Fundación Miguel Lillo
Tucumán
Argentina

Ecohydrological signatures as a management tool for the Upper Paraná forests

Firmas ecohidrológicas como herramienta de gestión de los bosques del Alto Paraná

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Abstract

The species composition and distribution of the Upper Paraná River floodplain could be affected by changes in the hydrological regime. We assessed the influence of horizontal river flows on the distribution patterns of fluvial forests by determining the frequency of pulses and the number of flooding days across the topographic distribution of the most frequent tree species in a section of the Upper Paraná. Using density distribution curves as an indicator, based on the occurrence frequency of the dominant trees and its relationship with the hydrological regime, we established the response of the pioneer and plurispecific forests to a pulsing regime. This information was evaluated by comparing the hydrological level for the 1985-2015 period, obtaining attributes of the hydro-sedimentological pulse at different positions along the gradient. Our results show a significant overlap of the frequency distribution

➤ Ref. bibliográfica: Zambiasio, V. A.; Casco, S. L.; Aceñolaza, P. G.; Ordano, M. A.; Fontana, J. L. 2025. Ecohydrological signatures as a management tools for the Upper Paraná forests. *Lilloa* 62 (2): 697-719. doi: https://doi.org/10.30550/j.lil/1964
➤ Recibido: 3 de febrero 2025 – Aceptado: 20 de agosto 2025 – Publicado: 10 de noviembre 2025.
➤ URL de la revista: http://lilloa.lillo.org.ar
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curves in both forest types. They also indicate that over the 30-year study period, substantial changes occurred in the hydrological regime which affected the occurrence of species at each site and among sites within the study area. We conclude that the modifications to the hydrological dynamics strongly influence the biodiversity composition of the gallery forests by modifying the frequency, duration, and seasonality of the flooded soil/dry soil phases of the Paraná River.

Keywords: Ecohydrology; floodplain; riverine forests; topographic distribution; hydro-sedimentological pulse; large rivers.

Resumen

La composición y distribución de las especies en la llanura de inundación del río Paraná podrían verse afectadas por las alteraciones del régimen hidrológico. Evaluamos la influencia de los caudales fluviales horizontales sobre los patrones de distribución de los bosques fluviales determinando la frecuencia de pulsos y el número de días de inundación a través de la distribución topográfica de las especies arbóreas más frecuentes en una sección del Alto Paraná. Utilizando como indicador las curvas de distribución de densidades basadas en la frecuencia de los árboles dominantes y su relación con el régimen hidrológico, establecimos la respuesta de los bosques pionero y pluriespecífico al régimen de pulsos. Esta información fue evaluada comparando el nivel hidrológico para el periodo 1985-2015, obteniendo atributos del pulso hidrosedimentológico en diferentes posiciones del gradiente. Nuestros resultados muestran que hubo un solapamiento significativo de las curvas de distribución de frecuencias en ambos tipos de bosque. También indican que, en 30 años, hubo cambios significativos en el régimen hidrológico que afectaron la ocurrencia de especies en cada sitio y entre sitios en ambos límites del área de estudio. Concluimos que las modificaciones de la dinámica hidrológica influyen fuertemente en la composición de la biodiversidad del bosque de galería al modificar la frecuencia, duración y estacionalidad de las fases suelo inundado/suelo seco del río Paraná.

Palabras clave: Ecohidrología; llanura de inundación; bosques ribereños; distribución topográfica; pulso hidrosedimentológico; grandes ríos.

INTRODUCTION

Functioning and structure of large rivers with floodplain are conditioned by hydrologic dynamics (Junk *et al*., 1989; Neiff, 1990; Puckridge *et al*., 1998) that regulate biotic processes in riverine wetlands (Tabacchi *et al*., 1998). Riparian vegetation is a key element in river ecogeomorphological processes (Vesipa *et al*., 2016) as it interacts through several hydrological, geomorphological, and ecological processes. Together, these factors are critical to maintaining the ecological integrity of the ecosystem and its social relevance (Steiger *et al*., 2005, Corenblit *et al*., 2007; Perucca *et al*., 2007; Corenblit *et al*., 2015).

Floods and droughts are forcing factors in spatial distribution, abundance and composition of fluvial forest in the topographic gradient (Furness & Breen, 1980; Brinson *et al*., 1981; Rosales *et al*., 2001; Budke *et al*., 2008; Casco *et al*., 2010; De Assis & Wittmann, 2011; Marchetti & Aceñolaza, 2012; Stevaux *et al*., 2012; Marchetti *et al*., 2013; Marchetti *et al*., 2016, Brumnich *et al*., 2019).

Riparian vegetation is a key element in a number of processes that determine the ecogeomorphological features of the river landscape. In the Paraná River, species have different response to pulse regime attributes: frequency, intensity, tension, regularity, amplitude and seasonality of the flood and drought phases (Neiff, 1990, 1999) and the presence and permanence of each type of vegetation and each species is conditioned by them. The trees of the Paraná floodplain are eurytypical, meaning that they present a high ecological tolerance and can thrive in a wide range of environmental conditions, particularly in relation to variations in water availability (Neiff, 1990, 2005; Casco & Neiff, 2013; Zambiasio, 2020).

Hydrologic signatures are defined as metrics that quantify various aspects of flow response, such as magnitude, frequency, duration, temporality, and rate of change (McMillan, 2021). These metrics have been widely used to characterize hydrological conditions that determine ecological habitats (Olden & Poff, 2003). In this context, ecohydrological signatures refer to those hydrological characteristics that directly influence the distribution, abundance and dynamics of organisms (Neiff, 1990; Zambiasio, 2020), allowing the establishment of relationships between hydrological variability, for example, attributes of flood pulses and biological variability, such as the spatial distribution of trees. Each vegetation physiognomy has a characteristic hydrological signature that determines its presence, expansion or retraction in space and time. The alterations that occur in the runoff and in the time of permanence of water in and on the soil, determine the phases of drought and flood, which will be marked by changes in the vegetation and its associated elements.

Thus, the study of riparian forests can be used as a tool to understand the changes that occur in the river as a result of disturbances, to predict risks to biodiversity (Kuiper *et al.*, 2014), and to implement appropriate policy management (Dixon *et al.*, 2019; Neiff *et al.*, 2020; Henriques *et al.*, 2021).

The aim of this paper was to study the ecohydrological signature of eleven tree species in Upper Paraná River. We focus on (1) to analyze distributional patterns along a topographic gradient; and (2) to determine the frequency of pulses and the number of flooding days across topographic distribution. We hypothesized that each species, on the islands and river banks, has its distributional pattern conditioned by the temporal and spatial fluctuation of water level, which constitutes its ecohydrological signature. Therefore, we consider that the populations of each tree species in riparian forests present a hydrological signature characterized by their response to periods of flooding and drought.

