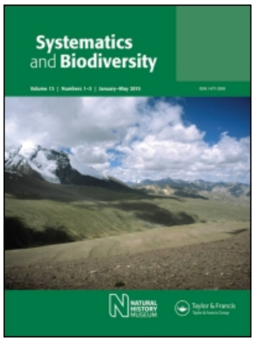

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Research Article

Hidden areas of endemism: Small units in the South-eastern Neotropics

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This study aimed to establish if the Lower Río de la Plata Basin (LRPB) wetlands can be considered a biogeographic unit. The species of this area were compiled and segregated according to the habitat, selecting only 87 endemic taxa restricted to the LRPB and linked to wetlands. Distributional data of species obtained from the literature, web databases, biological collections, and field trips were georeferenced. The areas of endemism were established as those areas where the distribution of two or more taxa overlaps in groups of rivers' sections with geographic continuity and were tested with a cluster analysis. This congruence is due to ecological, geomorphological, and historical factors. Four areas of endemism were found: a broad area that comprises the whole study area (Riverine district), which is divided into three nested smaller areas (Paraguay–Paraná Flooding Valleys, Uruguay Basin, and Paraná Delta subdistricts). Then, we analysed 170 taxa distributions to evaluate the relationship between the study area and the neighbouring biogeographic units. According to the results, the study area belongs to the Paraná biogeographic province. Some areas of endemism are hidden inside broader areas and are hardly detected with the currently used biogeographic grid-methods. We propose to combine the information about ecological requirements of each taxon with its georeferenced records to estimate their areas of distribution as a primary step for searching areas of endemism in intracontinental studies.

Key words: areas of distribution, areas of endemism, nested areas, regionalization, Río de la Plata Basin, southern South America, wetland biota

Introduction

The identification of areas of endemism is a basic step to develop natural regionalizations (Crisci, Katinas, & Posadas, 2003; Noguera-Urbano, 2016), with the distribution of organisms as a reflection of historical (such as the evolution of the Earth and its biota) and ecological factors. Among the most popular methods for endemism areas delimitation, are those that divide the region to be analysed into grid-cells, construct a data matrix of grid-cells per taxa from their distributional information, and apply an algorithm to the matrix (e.g., Parsimony Analysis of Endemicity, Endemicity Analysis, Nonmetric Multidimensional Scaling, Ordination and Clustering; Ferrari, 2017; Garraffoni, Moura, & Lourenco, 2017; Morrone, 2018). Many works use, in general, large databases of species (or other taxa) distribution (e.g., Holt et al., 2013; Kreft & Jetz, 2010; Rueda, Rodríguez, & Hawkins, 2013), facing the problem of the data quality. Among the main factors that influence the quality of data, are the correct determination of specimens and the accuracy of the geographic distribution of those specimens (Beck, Ballesteros-Mejia, Nagel, & Kitching, 2013; Goodwin, Harris, Filer, Wood, & Scotland, 2015; Hortal, Lobo, & Jiménez-Valverde, 2007). In the latter, besides errors and inaccuracies in the georeferencing, there may be a lack of integration between the spatial distributions of organisms with their ecological information.

Another point of concern is that most of these works usually cover very large land surfaces where small and distinctive unit areas remain hidden in the analyses, as a result of the use of a small scale. All these issues constitute an obstacle when performing regionalizations in relatively reduced areas with contrasting ecosystems, such as those that combine terrestrial and aquatic habitats (Guerrero, Apodaca, Dosil, & Cabanillas, 2018). In these cases, other methodologies such as the overlapping

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method formalized by Müller (1973) may be more appropriate. The method basically consists of superposing the taxon distribution areas and establishing the overlapping area or areas, which constitute the areas of endemism (Crisci et al., 2003). The overlapping method was performed in papers based only on a single taxon (e.g., Chelonia: Ippi & Flores, 2001; Scorpiones: Maury, 1979; Decapoda: Morrone & Lopretto, 1995; Coleoptera: Morrone, Roig Juñent, & Crisci, 1994; Mammalia: Noguera-Urbano & Escalante, 2015; Opiliones: Ringuelet, 1959), and in several taxa (Morrone, Katinas, & Crisci, 1997). In these papers, the overlapping method was employed for establishing regionalization schemes or as a preliminary step in the application of another biogeographic method, such as PAE, NDM/VNDM, and cladistic biogeography, with the objective of finding secondary endemism areas, or transition areas. Also, multivariate analyses were very useful for revealing overlapping in spatial distributional patterns, for example in aquatic communities (e.g., Arzamendia, Giraudo, & Bellini, 2015; López et al., 2008; Sepkoski & Rex, 1974; Vieira et al., 2014).

