided channels separated by sand bars. Movements within the Earth's crust during the Cretaceous Period led to sweeping changes in the regional topography, modifying the slope and direction of surface run-off. Paleo-river Parana gradually migrated from the basin now occupied by Ibera to the current channel placed between Paraguay and Argentina at the end of Pleistocene roughly 10,000 years ago (Castellanos 1965; Iriondo, 1991; Popolizio 1977; 2004; Neiff 2004; Orfeo and Neiff 2008; Iwaszkiw et al. 2010). The ancient riverbed of Parana now known as the Ibera depression is now a basin of 30,000 km^2 fed by rainfall (Herbst and Santa Cruz 1999. Currently any excess water drains into the Parana River through Corriente River in the south of the Ibera system.

Its biological diversity is similar to that of the Parana River, in despite of the absence of a geographical connection between them. The Iberá region was a wide fluvial belt from the Pliocene with low sinuosity braided channels separated by sandy natural levees. This fluvial system related with the origin of the Parana River, deposited the extense Ituzaingó Formation (fine sandy sediments with iron compounds) with outcrops in the inner part of the studied area. During the Cre-

taceous Period, the epirogenic movements of the sub-surface basaltic blocks generated local changes of the slope, modifying the drainage direction. The Parana paleochannel gradually abandoned the central depression of Corrientes, changing to the present course that shows structural control. The fluvial belt was transformed into a series of interconnected waterbodies that receive the influence of local rains.

The local climate is Humid Subtropical, with rainfall of 1500 mm/yr, athough rainfall can exceed 2500 mm in years influenced by ENSO events (Poi et al. 2017). During most of the year, temperature typically ranges from 20ºC to 30ºC, with a maximum absolute temperature of 44ºC and minimum absolute temperature of 1ºC.

Rainfall has driven the geomorphology and hydrology of Ibera for millenia. No differences have been found in the pollen analyses in the whole area of study (Cuadrado and Neiff 1993), and [14]Carbon analyses gave an age of 3000 to 3700 years for the current landscape of Ibera and the older islands in Parana River. However, geomorphological and sedimentological studies agree that Ibera lost its connection with the Parana River 10,000 years ago. Therefore, the Ibera wetland represents a unique and long-lasting environment for the collection of Amazon species that settled there (Cabrera 1951; 1976; Cabrera and Willink 1973; Carnevali 2003; Zalocar de Domitrovic 2003).

It is important to note that the forms of life found in the Paleo Iberá date from 3000 to 4500 years BC (Cuadrado and Neiff, 1994; Morton, 2004; Pacella and Di Pasquo, 2020) and there are no records of plant or animal life between that date and the time of Iberá's disconnection from the river regime. Paleontologists still do not have an answer to this absence of preserved paleontological materials, although it is known that it was a period of very contrasting climatic changes. There is a significant gap in the geological and biological history of Corrientes Province from the recent Holocene to the late Pleistocene with the 40,000-year-old Toropí Formation. Unfortunately, the sequence of the Late Pleistocene and Early Holocene has not been preserved[1].

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TABLE 1. Information published about Ibera and Parana wetlands

Areas	Scientific contributions
Geology and Geomorphology	Castellanos (1965); Popolizio (1977; 1981); Herbst and Santa Cruz (1999); Iriondo (2004); Orfeo and Stevaux (2002); Orfeo and Neiff (2008)
Climatic Change effects	Neiff et al. (2011); Neiff and Neiff (2013); Úbeda et al. (2013)
Phytoplankton	Zalocar de Domitrovic (1990; 1992; 2003); Cózar et al. (2003); Zalocar de Domitrovic et al. (2007)
Zooplankton	Corrales de Jacobo and Frutos (1982); Frutos (2003; 2008; 2017); Cózar et al. (2003); Frutos et al. (2009)
Benthic invertebrates	Varela and Bechara (1981), Varela et al. (1983); Bechara and Varela (1990)
Invertebrates associated to aquatic plants	Poi de Neiff (2003); Poi de Neiff et al. (2006); Poi (2017)
Ichtyofauna	Bonetto et al. (1981); Bonetto (1986a,b); Jacobo (2002); Almirón et al. (2003), Casciotta et al. (2005); Neiff et al. (2009); Iwaszkiw et al. 2010; Contreras et al. (2017)
Vegetation	Cabrera (1976); Neiff (1986; 2003); Arbo and Tressens (2002); Carnevali (2003); Neiff and Casco (2017)
Wildlife and Biogeography	Cabrera and Willink (1973); Alvarez et al. (2003); Giraudo and Arzamendia (2003)
Ecology and Limnology	Cuadrado and Neiff (1993); Neiff et al. (1993); Canziani et al. (2003); Gantes and Torremorel (2005); Poi de Neiff (2003); Neiff (2004); Poi et al. (2017)

FIGURE 2. Satellite image of Parana River paleo-fan indicating the location of the different wetland groups identified in this study according to their connectivity to the Parana River. I: Isolated lakes and marshes; E: Eventually connected wetlands; C: Close connected wetlands.

APPROACH

Forests and aquatic communities of different individual sizes and turnover rates were analyzed in the present study, ranging from phytoplankton and zooplankton to benthos and fishes. Using our own information and findings published by others over the last decades (Table 1), we compared the two wetland systems: the current floodplain of Parana River and its paleo-floodplain (Ibera) that was disconnected from the river 10,000 years ago.

To detect changes at ecosystem level and their components, we use common indicators such as total number of species cited, total abundance, and dominant taxa, especially those marking functional differences. On this basis, we aim to identify which wetland "compartments" changed and which did not, how they were modified, and then try to explain "why". We analyze whether the causes of change lie in habitat variability, the breadth of niches, or other factors.