METHODS

Study area

The Upper Paraná in the Argentine stretch covers from its confluence with the Iguazú River at Misiones city (25°35'31"S; 54°35'32"W, Fig. 1) to the confluence of Paraguay and Paraná Rivers at Corrientes city (27°17'27"S; 58°36'27"W, Fig. 1). In this section, the design of the course is anastomosed (Orfeo & Stevaux, 2002) with a narrow floodplain and interconnected channel enclosing large islands (Bonetto *et al.*, 1986).

The local climate is Subtropical Humid, with temperature ranges from 20°C to 30°C, and a maximum of 42°C and annual mean precipitation is 1670 mm (Bruniard, 1981; Barros *et al.*, 2008). The hydrological regime is irregular; with normal floods in summer, with maximum levels in February–March and a period of low waters, with minimum values between August and the beginning of September (Bonetto *et al.*, 1986; Depetris & Pasquini, 2007). When extraordinary floods occur island soils can be covered with more than 4 m of water (Neiff *et al.*, 2000).

Since the middle of the 20th century, numerous dams have been built in the Upper Paraná basin: 27 large dams (Taylor-Golder-Consular-Connal [TGCC], 1996) and 60 small reservoirs (Souza Filho *et al.*, 2004), the discharge regime changed, regulating the river hydrometric level (Rocha *et al.*, 1998, 2001; Souza Filho, 2009).

Although from the edaphic point of view there are two types of soils, red and sandy, it has been decided to divide the sands into two sub-regions: Paraná River sandy banks and sandy hills of old Paraná riverbeds that present different characteristics (Carnevali, 1994).

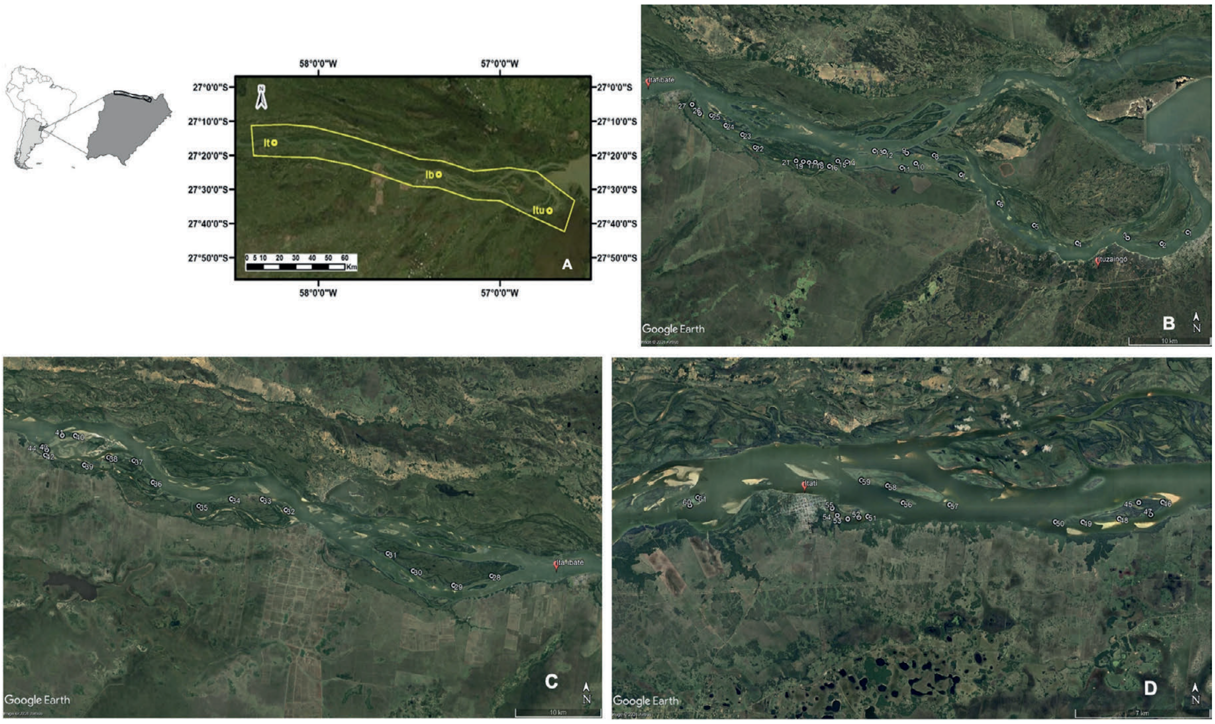

Fig. 1. Study area. Satellite image from Google Earth Pro. Letters indicate the sites of sampling; study sites are indicated by numbers. (A) Floodplain of the Upper Paraná River, Argentina: View of the Complexes in the Ituzaingó-Itatí transect. (B) Study site Ituzaingó (Itu), (C) Study site Itá ibaté (Ib), (D) Study site Itatí (It).

Fig. 1. Área de estudio. Imagen satelital de Google Earth Pro. Las letras indican los sitios de muestreo, y los sitios de estudio se indican con números. (A) Llanura de inundación del Alto Paraná, Argentina: se muestran los complejos en el transecto Ituzaingó-Itatí. (B) Sitio de estudio Ituzaingó (Itu). (C) Sitio de estudio Itá ibaté (Ib) (D) Sitio de estudio Itatí (It).

The Paraná riverbed, in the study area, has well-drained deep sandy and sandy loam soils, from which sandy, imperfectly drained ridges of varying depth fan out, interspersed with grasslands, marshes and lagoons (Carnevali, 1994). Fluvial deposits, which emerge in the eroded coasts, are silty sand to reddish clayey silt and interspersed among this material, white sand banks, also of fluvial sedimentation (Eskuche & Fontana, 1996). The islands soils are characterized by a very low degree of edaphization (Entisoils) and they are sediment deposits originated by river floods which generate layers of different texture (Orfeo, 1995). They have very low organic matter content and poor exchange capacity. They can remain submerged for weeks or months during which reducing conditions are produced (Neiff, 2005).

In the Paraná River, landscape complexes, systems and units can be distinguished according to the physiognomy and structure of the vegetation, soil types and response to hydrological conditions.

The Paranaense rainforest involves marginal hydrophilic forests that extend along the Paraná River and its tributaries, with species such as *Ocotea acutifolia* (Nees) Mez, *Nectandra angustifolia* (Schrad.) Nees & Mart., *Erythrina crista-galli* L., *Inga uruguensis* Hook. & Arn., *Pouteria salicifolia* (Spreng.) Radlk., *P. gardneriana* (A.DC.) Radlk., *S. humboldtiana*, *Sapium longifolium* (Müll.Arg.) Huber, *S. haematospermum* Müll.Arg., *Cecropia adenopus* Mart. ex Miq., *Croton urucurana* Baill., *Guadua angustifolia* Kunth and *G. paraguayana* Döll, among others (Neiff, 2005).