Among regions that combine terrestrial and aquatic habitats, it is the lower part of the Río de la Plata Basin (i.e., the Río de la Plata Basin south of −25° latitude; LRPB onwards). Located in south-eastern South America (Fig. 1), its main rivers are the Paraná, the Paraguay (which merges with the Paraná and is its main tributary), and the Uruguay Rivers, encompassing the wetland ecosystems of the Delta and Islands of the Paraná and Uruguay Rivers ecoregion and the Iberá ecoregion (Matteucci, 2012a,b). It holds endemic species and biological communities that differ strikingly from those of the surrounding habitats. The LRPB is an attractive area not only because it combines terrestrial, riparian, and aquatic habitats. It is unique because its rivers originate in the humid tropics of Brazil and drain their waters into the humid temperate Pampas region, at ~34.25°S, 58.33°W (Oakley, Prado, & Adámoli, 2005). Other major rivers either have their lower basins and mouths in deserts (e.g., Nile River), are inter-tropical (e.g., Orinoco and Amazonas Rivers) or have their origin in temperate regions (e.g., Mississippi, Yellow, and Ganges Rivers). Although the main rivers of the LRPB run downstream through grasslands and xerophytic forests, their margins maintain the forested appearance (gallery forests) that is characteristic in the north, constituting a distinctive ecosystem which holds high biological diversity relative to the surrounding regions. In addition, it constitutes a biotic dispersal route that plays an important role in the establishment of distributional patterns. This also leads to a similarity in the species composition between upstream and downstream localities (Neiff, 2001), but different from the species composition just a few metres away from the river banks. In these cases, the segregation of species according to their ecological similarity is fundamental in biogeographic studies.

The LRPB apparently contains an area of endemism that remains hidden between the biogeographic limits among three provinces, i.e., the Chacoan, the Pampean, and the Paraná provinces. Thus, there are two unsolved questions regarding the LRPB wetland ecosystems area: does it constitute a biogeographic unit? And, how is it related to the other biogeographic units of the prevailing regionalization schemes?

The current ecology-based biogeographic regionalization schemes (e.g., based on physiognomy, communities, or ecoregional criteria; Dinerstein et al., 1995) consider just parts of the study area as distinctive units, such as the ecoregions (Morello, Matteucci, Rodríguez, & Silva, 2012) mentioned above, but not the whole area. Other schemes merge the study area inside larger vegetational units (e.g., Hueck, 1972).

In the historically based regionalizations (i.e., implicitly or explicitly based on areas of endemism) this area is not distinguished from the neighbouring provinces. Parts of it were biogeographically related, for example, with the Chacoan province (e.g., Cabrera, 1971; Cabrera & Willink, 1973; Giraudo & Arzamendia, 2018; Morrone, 2014; Ragonese & Castiglioni, 1970), with the Pampean province (Cabrera & Willink, 1973; Morrone, 2014), or with the Paraná province (e.g. Acosta, 2002; Arzamendia & Giraudo, 2009; Burkart, 1957; Cabrera & Dawson, 1944; Di Giacomo & Contreras, 2002; Guerrero et al., 2018; Nores, Cerana, & Serra, 2005; Ringuelet, 1955, 1959). Other parts of the study area were considered as transition zones between provinces (Arzamendia & Giraudo, 2009; Di Giacomo & Contreras, 2002; Prado, 1993).

The objectives of this contribution are to find out if: (1) the wetland ecosystems of LRPB constitute a geographically distinct assemblage of endemic species and communities, and (2) to establish which is the biogeographical connection between this area with the surrounding provinces. We propose to identify sympatric patterns through the overlapping distribution of terrestrial and amphibian plants, vertebrates, and invertebrates that inhabit the LRPB.