Based on our previous palynological and paleoecological research, we confirmed the fluvial origin of the current Ibera wetland system (Cuadrado and Neiff 1993; Morton 2004; Pacella and Di Pasquo 2020). In the present work, we

try to show the biotic divergence derived from the isolation of the fluvial dynamics. We think that the indicators used here can be easily replicated in other areas as they relate to water and nature conservation management projects.
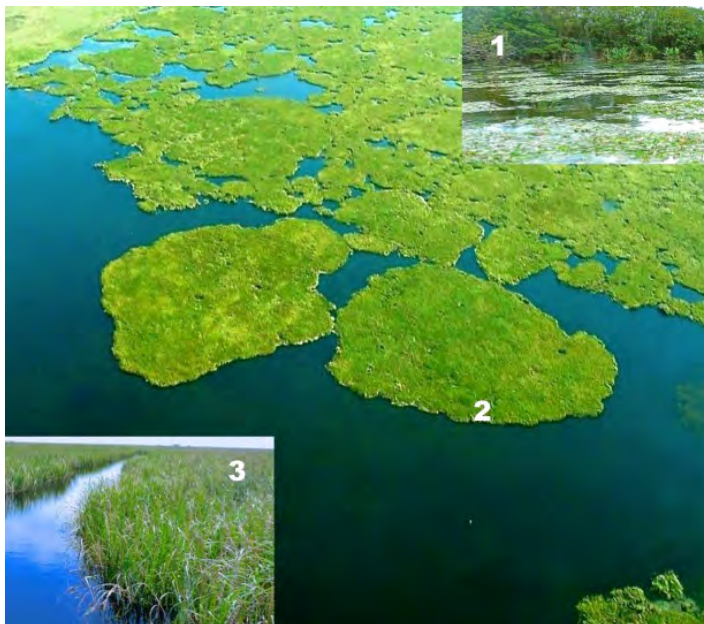
Finally, we will mention what knowledge is needed based on our analysis and when it is necessary to evaluate environmental impacts of wetland isolation on a long time scale.

WETLAND TYPES AND DISTRIBUTION

For this region, the Parana River ecosystems contains three types of wetlands based on differences in water supply and pulse regime (Figures 2-5): isolated, eventually connected, and close connected.

Isolated wetlands (Group I). They correspond to the Ibera lakes and are locally called as "esteros". Ibera lakes are located in the fluvial paleo flatland very close to the current course of the river in the Ibera region (27°30–29°00S, 56°25–58°00W). The lakes are large (8 to 95 km²) and surrounded by extensive marshes with sudds (floating islands; Figure 3). The water was relatively transparent, slightly acidic or neutral, the conductivity ranged between 9 and 52 μS.cm^{-1} and the dissolved oxygen concentration varied between 5.3 and 7.5 mg/l (Neiff et al. 2011). The lakes are articulated with each other through channels of varied development, to finally resolve into a diffuse drainage system in the headwaters of the Corrientes River. This river transports water and information from the Ibera to the Parana River but it is disconnected from the hydrological pulses of this river. The water fluctuation is exclusively due to the effect of local rainfall, which is relatively predictable on annual and interannual bases. Water fluctuations are smoother (less) than in the lakes connected to Parana River. Water flows are predominantly vertical, from and to the atmosphere with strong influence from the extensive vegetation (Neiff 2004). There are laminar flows between the marshes and the large lakes and vice versa that provide a buffer against the drastic changes in the water table. The wetlands included in the Ibera depression occupy 12,000 km². They are gently concave (0.10 to 2.5 m deep) with dense and continuous marsh vegetation covering about three quarters of total surface. General NE-SW runoff is very slow and connects with the large lakes (Galarza, Luna, Ibera, Fernández, Trin, Medina, and Itati) to finally discharge into the Parana River through the Corriente River (Figure 2). These large lakes are 2.5-4.0 m deep and the water level fluctutates from 0.5 to 0.7 m throughout the year. The western border of Ibera contains low hills of sand deposited by the Parana River and a gentle slope. Thousands of small lakes of 1-5 ha (Contreras et al. 2014) with a depth of 1.5-2.5 m are scattered across this area. Since their source of water, physicochemical characteristics, vegetation and fauna are similar to those in the large lakes of Ibera (Neiff 2004; Poi et al. 2017) they are included in Group I.

FIGURE 3. Examples of Group I (Isolated) wetlands: 1) peatland forest surrounding Galarza Lake, 2) sudds (floating islands) in Luna Lake, and 3) "esteros" landscape in Ibera Lake.

FIGURE 4. Examples of Group E (eventually connected) wetlands (from left to right): 1) marginal riparian forest, 2) bulrush marsh (*Schoenoplectus californicus, Cyperus giganteus*, and others) around the lakes, and 3) submerged meadows (*Egeria naias, Ceratophyllum demersum* and others) in lakes. Note: Inset E shows the geographic location of these wetlands. (Source of base image: Google Earth.)

FIGURE 5. Examples of Group C wetlands: 1) Parana River floodplain with shallow and connected wetlands, 2) oxbow lakes with *Pistia stratiotes* floating meadows, surronded by palm forests (in the distal area of the floodplain), and 3) meander scroll covered by dense floating meadow of water hyacinth (*Eichhornia crassipes*).

Eventually connected wetlands (Group E). These wetlands, including island levee lakes, are located on ancient riverine islands. The lakes are surrounded by marshes included in high riverine islands originated by the old Parana River. These islands are near Ituzaingó city (27°31'19"S, 56°42'55"W, Figure 4). They are situated almost 3 m above the river course hence they are only connected to the river by extraordinary floods, that is, once every ten years or more. These occasional flooding events trigger an exchange of information (nutrients, organisms, seeds, eggs, etc.) between the lakes and the Parana River. Most of the time, however, the lakes are fed by rainfall. The local landscape is very similar to the Ibera region, at least in the last 3,000 years (Cuadrado and Neiff 1993). Lake waters show very low concentrations of suspended solids and a black-brown color due to the high concentration of dissolved organic matter.

Close connected wetlands (C). These wetlands include shallow lakes, oxbow lakes and ponds that occur on recent lateral riverine islands that emerged in the last few centuries. They are part of the active Parana floodplain and fed by river overflows at least once a year. These waterbodies are located in the tract comprised from the wetlands in Group E to the south, at Itatí city (27°15'34"S, 58°14' 35"W; Figure 1). Silty-sandy sediments and "white waters" (with suspended silt, fine sand and clay) predominate. The most frequent vegetation is free floating and reed swamp plants. These lakes have a high turnover of plant and animal organisms with different phases of the river pulses. The water in these wetlands is similar to that of the Parana River.

PHYTOPLANKTON

Phytoplankton composition shows relevant differences between the Ibera lakes (Group I) and the lakes of the current Parana floodplain, with ten times more species in Ibera (796 species found by Zalocar de Domitrovic 2003) than in Parana floodplain. In wetlands of Group E and C, density and diversity of phytoplankton decrease during the connection periods in relation to the disturbance and dilution produced by the river water entering into the floodplain.

Chlorophyta is the most important group in Ibera lakes (Table 2, Group I), while Bacillariophyceae was more important in the floodplain lakes of the Parana River (Table 2, Groups E and C) during the connection period (Zalocar de Domitrovic et al. 2007).