The forests of Upper Paraná occupy sand banks and marginal dikes in the meander scrolls. The pioneer forest is dominated by one species, generally *Salix humboldtiana* Willd, while the higher islands have communities with 10 or more species in two or three strata 12-15 m high. The forest with *Salix humboldtiana* (willow) grows on sandy soils on newly formed islands, in lower positions of the topographic gradient, whereas in marginal dikes of the meander scrolls, gallery forests pluri-specific and multistratified are distributed.

We recorded the occurrence of canopy trees defined as stems>10 cm DBH (diameter at breast height), on 61 sites (Fig. 1) distributed along a 175 km stretch of the river in islands and gallery forests in the main channel of the Paraná River during high and low water phase. The area includes the sites of: a) Ituzaingó (27°31'19"S; 56°42'55"W); b) Itá Ibaté (27°25'04"S; 57°24'43"W) and, c) Itatí (27°15'34"S; 58°14'35"W).

Eleven key species were selected: in the lower position of the topographic gradient, we recorded the occurrence of pioneer forest of *Salix humboldtiana* and in the highest positions of the topographic gradient, we selected the most frequent species that grow in mixed gallery forests (Neiff, 1986; Eskuche & Fontana, 1996; Eskuche, 2004; Neiff *et al*., 2020). *Albizia inundata* (Mart.) Barneby & J.W. Grimes, *Banara arguta* Briq., *Cecropia pachystachya* Trécul, *Celtis tala* Gillies ex Planch., *C. urucurana*, *Inga affinis* DC., *Myrcianthes pungens* (O.Berg) D. Legrand, *Nectandra angustifolia* (Schrad.) Nees & Mart. ex Nees, *Ocotea diospyrifolia* (Meisn.) Mez, *Peltophorum dubium* (Spreng.) Taub., and *S. haematospermum* are continuous and pluri-estratified tree formations with mature trees up to 12 m high and up to 90 cm of diameter at breast height.

Hydrological regime and Hydrosedimentological Pulse regime analysis

To analyze water level fluctuations of the Paraná River, we used the daily hydrometric information (1970-2015 period) provided by the National Division of Navigable Ways and Ports at Ituzaingó, Itá Ibaté and Itatí gauges.

We determined the topographical position of each site in which the trees grew in relation with the water level of Paraná River. Overflow level was related with the zero value of the nearest gauge: Ituzaingó 57.4 m a.s.l., Itá Ibaté 51.8 m a.s.l. and Itatí 45.1 m a.s.l. above sea level.

Because of each floodplain site where trees grow has different connectivity to river flow depending on its topographic position (Mitsch & Rust, 1984; Hughes, 1990; Neiff, 1990; Pringle, 2003; Turner *et al*., 2004; Johnson *et al*., 2012), we used Pulse 2.0 software (Neiff & Neiff, 2004), to calculate the hydrosedimentological pulse attributes: frequency of pulses, number of flooding days (potamophase) and number of emergent soil days (limnophase) based on the overflow level that represents the hydrological connectivity between each site of the floodplain and the river flow (Neiff, 1990; Neiff *et al*., 2020).

Species distribution and flooding days in the topographic gradient

As with the topographic position, the frequency and distribution of each species was characterized as a function of the number of days of flooding.

To analyze the frequency of each species in the topographic gradient we grouped the occurrence of trees at 10-cm height above water level intervals. This value was considered as a frequency. In order to characterize the distribution of densities based on frequencies in each topographic position, all data >0 were considered, is to say, only tree presence data. Otherwise (use of zeros) the calculation of the range would result in topographic positions that include absence (Zambiasio, 2020).

The value of the statistical median was used as an indicator of "ecological optimum" considering the reference value and the distance between the extremes of the distribution in each curve was interpreted as an expression of the "spatial niche" following Gleason (1926) developed later by Whittaker (1970), in this study refers to the range of ecohydrological conditions of each tree species that makes maximum development and growth in their natural environment.

Because to higher frequency of zeros we applied a Zero-inflated Generalized Linear Mixed Modeling using Poisson error structure (Bolker *et al*., 2008; Zuur *et al*., 2009), to determine the tree frequency variation in a function of forest type (pioneer or pluri-specific forests) and the topographic position. A zero inflated distribution allows accounting for a more realistic probability distribution (Zuur *et al*., 2009). In the models, the fixed structure considered the effects of zone, forest type and topographic position, and their interactions on tree species frequency. The model random structure considered the effects of site. The analyses were implemented in R 4.2.1 (R Development Core Team 2022) with the glmmTMB package (Brooks *et al*., 2017). R scripts are available upon request.

RESULTS

Hydrological regime and Hydrosedimentological Pulse regime analysis

Between 1970 and 2015, water level fluctuation range of Paraná River was comprised between 0.08 m (Itá Ibaté gauge) and 10.13 m (Itatí gauge). After Yacyretá dam operation (since 1994) the variability of maximum and minimum flows are attenuated, mainly in Ituzaingó and Itatí (Fig. 2).

Pulse attributes were different in the three gauges with the lowest frequency of pulses in Ituzaingó -189- and the highest in Itá Ibaté -374- (Fig. 2). The number of days with soil flooded was higher in Itatí (7511) and Ituzaingó recorded the highest number of days with emergent soil (13933).

Species distribution curves in topographic gradient

We differentiated the frequency distribution of tree species in the Paraná River by sector, sampling site and forest type, according to topographic position. Pioneer forest is represented by *S. humboldtiana* and/or *T. integrifolia*; and mixed or multi-species forest is represented by *A. inundata, N. angustifolia, O. diospyrifolia, C. pachystachya, B. arguta, I. uruguensis, C. urucurana, P. dubium*, for each sector of the river, the sites are ordered from left to right, upstream to downstream, respectively (Fig. 3).

S. humboldtiana trees were found between 48.3 and 59.3 m a.s.l. (Fig. 4), showing leptokurtic distribution curves in Ituzaingó (58.5 and 59.3 m a.s.l.) and in Itá Ibaté (53.6 and 55.4 m a.s.l.), while in Itatí their distribution was less restricted, reflecting a platykurtic curve (48.4 and 49.9 m a.s.l.).