Materials and methods

Study area

The study area comprises the wetland ecosystems from the southern half of the Río de la Plata Basin (LRPB) ranging in parts of Argentina, Brazil, Paraguay, and

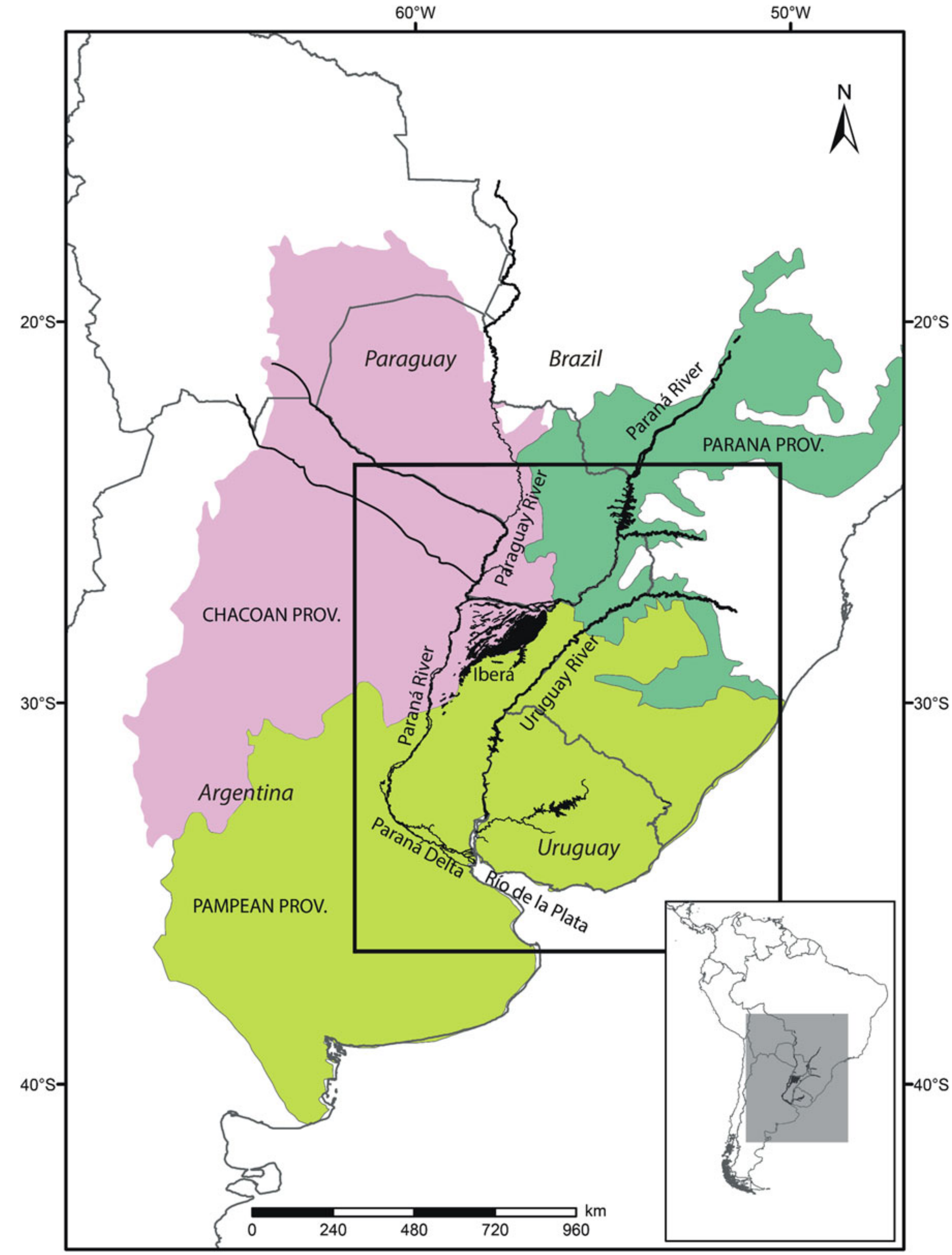


Fig. 1. Main rivers of the Río de la Plata basin, and the biogeographic provinces involved (Morrone, 2014). Pink = Chacoan province; green = Paraná province; light green = Pampean province. The rectangle shows the LRPB. Please see the pdf version for colour reference.