Phytoplankton density in Ibera is highly dependent on the type of environment where the sample is taken, ranging from 100 to more than 4000 cells/ml. In wetlands of Parana River (Groups E and C), the density can vary between 1000-2020 (Zalocar de Domitrovic 1990; 1992) or, 588-2598 cells/ml (Zalocar de Domitrovic et al. 2007) depending on the hydrological phase considered (Table 2).

ZOOPLANKTON

In Group I, the species richness ranged from 7 to 41 (Frutos 2003, 2017), with the highest species richness in lakes with submerged vegetation. Zooplankton abundance increased in summer (50-450 individuals/L) and decreased in winter (20-350 individuals/L). Rotifers of the genera *Keratella*, *Ptygura*, and *Trichocerca* were always numerically dominant (80-95%). Cladocera and copepods had variable representation in the samples (Cózar et al. 2003; Frutos 2003, 2008). The low density of cladocera and copepods in the Ibera lakes is reportedly due to high fish predation

(Cózar et al. 2003). Spatial differences in species richness were less than 38% in the Ibera lakes and the variation between high rainfall and dry periods was only 6%. The rotifers *Lecane proiecta* and *Filinia* sp. were very abundant in severe droughts.

In Parana River floodplain (Group C, Table 3), zooplankton abundance is related to seasonal hydrological fluctuations, with higher concentration at the end of the low-water seasonal period (usually in spring) and lower density during the high-water peak, due to dilution effect. Density values are often between 1 and 75 individuals/L in the river proper (Paggi and José de Paggi 1974; Corrales 1979), although these values can double in floodplain lakes (Bonetto 1986a). Rotifers are numerically dominant at all times, and cladocerans and copepods alternate as subdominants, both in considerably low abundance. Despite the difference in diversity, the dominant species are similar to those in Ibera. For instance, the most abundant rotifers include *Keratella cochlearis*, *Trichocerca similis* and *Poliarthra trigla*. The main difference with the lakes of Group I is the occurrence of cladocerans (e.g., *Ceriodaphnia cornuta, Diaphanosoma bracyurum,* and *Eubosmina hagmanni*) and copepods (e.g., *Notodiaptomus incompositus* and *Mesocyclops longisetus*, among others) in wetlands of Group C

FIGURE 6. Daily water fluctuation at Ibera lakes (red) and Parana River (black) measured at Itatí city from 1970 to 2019. The straight black line shows the overflow level for Ibera lakes (black), while the dashed lines show overflow levels at Parana River – the lower line indicates overflow into Group C lakes, while the upper line represent the level at which lakes in Group E are flooded with water from the Parana River. The latter lakes are rarely overflowed.
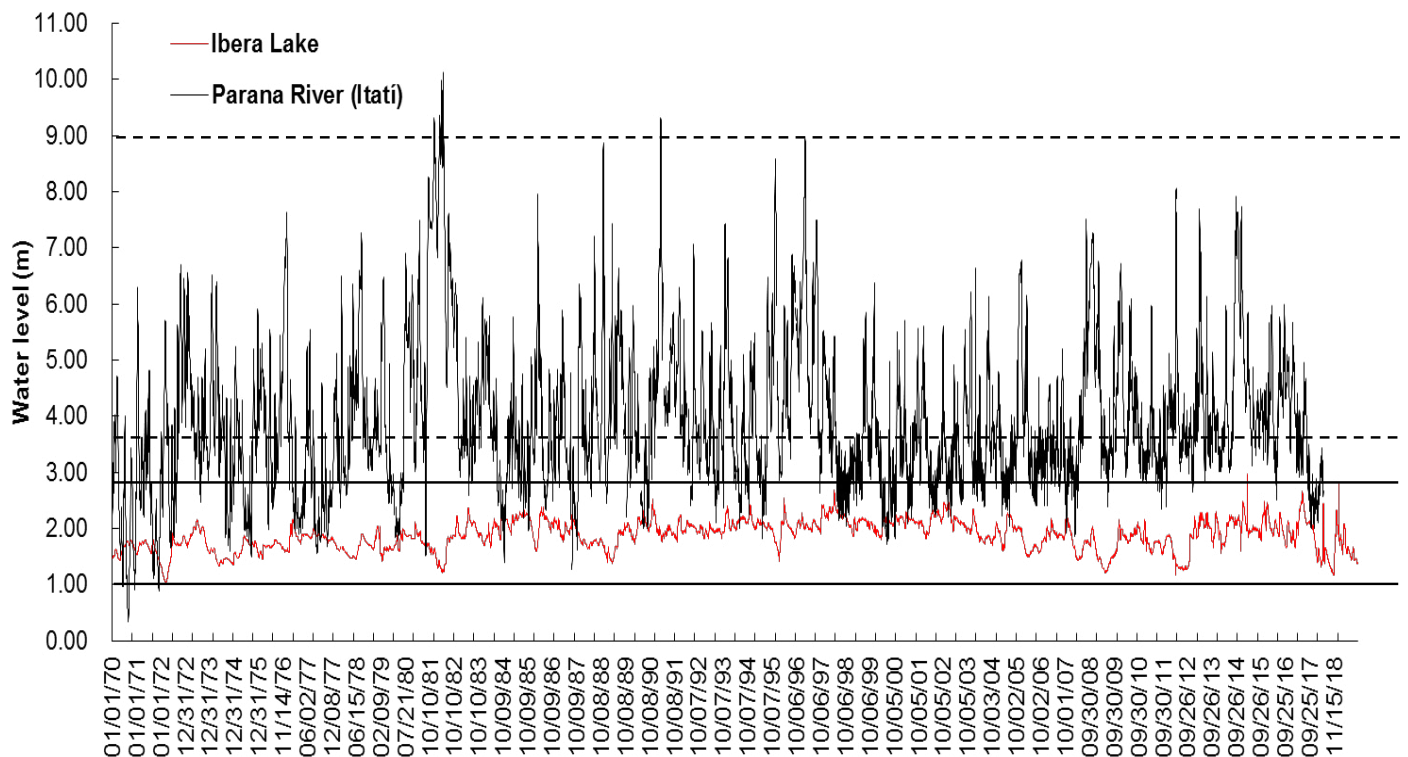
BENTHOS

The bottom substrate is an important factor influencing the benthic fauna. In Group I lakes, the bottom fauna is mainly determined by the presence of organic detritus. Since all lakes have a sandy floor, the limnetic area generally has a mobile bottom due to wind effect, so the benthic fauna is not very abundant. In the littoral zone, or in sites with dense submerged vegetation, however, the fauna is more abundant and shows a greater number of species (Varela et al. 1983; Bechara et al. 1990; Casciota et al. 2005). In Parana floodplain lakes (Groups E and C in this study), the bottom is sandy and dynamic due to the current. In the wetlands of Group C, 75 species were recorded, and in the wetlands of Group I (without connection to the river) 67 species are mentioned (Table 4). The abundance of fauna is much more variable in wetlands connected to the river course, which have a greater amount of Oligochaeta, while in Group I lakes (Ibera) Chironomidae is the dominant taxa, especially in sites with submerged vegetation.