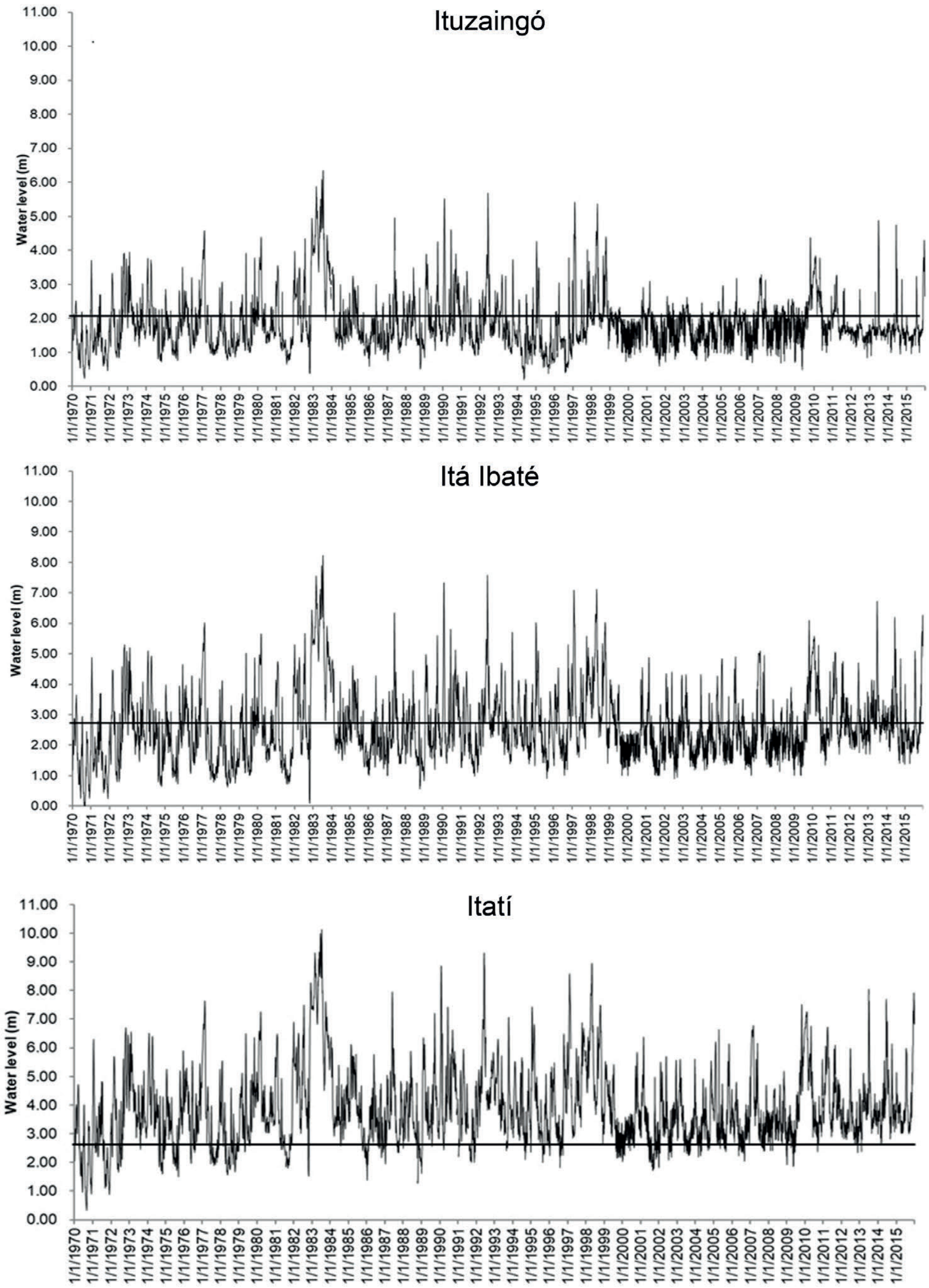

Fig. 2. Water level fluctuations (m) of the Upper Paraná River at the tree sites: Ituzaingó gauge, Km 1454 from the Atlantic Ocean. Itá Ibaté gauge, at Km 1380. Itatí gauge at Km 1279. The grey line: overflow level (m).

Fig. 2. Fluctuaciones del nivel del agua (m) del Alto Paraná en los siguientes puntos: Estación Ituzaingó, km 1454 desde el Océano Atlántico. Estación Itá Ibaté, km 1380. Estación Itatí, km 1279. Línea Gris: nivel de desbordamiento (m).

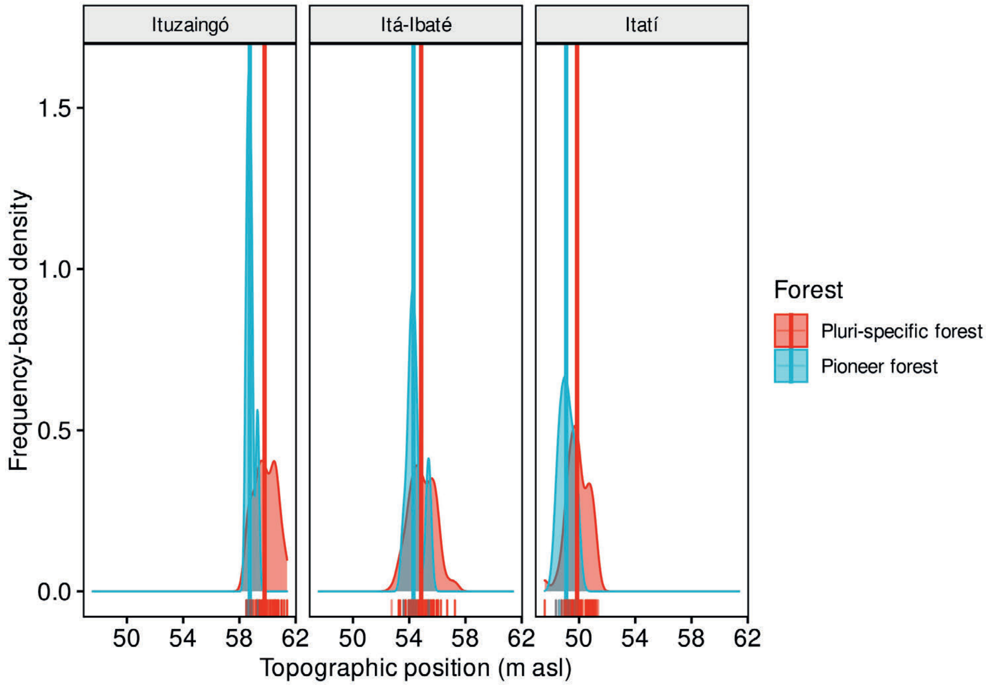

Fig. 3. Frequency distribution according to topographic position of tree species of the Paraná River by sampling site and forest type.

Fig. 3. Distribución de frecuencias de especies arbóreas del río Paraná por sitio de muestreo y tipo de bosque, de acuerdo a la posición topográfica.