Uruguay. It covers the depressed areas adjacent to the Paraná, Paraguay, and Uruguay Rivers, the whole Iberá swamps, and the delta and islands of the Paraná and Uruguay Rivers (Fig. 1). These ecosystems dissect the grassland and xerophytic forest of the pampas plains.

The depressed areas associated with the rivers have a particular geomorphology and a wetland vegetation which is completely different from that found in adjacent, topographically higher plains (Figs 2, 3). It includes riverine scrubs (Fig. 4), gallery forest (Figs 4, 5), tropical-subtropical megathermic swamp grasslands (locally called '*pajonal*'; Figs 3, 4, 6) and particular aquatic communities such as the swamps or '*esteros*' (Fig. 6) (Burkart, 1957, 1975; Franceschi & Lewis, 1979; Matteucci, 2012a,b; Ragonese, 1941).

The biogeographic scheme follows Morrone (2014). According to this author, our study area is located in the Chacoan subregion of the Neotropical region; one half in the Paraná dominion (which includes the Paraná province) and the other half in the Chacoan dominion (which includes the Chacoan and Pampean provinces). The division of the rivers in sections follows Arzamendia and Giraudo (2009): Lower Paraguay River, Upper and Middle Paraná River, Upper and Lower Paraná Delta, Upper and Middle Uruguay River and Río de la Plata. These sections correspond to different geomorphological, hydrological, and geological characteristics of the area crossed by the rivers (Bonetto, Neiff, & Di Persia, 1986; Di Persia & Neiff, 1986). We unified the lower course of the Uruguay River with the Lower and Middle Delta due to their floristic and geomorphological similarity (Burkart, 1957; Menalled & Adamoli, 1995), and included the Iberá wetlands as another section.

Taxa analysed

Distributional data of species were obtained from several sources, i.e., literature, web databases, biological collections, and field trips. The literature search includes the flora of southern South America, other local floras, vertebrate checklists, Hexapoda, Myriapoda, and Arachnida revisions and other reports (Appendix S1, see online supplemental material, which is available from the article's Taylor & Francis Online page at http://dx.doi.org/10.1080/14772000.2019.1646833). The Global Biodiversity Information Facility (GBIF, 2018) database and the following biological collections of Argentina were consulted: vascular plants, Arachnida and Myriapoda, and Herpetology at Museo de La Plata; vascular plants and Arachnida at Museo Argentino de Ciencias Naturales; arthropods at Fundación de Historia Natural 'Félix de Azara'. Our field trips covered several locations at the Argentinian provinces of Corrientes (e.g., Corrientes, Colonia Carlos Pellegrini, Río Corrientes, Esquina), Entre Ríos (e.g., Concordia, El Palmar National Park, Colón, Paraná, Gualeguay, Ibicuy, Paranacito) and Buenos Aires (e.g., Isla Martín García, Paraná Delta, Río de la Plata coast), and some localities of Uruguay (e.g., Salto, Daymán, Colonia).