VEGETATION

Of the 115 macrophytes cited for the floodplain of Parana River (Neiff 1986), only seven species are not found today in the wetlands of Ibera and they are members of the Podostemaceae - aquatic plants typically growing in the river rapids (habitats that do not exist in Ibera). These plants are only found in flowing waters and form a very specialized community known as "tachyrheophyton" (Neiff 1986).

In a more recent study (Neiff et al. 2011), 161 species were catalogued for the active Parana River floodplain. They also account for 40% of the total species reported for floating islands and marshland vegetation in Ibera (400 species) based on extensive surveys and historical records in herbaria (Arbo and Tressens 2002). The comparison is especially significant since the main environmental difference between Ibera (Group I) and Parana River floodplain (Groups E and C) is related to the regime of pulses, namely amplitude, frequency and predictability of the water level fluctuations.

Table 5 shows the biological spectrum of the vegetation for Groups I and C, for which information of similar amount and quality is available. The total number of species in both groups does not differ by much. The difference is the distribution of species richness in each plant bioform, which is due to the different geomorphology of both wetland groups and the variability of the pulse regime. In the Ibera depression (Group I) the habitat favors the development of emergent plants (helophytes) that have rhizomes; they dominate the marsh landscape. In Group C reed bed plants are successful because they are highly resilient to the irregular hydrological regime of the river (Neiff 1978, 1990). The number of free-floating plant species is similar

TABLE 2. Phytoplankton in Ibera lakes (grouped as I, isolated) and lakes of current Parana floodplain (grouped as E and C, eventually and closely connected respectively). Data of the taxonomic group (expressed as relative abundance (percentage of total abundance), species richness (total number of species) and abundance range (cells/ml).

Taxonomic group (%) or Other metric	I (isolation)	E and C (eventually and close connection)
Chlorophyta	65.7	49.90
Bacillariophyceae	11.93	26.95
Euglenophyta	11.80	6.50
Cyanophyta	6.91	8.51
Xanthophyceae	1.63	----
Chrysophyceae	0.75	1.63
Chryptophyta	0.75	6.51
Dinophyta	0.50	----
Relative abundance	100%	100%
Total abundance range (cells/ml)	140-4,033	588-2,598
Species richness	796	74

(Data Sources for Group I: Zalocar de Domitrovic 2003; for Group E: Zalocar de Domitrovic 1990 and 1992; and for Group C: Zalocar de Domitrovic 1992; Zalocar de Domitrovic et al. 2007.)

TABLE 3. Zooplankton in the lakes of Ibera (group I, isolation) and shallow lakes of current Parana floodplain (group C, closely connected). Data of the taxonomic group (expressed as a percentage of total abundance, %) and abundance (individuals/L).

Taxonomic group or Other metric	Zooplankton fauna in ecological groups according its connectivity	
	I (Isolated)	C (Closely connected)
Rotifers	79.36	63.5
Cladocerans	14.28	17.22
Copepods	6.36	19.28
Abundance (individuals/L)	20-450	2-88

(Data Sources: CECOAL 1981; Frutos 2017.)

in Groups I and C, and the species recorded are common to both (Table 5). However, this group of plants achieves greater coverage in the wetlands of active Parana floodplain, due to the periodic input of nutrients during the annual and more frequent floods (Carignan and Neiff 1992; Carignan et al. 1994). Although these plants can be found in Ibera, they never reach 1% coverage in the lakes. On the other hand, submerged plants form extensive meadows in the Ibera lakes, while their presence is sporadic and limited to Group E in wetlands of the Parana floodplain.

TABLE 4. Composition of lake bottom fauna in the study area. Data of the taxonomic group (expressed as a percentage of total abundance, %), species richness (total number of species) and abundance range (individuals/m2).

Taxonomic group or Other metric	Benthos fauna in ecological groups according its connectivity	
	I (Isolated)	**C** (Closely connected)
Oligochaeta	52	43
Chironomidae	41	54
Ostracoda	3	1
Amphipoda+Turbelaria + Acari + Mollusca	4	2
	100%	100%
Abundance (individuals/m²)	5,000-10,000	1,000-100,000
Species richness	67	75

(Data Sources: Varela et al. 1983; Bechara et al. 1990; Casciota et al. 2005; Zilli et al. 2008.)

TABLE 5. Plant bioforms in wetlands with different connectivity (expressed as species richness). Emerging plants are always emerging (bulrush, cattails); "Reed bed plants" have life forms adapted to flooded soil (floating rooted form) and to the emerging soil phase (emerging rooted form).

Vegetation in ecological groups according its connectivity		
	I (Isolated)	**C** (Closely connected)
Emergent (cattail type)	76	38
Reed bed plants	18	29
Free-floating plants	9	10
Rooted submerged plants	7	3
Free submerged plants	6	3
Rooted with floating leaves	6	6
Trees on mineral or peat soils	5	15
TOTAL (Species richness)	127	104

(Data Sources: Neiff 1986, 1990, 2003; Neiff and Casco 2017.)

The main difference of the vegetation of Ibera in relation to that of Parana River is the area occupied by herbaceous and woody vegetation. On the islands of Parana River, forests cover about 10 to 15%, while the forest area is less than 1% in Ibera where the vegetation is virtually all herbaceous. Of the 15 tree species growing in the Parana gallery forests, only five species are found in small patches on organic (peat) or mineral soils (sand) in Ibera (Figures 7 and 8). The architecture of these trees is very different when they grow in the peaty soils of Ibera: the trees are less than 8 m high and their roots are distributed radially in the first 20 cm of the soil to avoid anoxia (Neiff and Casco 2017).

Overall isolation of Ibera has created a different environment – a lentic one – that supports rooted hydrophytes, while the Parana River favors free-floating plants and floodplain forests (Figures 9 and 10).