In the plurispecific forests most species have their population medians in different topographic positions (Fig. 4). *B. arguta*, presented a similar distribution range in Ituzaingó, Itá Ibaté and Itatí (between 49.1 and 60.4 m a.s.l.); *C. urucurana* in Ituzaingó presented a leptokurtic distribution curve, with a narrower range between 58.7 and 59.4m a.s.l. Curves distribution of *P. dubium* were different in the three sites, showing narrower range in Itatí (49.8 and 51.1 m a.s.l.) and Itá Ibaté (54.7 and 56.0 m a.s.l.) than in Ituzaingó (59.3 and 61.3 m a.s.l.). *S. haematospermum* was the species with wider distribution range (between 47.5 and 60.7 m a.s.l.).

Species distribution curves and number of flooded days

Because all species are tolerant to different dry or flooded soil conditions, a significant overlap of the distribution curves of both forest types was observed; however, willow forest is flooded longer than the pluriespecif forest (Fig. 5).

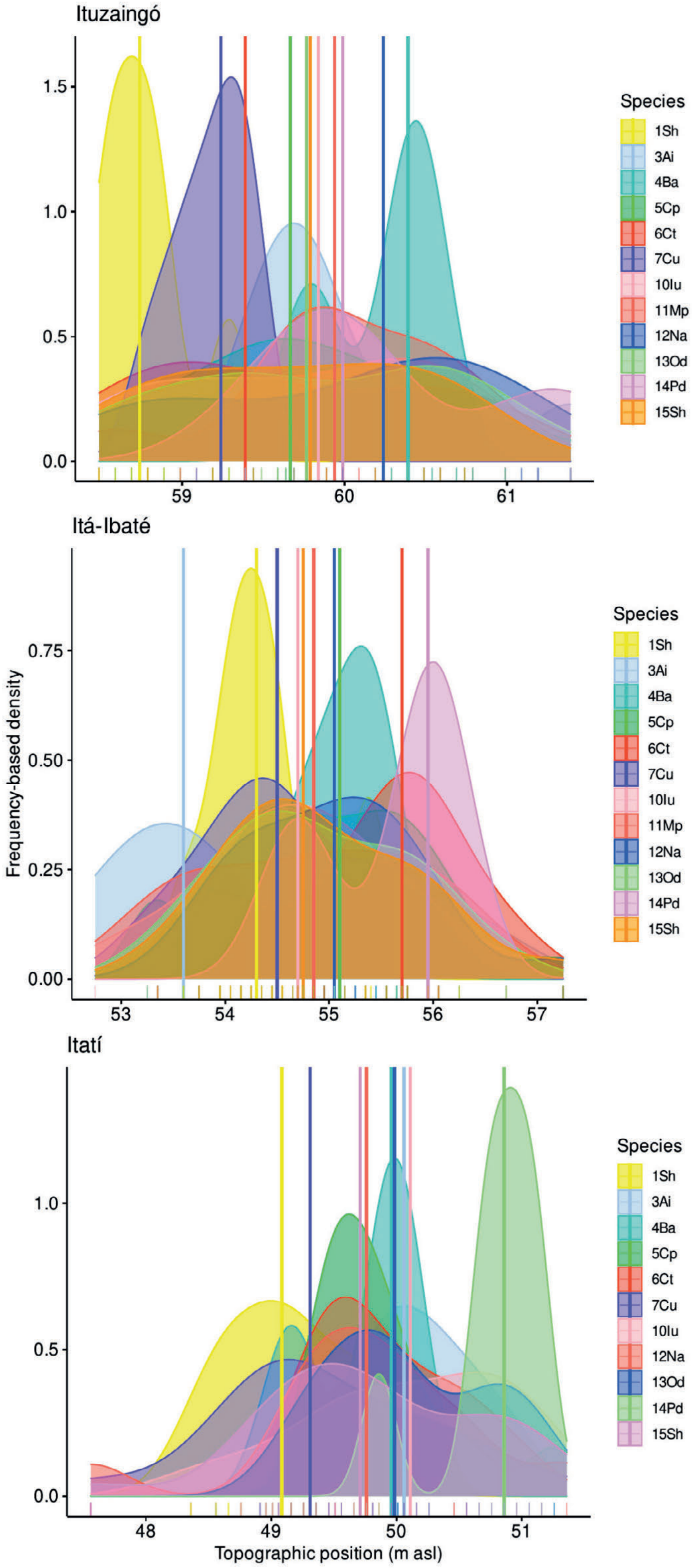

Fig. 4. Frequency distribution according to topographic position of tree species by sampling site (Ituzaingó, Itá Ibaté, Itatí) and species. The vertical line represents the mean density for each species at its corresponding topographic position. 1Sh: *S. humboldtiana*; 3Ai: *A. inundata*; 4Ba: *B. arguta*; 5Cp: *C. pachystachya*; 6Ct: *C. tala*; 7Cu: *C. urucurana*; 10Iu: *I. uraguensis*; 12Na: *N. angustifolia*; 13Od: *O. diospyrifolia*; 14Pd: *P. dubium*; 15Sh: *S. haematospermum*.

Fig. 4. Distribución de frecuencias de especies arbóreas por sitio de muestreo (Ituzaingó, Itá Ibaté, Itatí) y especie según su posición topográfica. La línea vertical representa la densidad media de la especie correspondiente según su posición topográfica. 1Sh: *S. humboldtiana*; 3Ai: *A. inundata*; 4Ba: *B. arguta*; 5Cp: *C. pachystachya*; 6Ct: *C. tala*; 7Cu: C. urucurana; 10Iu: I. uraguensis; 12Na: *N. angustifolia*; 13Od: *O. diospyrifolia*; 14Pd: *P. dubium*; 15Sh: *S. haematospermum*.

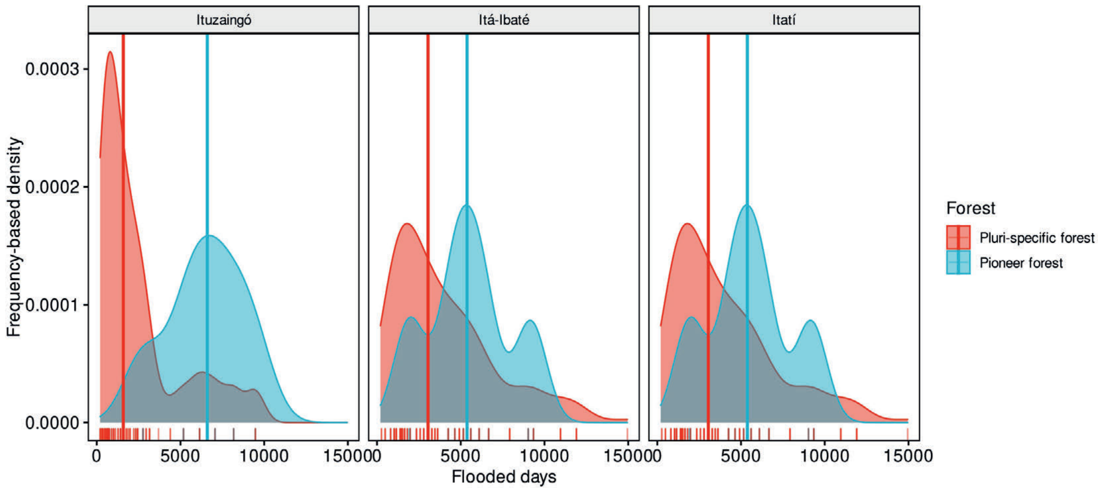

Fig. 5. Frequency distribution according to number of flooded days of tree species of the Paraná River by sampling site (Ituzaingó, Itá Ibaté, Itatí) and forest type.