Species geographic distribution

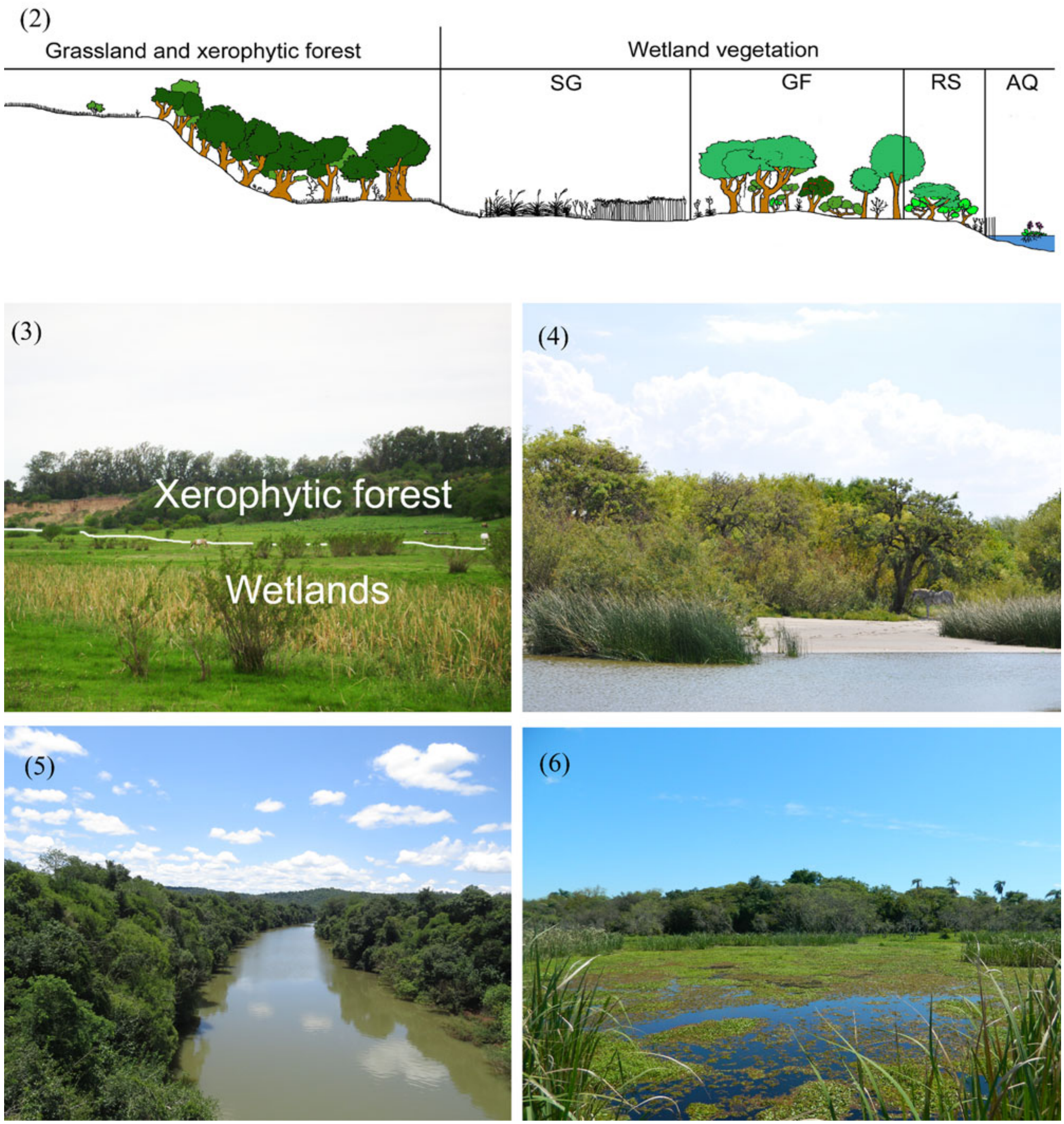
Each species locality was georeferenced using Google Earth and several gazetteers (e.g., Wilcox & Randall, 1992). Then, the distributional data were segregated according to the habitat, selecting only those taxa restricted to the LRPB and linked to wetlands, i.e., mostly following the adjacent areas to the course of the rivers (Fig. 2). For example, species associated with the semi-xerophilous forests and grassland communities of the Chacoan and Pampean biogeographic provinces were discarded.

Therefore, to determine the distribution areas, we started with two objective data: the known localities and the map of the region with the rivers' sections, and also the *a priori* hypothesis that the taxa will be distributed more or less continuously between the known locations where the environment is favourable to them (Delvosalle, 1959). This continuity will vary according to the fragmentation of the environment, the physiographic and geological characteristics of the area, and the biogeographic history of the taxa.

Detection of areas of endemism

With the aim to detect areas of endemism we applied two methodologies: the method of Müller (1973) and cluster analysis. Cluster analysis, coupled with classical geographic analysis, were suggested as the appropriate tools for delineating biogeographic areas (Legendre, 1990).