INVERTEBRATES ASSOCIATED WITH AQUATIC VEGETATION
In extensive surveys that include several species of aquatic and marsh plants, 152 morph species of invertebrates have been recorded in Parana River floodplain (Poi de Neiff and Neiff 2006) and 98 in Ibera (Poi de Neiff 2003). In both surveys identical techniques were employed on seven of the most frequent aquatic plants in wetlands (*Eichhornia crassipes*, *Eichhornia azurea*, *Pistia stratiotes, Salvinia biloba*, *Azolla caroliniana*, *Lemna gibba*, and *Paspalum repens*) and on five species in lakes of the large Ibera wetland (*Typha latifolia*, *Leersia hexandra*, *E. azurea*, *Egeria najas*, and *Cabomba caroliniana*).

It is difficult to compare abundance and composition of invertebrates to investigate the effects of river connectivity, because different bioforms of macrophytes were dominant in the Parana floodpain versus the Ibera lakes. Each plant bioform (submerged rooted, free floating, or emergent rooted) provides a different habitat for invertebrates. In floodplain habitat, both density and species richness are influenced by horizontal flows to and from the river course. Surveys of a floodplain lake with high connectivity to the High Parana (Sirena

Lake with floating meadows dominated by *Paspalum repens* and *Salvina biloba*; Poi de Neiff 1981) and two Ibera lakes (Galarza and Trin with dominance of *S. biloba* and *Eichhornia azurea*; Poi de Neiff 2003) recorded 82 morph invertebrate species and 61, respectively. The comparison of similar types of habitats confirms a higher taxon richness in the lake connected to the river than the isolated lakes of Ibera. Depending on the site and the mesh size (Table 6) the overall abundance varied between 18,388 and 72,056 individuals/m² in Ibera and High Parana, respectively.

Macroinvertebrates (> 500 μm) associated with the aquatic plants were dominated by oligochaetes (mainly Naididae), insects and copepods (Table 6) both in High Parana and in Ibera. When smaller invertebrates (size greater than 125 μm) were included, copepods had the highest relative abundance in Parana and cladocerans in Ibera wetlands. Copepod species were also recorded in the plankton of the more connected lakes (Poi de Neiff 1981; Table 3). Cladocerans typically associated with vegetated areas, such as *Diaphanosoma*, *Euryalona*, *Oxyurella*, and *Euricercus*, were registered in Ibera (Poi de Neiff 2003). Mollusks and mites were poorly represented, especially in Ibera. At both sites, the composition of insects was similar. Larvae of two families Ceratopogonidae and non-biting midges (Chironomidae) were the most abundant insects. Air fronds of *S. biloba* supported semi-aquatic species such as the grasshopper *Paulinia acuminata* that has a high specificity to this host plant. There was a high number of genera of Coleoptera (*Helochares*, *Enochrus*, *Derallus*, *Tropisternus*, *Paracymus*, *Berosus*, *Hydrochus*, *Desmopachria*, *Laccophylus*, *Liodessus*, and *Hydrochanthus*) and Hemiptera (*Belostoma*, *Pelocoris*, *Neoplea*, and *Ranatra*) at both sites.

As described above, submerged plants form extensive meadows in the Ibera lakes. The freshwater prawn *Pseudopalaemon bouvieri* (Decapoda) is adapted to freshwater oligohaline waters covered by submerged vegetation. It is restricted to Ibera (Group I) and other water bodies of the Corrientes province (Lopretto 1995) fed by rain; this prawn has not been reported for the Parana River floodplain (Group C).

FISH FAUNA

According to Bonetto (1986b), the fish fauna of this area of the Parana River contains about 200 species and does not differ much from that of other large South American rivers. As in other floodplain rivers in South America, characiforms (e.g., toothed fish) comprise almost 40% of the river fish, with many species of *Tetragonoptera*. Silurids (catfish) make up 20% or more of the total taxa with some being quite large fish. For example, "surubí" (*Pseudoplatystoma coruscans*; a long-whiskered catfish) reaches 2 m in length and may weigh 120 kg.

FIGURE 7. Gallery forest of Parana River (Group C) near of Ituzaingó: 1) high, closed, continuous forest, up to 20 m tall, and 2) Trees spaced by 4-6 m each, DBH 0.30-0.90 m; shrubs and grasses are scarce or absent as a result of frequent flooding.

FIGURE 8. Peatland forest in Group I: 1) irregular, low forest, up to 8 m high, with species as the Parana riverine forest, although with less diversity, and 2) irregularly shaped trees separated by 4-6 m (DBH 0.15-0.30m) with dense herbaceous vegetation up to 2 m high.

Some assemblages of the fish fauna are considered "sedentary fauna" - smaller fishes that live in ponds and floodplain wetlands on the islands of Groups E and C. Another group of species is the potamodromous (migratory freshwater) fishes that as adults (1-2 m long) make extensive migrations upstream in spring and downstream in late summer (Bonetto 1986). Available information shows that potamodromous species have their immature states living in lakes of Group C (Bonetto 1986b; Casciota et al. 2005; Iwaszkiw 2010; Contreras et al. 2017). These species

TABLE 6. Relative abundance of the main taxa (%) and overall abundance expressed as individuals/m2 of macro- (>500μm) and meso-invertebrates (>125μm) in the Galarza, Sirena and Trin lakes. (Sources: Reconstructed from Poi de Neiff 1981, 2003 data)

	Ibera >500μm	Ibera >125μm	High Parana floodplain >500μm	High Parana floodplain >125μm
Oligochaeta	25	10.5	33	24
Cladocera	5	36	1.5	9
Copepoda	15	25	18.5	29
Amphipoda	1	0.5	4.5	26.5
Ostracoda	1	+	5	6.5
Insecta	45	18	31	18
Mollusca	+	+	1.5	0.5
Hidrachnidia	+	0.5	4	2.5
Other taxa	8	9.3	1	8
	100%	100%	100%	100%
Mean overall abundance individuals/m²	18,388	47,494	38,096	72,056

The + sign indicates that the taxa were present but in a very low percentage (<0.5)

include *Prochilodus lineatus, Pterodoras granulosus, Oxydoras kneri, Trachydoras paraguayensis, Serrasalmus spilopleura, S. marginatus, Pygocentrus nattereri, Hypostomus latifrons, Loricariichthys melanocheilus, Schizodon borelli, Leporinus lacustris, Pachyurus bonariensis, Triportheus paranensis, Odontesthes perugiae*, and *Potamotrygon motoro*. Some larger fish (*Salminus brasiliensis, Pseudoplatistoma coruscans, P. fasciatum,* and *Lucypimelodus pati*) of the Parana River are migrants each year during high flows that occasionally also go upstream via the Corriente River to the southern lakes of the Ibera (Itatí, Medina lakes); they are, however, not found in the isolated lakes of northern Ibera (Galarza, Luna, and Ibera lakes).