Fig. 5. Distribución de frecuencia según número de días de inundación, de las especies arbóreas del río Paraná, por sitio de muestreo (Ituzaingó, Itá Ibaté, Itatí) y tipo de bosque.

Salix humboldtiana, *A. inundata* and *C. urucurana* were the species that could be found in soils with the highest number of flooded days (between 205 and 9474) in all the sampling sites (Fig. 6).

The number of days of flooded soil in which each species has most of its population varies in a very wide range, between 5000 and 11909 days (Fig. 7 and Fig. 8).

When the frequency-based density curves related to days of flooded soil of *S. humboldtiana* in the three sites analyzed were plotted on the topographic gradient, the median distribution on the curve was 5601 days (Fig. 7A).

A. inundata (Fig. 7B) was found in soils that were flooded 11909 days and it median was registered in 1760 days.

Species curves were analyzed based on frequency of days with flooded soil and the median in the different places studied for the following species: *B. arguta* (Fig. 7C) the median was 2793; *C. pachystachya* was 2374 and *C. urucurana* the median was 3687 (Fig. 7D, F); while *C. tala* was recorded with a median equal to 1586 and remaining in sites with flooded soil between 358 days and 9474 days (Fig. 7E).

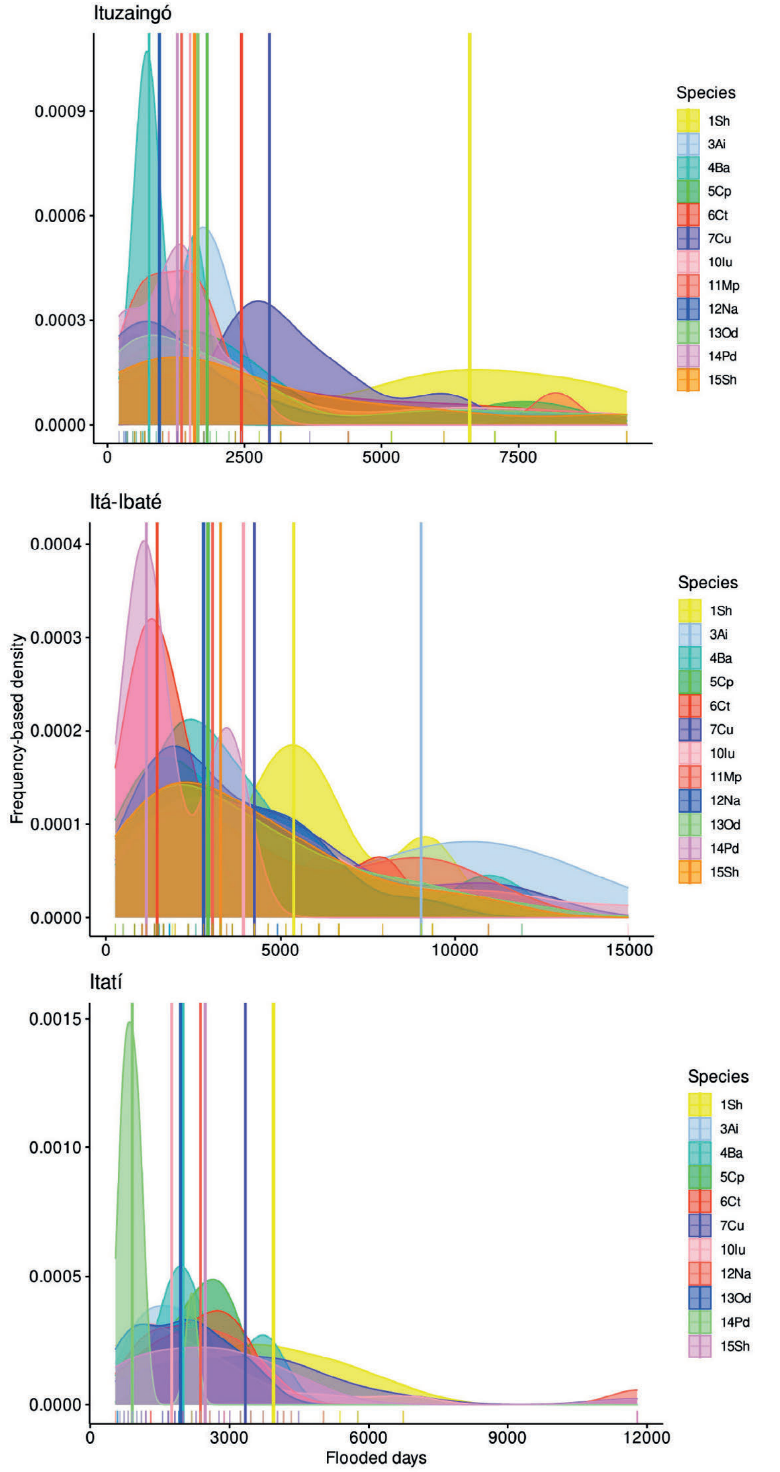

Fig. 6. Frequency distribution of tree species by sampling site and species, as a function of the number of days of flooding between 1970 and 2015. The vertical line represents the mean number of days of flooding for the corresponding species. 1Sh: *S. humboldtiana*; 3Ai: *A. inundata*; 4Ba: *B. arguta*; 5Cp: *C. pachystachya*; 6Ct: *C. tala*; 7Cu: *C. urucurana*; 10Iu: *I. uraguensis*; 12Na: *N. angustifolia*; 13Od: *O. diospyrifolia*; 14Pd: *P. dubium*; 15Sh: *S. haematospermum*