Müller's (1973) protocol determines areas of endemism by analysing species ranges in a way that: (a) species ranges must be relatively small compared with the region itself; (b) their distributional limits must be accurately known; (c) the validity of the species must not be in dispute; (d) substantial overlapping in ranges of ≥ 2 species determines an area of endemism. After the species geographically and ecologically restricted to the study area were selected, we noticed that there was a strong correspondence between the taxa distribution and specific rivers' sections that had geographic continuity. Therefore, we classified the taxa according to the section of the river with which they were associated (Appendix S1, see supplemental material online). This



Figs. 2–6. (2) Schematic profile showing the relationship of plant communities and the topographic gradient. The grassland and xerophytic forests represent the Chacoan dominion plant communities. The wetland vegetation of the LRPB constitutes the study area and includes: SG = swamp grasslands; GF = gallery forest; RS = riverine scrub; and AQ = aquatic communities. (3) The limit between xerophytic forest biota and the LRPB wetland biota (Photo: E. L. Guerrero). (4) Riverine scrub (RS) and gallery forest (GF) in the Río de la Plata coast (Photo: P. Carrión). (5) Gallery forest (GF) in a tributary of the Uruguay River at 27°50′ south latitude (Photo: L.G. Pagano). (6) Aquatic communities (AQ), swamp grasslands (SG) and gallery forests (GF) in the Iberá wetlands (Photo: F. Suazo Lara).

is a general, not an exact correspondence, since areas of endemism are mostly of a polythetic nature, i.e., geographic congruence does not demand complete agreement on the boundaries of those taxa's distributions at all possible scales of mapping (Apodaca & Crisci, 2018). Thus, the endemism areas were established as those areas where the distribution of two or more taxa coincide or overlap in groups of rivers' sections with geographic continuity. This congruence is due to the following factors: (a) ecological: taxa depend on the biotic and abiotic factors of particular sectors of the rivers; (b) geomorphological: the conditions of the rivers change from the river origin area to the mouth, and this variation influences taxa distribution; and (c) historical: the geological history of the rivers (Albert, Val, & Hoorn, 2018; Arzamendia & Giraudo, 2009; Cavalloto, 2002; Orfeo, 2005; Orfeo & Neiff, 2008) affected past and current taxa distribution.

In order to perform the cluster analysis, we constructed a presence/absence data matrix based on Appendix S1, where presences were computed with 1 and absences with 0. We used the Jaccard index to construct the similarity matrix, and UPGMA (unweighted pair-group method using arithmetic averages) to obtain the dendrogram (Sneath & Sokal, 1973). We also computed the co-phenetic coefficient (Sokal & Rohlf, 1962) to evaluate the degree of distortion of the analysis. The analysis was implemented with the program PAST (Hammer, Harper, & Ryan, 2001).

Biogeographic connections

To establish biogeographic relationships between our resulting endemism area/s and the surrounding biogeographic units we followed Guerrero et al. (2018). We selected 170 plant species of the life forms that define each community (i.e., trees of the gallery forest, bushes of the riverine scrub, and tall dominant Poaceae or Cyperaceae of the swamp grasslands). Their distribution was obtained from the literature (e.g., Zuloaga, Morrone, & Belgrano, 2008) and GBIF records. Then, each species was analysed and classified according to Morrone's (2014) units into the following categories: (a) Widespread, species distributed in several provinces of the Neotropical region or the Chacoan subregion; (b) Chacoan dominion, species distributed in the Chacoan dominion provinces; (c) Chacoan province, species distributed in the Chacoan province and our study area; (d) Pampean province, species distributed in the Pampean province and our study area; (e) Paraná dominion, species distributed in the Paraná dominion provinces and our study area; (f) Paraná province, species distributed in the Paraná province and our study area. Finally, we analysed with which of those subregions, and provinces within subregions, the taxa of our study area have the strongest link, i.e., major number of shared taxa, for establishing a biogeographic connection.

Results

Areas of endemism

Appendix S2 (see supplemental material online) summarizes the distributions of endemic taxa in the study area. Figure. 7 shows the dendrogram that resulted from the cluster analysis.