In Group E lakes, fishes associated with littoral, emergent or rooted floating vegetation are very common (Iwaszkiw et al. 2010). These fishes include *Poptella paraguayensis, Hyphessobrycon eques, Moenkausia* spp., *Acesrorhynchus pantaneiro, Hypostomus latifrons, Hypoptopoma inexpectata, Cichlasoma dimerus, Gymnogeophagus balzanii, Apistogramma* spp., *Crenicichla* spp., *Hoplerythrinus unitaeniatus, Hoplias malabaricus, Hoplosternum littorale*, and *Lepthoplosternum pectoral*. Many of these fish are also found in Group I where the most frequent fishes are *Hyphessobrycon eques, Moenkausia* spp., *Acesrorhynchus* sp., *Cichlasoma dimerus, Gymnogeophagus balzanii* and *Apistogramma* spp. The migratory fish of Parana River (*Salminus brasiliensis, Pseudoplatistoma coruscans, P. fasciatum; Lucypimelodus pati*) are of occasional presence, as they enter some lakes only during the extraordinary floods of Parana River.

As shown in Table 7, fish fauna appears similar across the region regardless of connection to the river. Although the percentage of characiforms is higher than that mentioned by Bonetto (1986b), the percentage of species included in the different taxonomic groups has a similar proportion in the three connectivity vari-

ants (Groups I, E and C). Of the 200 species reported by Bonetto (1986a) for the Upper Parana River, there are 111 species in Ibera (Casciotta et al. 2005). This total accounts for those upstream-migrating species found in lakes and streams of the southern Ibera basin (Group I) which are still linked to Parana River, at south of Itatí lake (Figure 2). However, in the lakes of northern Ibera, which are completely isolated from the pulses of the Parana River (lakes Galarza, Ibera and Luna), the same authors reported only 51 species, reflecting the impact of isolation from the river. The loss of connectivity of the wetlands of Ibera (Group I) has resulted in a reduction of the number of fish species to a third or a quarter and a loss of species of large migratory (potamodromous) fish that are restricted to the Parana River and its active floodplain wetlands.

COMPARISON OF FLUCTUATION REGIMES UNDER DIFFERENT CONNECTIVITY 10K YEAR LATER

Daily data on water level fluctuations have been collected since 1929. The fluctuation of the water level in wetlands of Group I has maintained a pulse regime as a consequence of the seasonality of the rains (Neiff 2004). The range of fluctuation between maximum and minimum absolutes was close to 1.5 m (Figure 6). The pulse rate in Parana River is very irregular and the extreme range of fluctuation between highs and lows is greater than 8 m historically. When the water level reaches around 3.5 m, Parana River spills over into many of the lakes classified as Group C, receiving new water and information. If the riverwater level exceeds 9 m line, the lakes of Group E are then flooded; since 1970, this happened in 1983 and again in 1992 (Figure 6).

The pulse regime in wetlands indicates horizontal movements of water from the river and allows some horizontal circulation of information (nutrients, eggs, seeds, plankton, etc.). Water turnover produces renewal in biotic assemblages through water circulation but also through change in habitat conditions (e.g., transparency, oxygen, and nutrients). In Group I (total isolation; at least for lakes at north of Itatí Lake) there is no exchange of information with the river, nor is there a washout effect, and less variability of the habitat is maintained, favoring the permanence of a greater number of species, with the taxonomic configuration of Amazonian origin, especially in the plankton, benthos, aquatic and marsh vegetation. Interestingly, the isolation did not manage to produce any endemic species

exclusive to Group I. Perhaps time (3,000-4,000 years) was not sufficient or the differences in environmental conditions (e.g., climate and water quality), except for flooding and soil saturation, were not significantly different between the Groups.

For some components of the system (Group I) such as phytoplankton, there was even an increase one order in magnitude in species richness, due to the lower rate of water renewal resulting from lower water level fluctuations. Despite this, there is no unique species in Group I. All the species recorded there were found in other environments in the Parana River basin.

In the Group I, more than 80% of the marsh area is occupied by plants with rhizomes (helophytes). This type of macro-vegetation in the lacustrine scenario is surprisingly not affected by flooding because the entire marsh with its peaty soils simply floats, rising with the increase in water level (i.e., floating islands called "embalsados") and falling when water levels decline. The marsh vegetation is sensitive to prolonged dry periods, yet since most of the species are helophytes with rhizomes that are able to root in the substrate, allowing the plants to persist during the dry period.

Most of the forests species in Parana River area are adapted to flooding periods. The floodplain trees lack adaptations for survival during periods of prolonged dryness. This fact likely explains both the small area of forest and its low species richness.

FIGURE 10. Lentic habitats of Ibera wetlands (Group I): 1) view of open water of the Ibera Lake and 2) marsh vegetation in littoral zone.

TABLE 7. Percentage of fish fauna represented by taxonomic group for the three wetland groups.

Taxonomic group	Fish fauna in ecological groups according its connectivity		
	I (Isolated)	**E** (Eventually connected)	**C** (Closely connected)
Characiforms	66	46	63
Siluriforms	15	27	23
Perciforms	10	16	9
Gymnotiforms	4	4	3
Cyprinodontiforms	4	4	-
Pleuronectiforms	-	2	1
Beloniforms	1	1	1
Total	100	100	100

(Data Sources: Casciota et al. 2005; Iwaszkiw 2010; Contreras et al. 2017.)