Fig. 6. Distribución de frecuencias de especies arbóreas por sitio de muestreo y especie, en función del número de días de inundación entre 1970 y 2015. La línea vertical rep-

resenta la mediana del número de días de inundación para la especie correspondiente. 1Sh: *S. humboldtiana*; 3Ai: *A. inundata*; 4Ba: *B. arguta*; 5Cp: *C. pachystachya*; 6Ct: *C. tala*; 7Cu: *C. urucurana*; 10Iu: *I. uraguensis*; 12Na: *N. angustifolia*; 13Od: *O. diospyrifolia*; 14Pd: *P. dubium*; 15Sh: *S. haematospermum.*

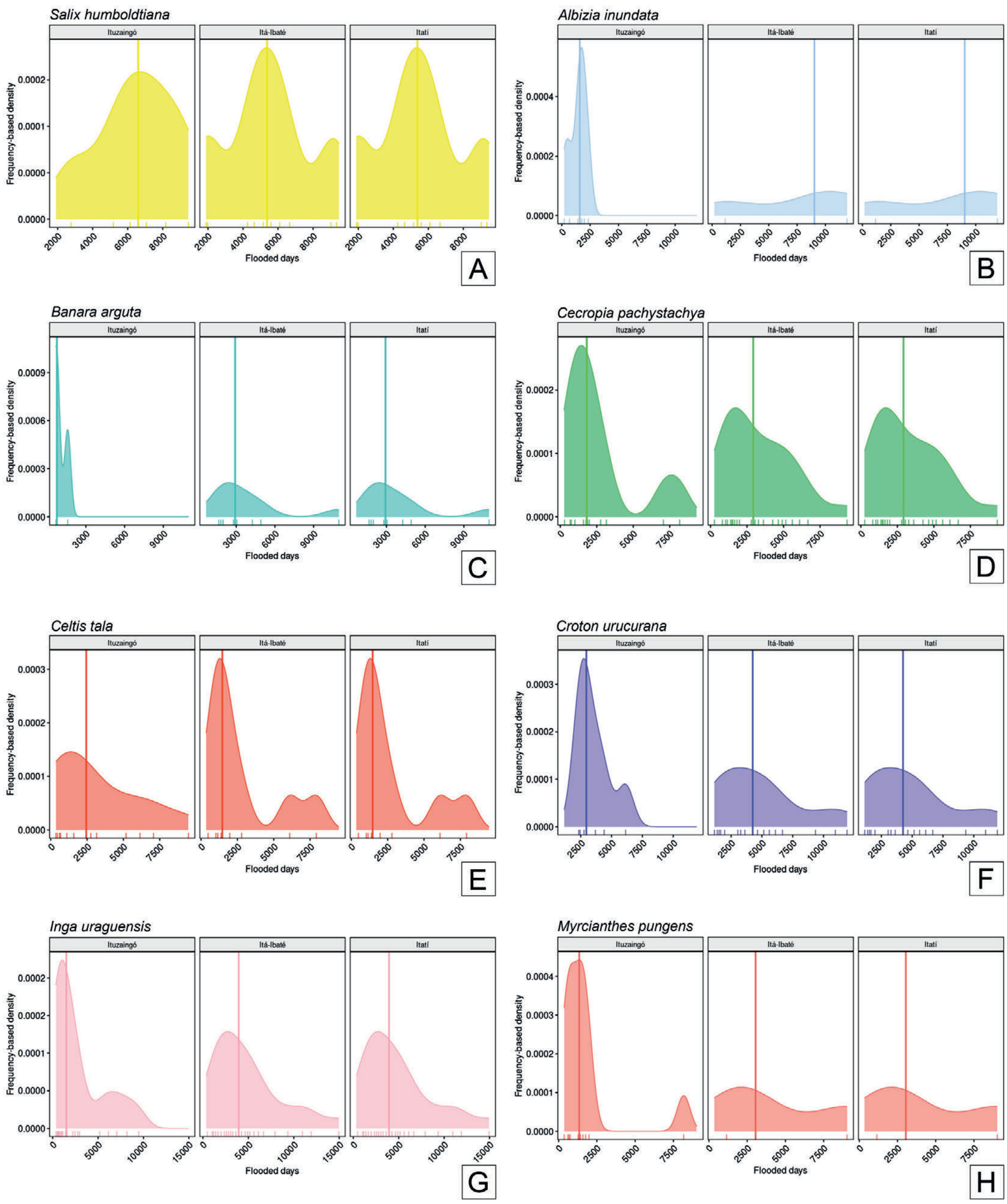

Fig. 7. Ecohydrological signature of each species, taking the density based on frequency related to the days of flooded soil at the different sites analyzed. A) *Salix humboldtiana.* B) *Albizia inundata.* C) *Banara arguta.* D) *Cecropia pachystachya.* E) *Celtis tala.* F) *Croton urucurana.* G) *Inga uraguensis.* H) *Myrcianthes pungens*.

Fig. 7. Firma ecohidrológica de cada especie, tomando la densidad en función de la frecuencia relacionada con los días de suelo inundado en los diferentes sitios analizados. A) *Salix humboldtiana.* B) *Albizia inundata.* C) *Banara arguta.* D) *Cecropia pachystachya.* E) *Celtis tala.* F) *Croton urucurana.* G) *Inga uraguensis.* H) *Myrcianthes pungens*.

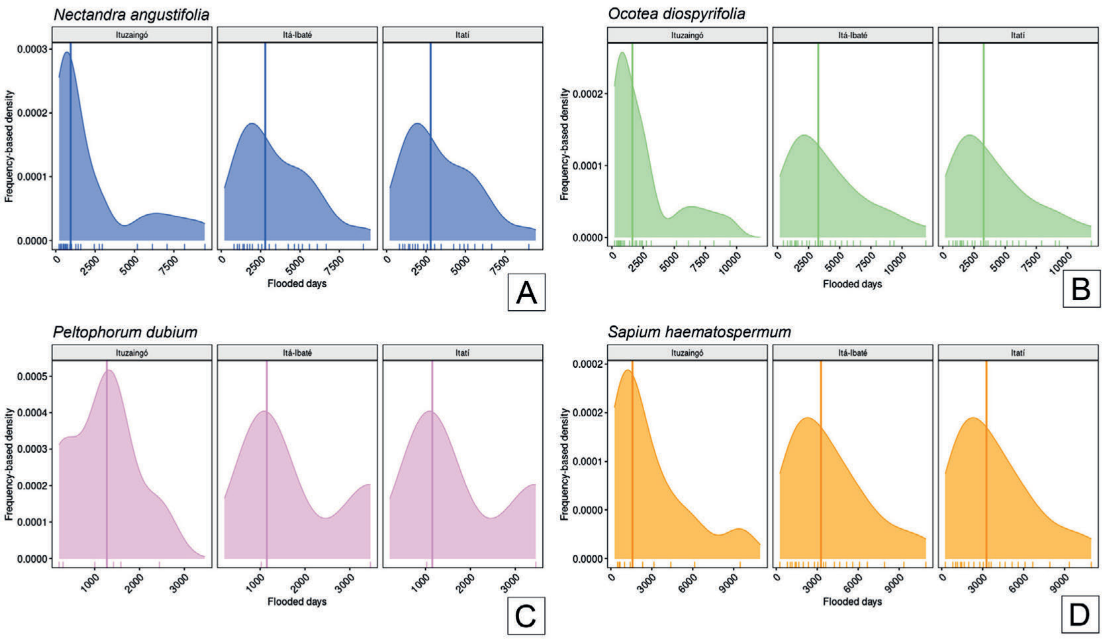

Fig. 8. Ecohydrological signature of each species, taking the density based on frequency related to the days of flooded soil at the different sites analyzed. A) *Nectandra angustifólia.* B) *Ocotea diospyrifolia.* C) *Peltophorum dubium.* D) *Sapium haematospermum.*

Fig. 8. Firma ecohidrológica de cada especie, tomando la densidad en función de la frecuencia relacionada con los días de suelo inundado en los diferentes sitios analizados. A) *Nectandra angustifólia.* B) *Ocotea diospyrifolia.* C) *Peltophorum dubium.* D) *Sapium haematospermum.*

B. arguta remained with flooded soil between 676 days and 10956 days; *C. pachystachya* between 266 days and 11100 days and *C. urucurana* varied in a wide range, between 586 days and 11909 days.

DISCUSSION

Our information shows that studied species occupy a wide range of floodable sites and the soil can be flooded for most of their existence as also observed by Neiff (1986) and Neiff *et al*. (2020) in the same Paraná River section. Agreeing with Garcia & Vargas (1998), this evidence shows that the possibilities of plants to colonize the alluvial plain are not the same in different landscape units in different hydrological phases.

Differences in the distribution of populations at the field scale are strongly associated with the geomorphological and physical characteristics of the river in the different sections, which influences the distribution of the dominant species assemblage, as pointed out by other authors (Reboratti & Neiff, 1987; Pero & Quiroga, 2019).

Because species are tolerant to different dry or flooded soil conditions, there was a significant overlap of the frequency distribution curves in both forest types in the three sites.

The possibilities of the analyzed woody population to resist prolonged droughts and floods are high, which determines the persistence of the landscape pattern even when contrasting hydrological conditions occurs, coinciding with what was indicated by Neiff (1999); Marchetti & Aceñolaza (2012); Mayora *et al*. (2020) for the Paraná River and by Junk & Piedade (1997) for the Amazon River.

In the Upper Paraná, *S. humboldtiana* forests are distributed between 46.7 and 62.8 m, which coincides with that described by Neiff (1986) for the same region, who defines forests dominated by *S. humboldtiana* as low, pioneer sandbank forests, flooded a large part of the year during prolonged floods (Zambiasio *et al*., 2018). The variants included in this work agree with the physiognomic, floristic and waterlogging descriptions according to the topographic gradient as obtained by Matteucci *et al*. (2004).

We found that the highest richness of tree species was recorded in intermediate sites, which remain flooded for up to 9474 days (57.68% of their life). This allows us to affirm that the vegetation of fluvial environments of the Paraná River is adapted to the flooding phases and their topographical distribution and richness is related to waterlogging duration. This coincides with what was described by Neiff (2005) and Zambiasio *et al*. (2018). Some authors such as Worbes (1985, 1997); Parolin *et al*. (2004a, 2004b) point out conditions similar to those found by us in the Amazon River basin, mentioning that many tree species can be completely covered by flood waters for several months and the trees normally continue their life cycle due to morphological (presence of lenticels, adventitious roots) and eco-physiological (water stress) adaptations.

As observed in our work given that the time of germination was recorded at the time of high water, coinciding with what was described by de Neiff *et al*. (2006); Marchetti & Aceñolaza (2012); Marchetti *et al*. (2013), where the floodplain forest needs the flooded soil for seed transport and nutrient transfers among other demands. Only during a period of more than 1000 days of continuous flooding, a high percentage of trees may die, as described by Neiff *et al*. (1985) in the lower basin of the Paraguay River during the 1982-1984 floods.

Our results suggest that the willow and mixed forests of fluvial environments of the Paraná River are populations with great amplitude of adaptation to the environment reflected in the distribution curves (Casco & Neiff, 2013; Zambiasio, 2020). These distribution curves are only a model fit between the vegetation distribution and the hydrological connectivity level with the river.

Several species, such as *P. dubium*, *S. haematospermum* and *O. diospyrifolia*, are not exclusive to riverine forests, as they are also found in the tropical rainforest called Mata Atlantica at the same latitude (Matteucci *et al*., 2004) and are found in soils with shorter or null flooding period.

Knowing that there is a relationship between the period of flooded soil and the distribution of trees in fluvial environments, we consider feasible to use this analytical procedure to relate the frequency of flooded soil to the frequency of each tree species at each level of the topographic gradient (Casco & Neiff, 2013; Zambiasio *et al*., 2018; Zambiasio, 2020). This makes it possible to establish the frequency and duration of the inundation period for each tree species at each floodplain site.

However, a model for spatial management and restoration of these forests also have to consider other factors that intervene in the distribution and abundance of tree populations, such as seed dispersal, soil seed reservoir, germination timing, biotic pressures, relief forms (Malvárez, 1997) among others (Junk *et al*., 1989; Rosales, 1996; Geissler & Gzik, 2010; Marchetti & Aceñolaza, 2012; Marchetti *et al*., 2013).

CONCLUSIONS

The results of this study demonstrate that the trees of the Paraná floodplain are eurytypical (Neiff, 1990; 2005; Casco & Neiff, 2013; Zambiasio, 2020) and tolerate the decrease in flooding time; agreeing with the literature consulted. There is a relationship between the distribution of trees and variables of the hydrological pulse, mainly flood duration and frequency. Progress was made in presenting an analytical procedure to associate the frequency of flooded soil with the frequency of each tree species at each topographic level. This makes it possible to establish the frequency and duration of the flooding period for each key species at each floodplain site in the analyzed sections.

Given that the woody species of fluvial environments of the Upper Paraná have wide distribution gradient in terms of days of flooded soil in its plain, we consider that there is no critical threshold of permanence that is related to this single variable (Hughes, 1990; Pero & Quiroga, 2019). Since it is feasible to assess the adjustment between the woody vegetation and the forcing factor such as the hydrosedimentological pulse, it is an excellent indicator for monitoring natural disturbances or anthropogenic disturbances that affect the hydrological regime (natural states of the system).

CONFLICT OF INTEREST

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

DATA AVAILABILITY STATEMENT

The data reported in this paper are available from the corresponding author upon a reasonable request.

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