DISCUSSION

After 3,000-4,000 years, it appears that the natural system of Ibera has maintained a part of its original configuration and adapted some elements and processes to a new habitat configuration, according to its capacity of self-design (Mitsch and Jørgensen 2003; Odum and Odum 2003). Since then Ibera has remained isolated from the Parana River with changes in the biota due to dry period climate changes in the Lower and Middle Holocene, and a progressively wetter period in the last three or four thousand years in the recent Holocene. Previous studies have demonstrated that the Parana River fed Esteros del Ibera produced a similar pattern of the landscape that was maintained over at least three thousand years ago for the entire Group I (Neiff 2004; Orfeo and Neiff 2008; Pacella and Di Pasquo 2020). Although sedimentological and geomorphological evidence has shown that the Ibera marshes (Group I) were isolated from the Parana River 10,000 years ago (Castellanos 1965; Orfeo 2005; Orfeo and Neiff 2008; Orfeo et al. 2014), palynological information shows that the current landscape corresponds to a recent humid tropical phase from 3000-3500 years old (Cuadrado and Neiff 1994; Pacella and Di Pasquo 2020). The same authors agree that there is no pollen evidence of older landscapes. In this contribution we point out that, although Esteros del Ibera was isolated from the Parana River for 10,000 years, experiencing long periods of dry and wet weather, they were able to maintain a fairly similar assemblage of plant and animal species although not all species were able to adapt to the new conditions. While the Parana River in its north-south direction has served as a vector for the dispersal of genetic information from the Amazon region to Parana River and surrounding ecosystems (Cabrera and Willink 1973) and, currently, as an ecological corridor for many species (Bonetto 1986a; 1986b; Giraudo and Arzamendia 2003), it also appears to have functioned as a meridian barrier to the dispersal of some birds as *Thamnophilus caerulescens, Cyclarhis gujanensis, Thraupis sayaca, L. angustirostris*, and *Colaptes melanochloros* (Kopuchian et al. 2020). According to these authors, large rivers as Parana, function as a barrier to genetic flow in a transverse direction between both banks for some terrestrial birds, leading to population differentiation and, ultimately, allopathic speciation. Isolation changed the landscape pattern with greater variety of habitat (large lakes, marshes, peatland areas, running waters, and riparian forests), and greater species richness in some communities (plankton, benthos, and aquatic plants) and simplification in others (disappearance of migratory fish and some tree species from the riparian forests).

The increased complexity that arose in Ibera from isolation can be explained from different perspectives: 1) the biogeographical context, 2) the extent of the niche of the resident species, 3) the nature of change in the environment, and 4) the ability of the system for self-design. From the first point, we consider that the impact of loss of floodplain connectivity to the river becomes particularly significant if the Ibera wetland system constitutes a species-endemic area. For this system, all species belong to the vast Amazon domain, which has remained a biogeographic dispersal center even during the glacial period. Since the Amazon bioprovince is among the most species-rich in the world, the lack of endemics is not surprising especially when wetland species generally have very broad niches. Despite this, the ecology of the Ibera has changed completely as a consequence of its isolation, with a greater extension and variety of lentic environments, although frequent species have disappeared from the river habitat of the Parana.

The breadth of the ecological niches also plays a key role in the pathway for the ecological change. Since the Upper Pliocene, the climate of the subtropical zone of South America has gone through very contrasting wet and dry periods (Iriondo 2004), driving a selection of plants and animals adapted to the irregular water regimes and drastic changes in the configuration of their habitat. Thus, an important number of fluvial species remain in the Ibera lakes (Group I) after 10,000 years of isolation and there is no re-

cord of species unique to Ibera. An example of the ecological plasticity of the wetlands in the region occurred in 1995, when the Yacyretá Reservoir was constructed by covering the marshes of ancient islands in Parana River (Group E) with an eight-meter-thick water layer. After seven months of being completely submerged, extensive "islands" of several kilometers of peat rose to the surface. Only 22 days later, the herbaceous and shrubby vegetation had sprouted from the buds of the plants that were lying on the surface looking "dead". It is expected that the floating islands of Ibera formed in a similar manner, thereby maintaining most of the plants found on the former Parana floodplain.

Ibera has experienced strong climate disturbances in the past, and global climate change is expected to have an impact on the region. We studied the possible effects on the Ibera lakes (Group I) under two future climatic scenarios (A2 and B2) proposed by the International Panel on Climate Change (IPCC; Neiff and Neiff 2013; Ubeda et al. 2013). Our results suggest that even though a reduction in lakes size could have negative effects on biota, affecting richness species at local scale (Ubeda et al. 2013), the biodiversity will not be significantly affected (Neiff et al. 2011; Neiff and Neiff 2013; Ubeda et al. 2013). The vastness of Esteros of Ibera wetland complex, with its huge variety of habitat types and ample niches for most species make it highly resilient from the biodiversity standpoint. We believe that knowledge of the breadth of niches and the resilience of the landscape are key aspects for the scientific assessment of global climate change risks.

The pulse regime has become more regular, showing shorter range of water fluctuations after isolation from the river (Figures 6 and 11). Water in Ibera comes from rainwater that has been draining through sand for thousands of years. However, the quality of Ibera waters is not very different from the waters of Parana River: low electrical conductivity (EC), slightly acid to neutral pH, low nutrient content (especially nitrogen) and the ionic balance is of the type: $HCO_3-> Na+> Cl-> Mg+> SO_4-> Ca+> K+$. The water exchanges between the marshes and Ibera lakes determine the contribution of chemical substances from the organic soils (Neiff 2004; Ubeda et al. 2013; Poi et al. 2017).

Ibera's self-designed response to loss of connectivity is interesting. Nature has selected those tree species that can persist in water-saturated soils for long periods and go through prolonged dry spells - trees that can occupy loose, acidic soils (pH 4.5), such as peat or sandy soils with very low nutrient concentration. Ibera wet-

lands changed from a lotic system dominated by river overflows to a lentic system of lakes with fluctuations due to local rainfall patterns. It is evident, for example, that Ibera wetlands (in Group I) have a greater number of Cyperaceae and other helophytes unlike riverine wetlands (Group C) that have a greater occurrence of free-floating plants. The species of trees that live in Ibera are smaller than those on the islands of Parana River and have a highly developed root system in the shape of a big dish, which allows them to be supported on organic soils (peat). The process of self-design seems to have selected species that are extremely tolerant of climatic change, which means that the structure of the Ibera landscape and its biotic components are maintained with a low rate of change in spite of extreme climatic events of drought and extraordinary waterlogging (Neiff et al. 2011; Ubeda et al. 2013). Yet, at the same time, the lower variability of the water sheet and the lower flow rate has favored the increase of numerous species of plankton and benthos that take advantage of the microenvironments of the waters with different types of vegetation.

The P/R ratio is higher in Ibera wetlands than in the wetlands of Parana River resulting in the accumulation of organic matter in the Ibera marshes ("esteros") that surround the lakes. This organic matter, although slowly degraded, releases substances that are recycled by the vegetation of the lakes.

At least in the time scale of our analysis, biodiversity does not seem to be a powerful indicator to evaluate the effect of the

FIGURE 11. Seasonal changes in the water levels for the Ibera wetlands (Group I) and the floodplain of Parana River (Group C). The meters represent the vertical variability of the water sheet in each gauge station. In Group I the seasonal fluctuation is lower than in Group C because it responds to the variation of local rainfall that occurs over a wide area. The vegetation of the marsh increases the roughness of the surface and decreases the runoff speed.
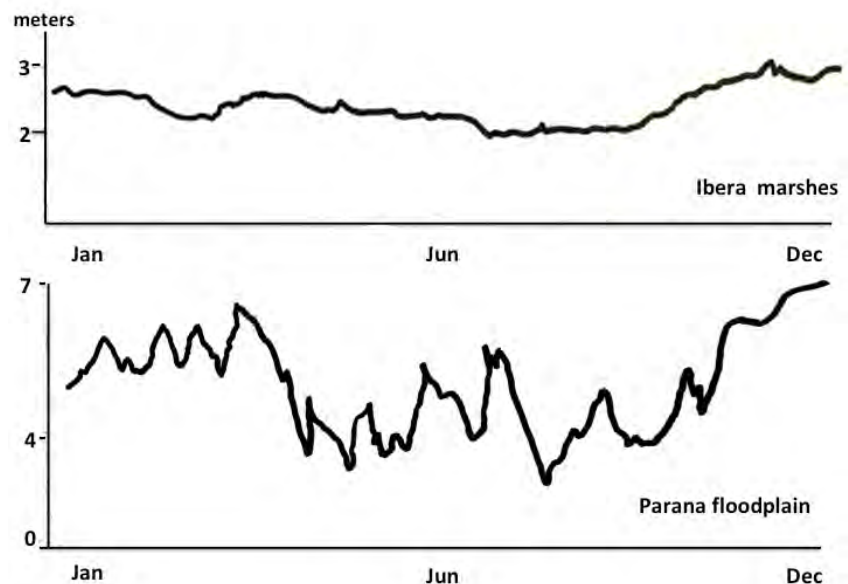
loss of connectivity. We know that all the biota of Parana River comes from the Amazon mega-basin where extensive floodplains have remained since geological-evolutionary times. So what biotic changes have occurred? The dominance of rotifers in the potamoplankton could be a consequence of isolation. Loss of connectivity with Parana River during Upper Pleistocene produced wetlands with an increase in different forms of organic matter, which is the favorable habitat for rotifers.

We think that the analysis of connectivity in terrestrial ecosystems based on topological relationships (as the spatial proximity of landscapes or as exchanges between populations or landscape gene banks) is inappropriate in river systems, due to differences in the response mechanisms of individual organisms and landscapes to changes to the pulse regime and variables associated with river connectivity. While in a terrestrial native forest the loss of landscape continuity is seen as fragmentation and increased distance between patches, in a floodplain of large rivers it is normal for the natural design of the landscape to include numerous patches of forest in the form of "galleries" or "patches" in the landscape matrix due to differences in the topographical position. This determines different eco-hydrological connectivity and, consequently, different assemblages of species, such as separate cells in the landscape.

We have a difficult challenge in the study of the niches (in Hutchinson`s sense) of plants and animals, in order to assess the relationships of river connectivity in different scales of time and space. Although the hydrological regime is one of the main characteristics that condition and define the functioning of aquatic systems, there are other attributes that determine the character of wetlands, as Tiner (2017) pointed

out. In the case of Ibera, there was a drastic change in the hydrological regime with a significant attenuation of the variability at interannual and seasonal scales (Figures 6 and 11). This change resulted in increased species richness for most biotic assemblages over the millennia time scale (plankton, benthos, and aquatic vegetation), except for forests where the number of species was less than ithe Parana gallery forests.

CONCLUSION

Generally, the connectivity of basin landscapes is analyzed on a current scale, or that of the recent past, without putting into a biogeographical context the events and changes that occur in the support system (physical-chemical environment), focusing the analysis on the effects of engineering works on the stability of riverine wetlands (e.g., damming of rivers or channelization of watercourses). Undoubtedly, any human action on the ecosystems produces disturbances that can alter the local, regional or global nature in different ways. Our challenge is to understand the impact of natural changes in connectivity between landscapes in a basin. We have compared a scenario in which the isolation of riverine wetlands occurred naturally 10,000 years ago. While the isolation of Ibera has clearly created a lentic environment on the former floodplain and a decline in fish species, this species segregation affected only the northern lakes of Ibera, because large migratory fish need to migrate in order to reproduce. We have not recorded the appearance of unique species typical of the new situation of isolation. Obviously, the absence of rapids in Ibera justifies the disappearance of typically rheophile species such as those of the Podostemaceae family cited for Parana River (Neiff 1986). Nor have we recorded in Ibera the presence of any invasive species that occur in the Parana River in recent decades, such as the golden mussel (*Limnoperna fortunei*) or the tilapia (*Tilapia niloticus*). We can think that the structure and functioning of the Ibera macro-wetland has retained its biodiversity and as a result of isolation, it will resist biological invasions, at least from riverine species. As a synthesis we present Figure 12 with the most notable changes in the long-term scale. ∎

FIGURE 12. Synopsis of the changes produced by the disconnection of "Esteros de Ibera" from the water regime of Parana River.
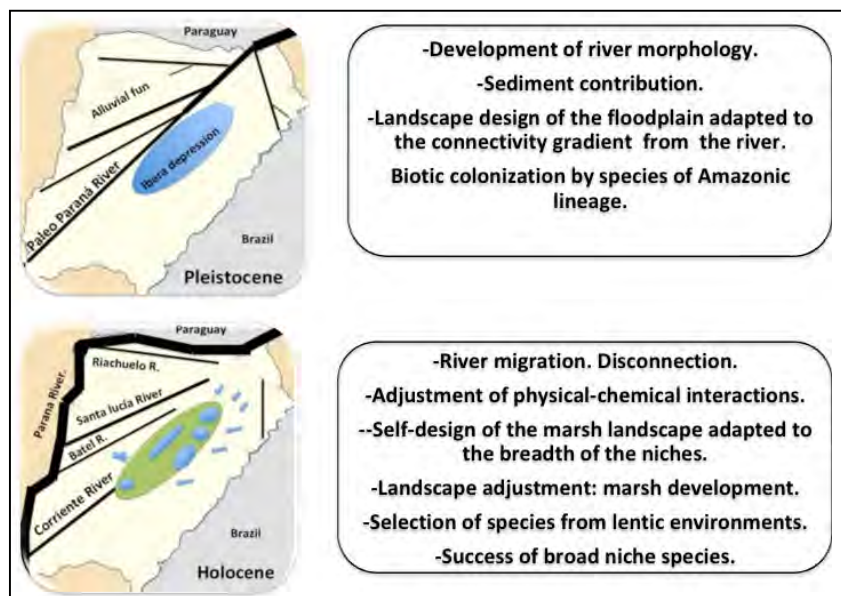
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