On the basis of the overlapping method (Müller, 1973) four common patterns were obtained and established as endemism areas (Appendix S2, see supplemental material online; Figs 8–15): (a) A broad area that comprises the whole study area (Figs 8, 9), which can be divided into the following three smaller endemism areas; (b) a southern area, that includes the Delta of the Paraná River and its extension to the Río de la Plata (Figs 10, 11); (c) an eastern area coinciding with the Uruguay River axis and its tributaries (Figs 12, 13); (d) a western and northern area, that coincides with the Paraguay–Paraná fluvial axis and its tributaries, and the Iberá wetland system (Figs 14, 15). The cluster analysis (Fig. 7) showed similar results, where groups (b), (c), and (d) can be easily recognized, with a co-phenetic coefficient value of 0.81.

Relationships of the endemism area with other biogeographic provinces

Thirty-two dominant plant species of the gallery forest and the riverine scrubs connect our area of endemism to the Paraná dominion and the Paraná province (Appendix S3, see supplemental material online). Five species inhabit the eastern (humid) Chacoan province, and in some locations reach the Paraguay and Paraná river banks as accessory elements of the gallery forests. The only community dominated by a Pampean province species is the *Paspalum quadrifarium* humid grassland. One hundred and thirty-two plants of the LRPB – mainly trees from the northern gallery forests – are widespread and thus non-informative (Appendix S4, see supplemental material online).

Some of the widespread species dominate the swamp grasslands. Among them, *Schoenoplectes californicus*, *Cyperus giganteus*, and *Tipha* spp. dominate the so-called 'juncales', 'pirizales', and 'totorales' respectively, all of which are typical communities of the riverine landscape. On the other hand, the swamp grasslands of *Panicum prionitis*, *Scirpus giganteus*, or *Zizaniopsis bonariensis* are dominated by these endemic species. Despite the fact that the dominant species of the swamp grasslands are non-geographically informative (*Panicum prionitis* community is related to all the surrounding

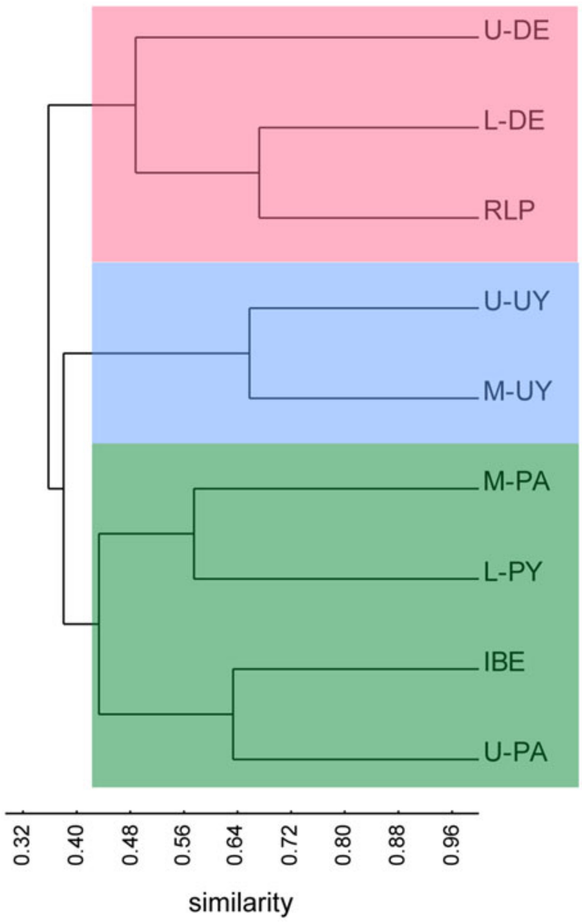


Fig. 7. Dendrogram resulting from the Jaccard matrix and UPGMA method. Co-phenetic correlation value = 0.81. Abbreviations: U-PA = Upper Paraná River; IBE = Iberá Wetlands; M-PA = Middle Paraná River; L-PY = Lower Paraguay River; U-UY = Upper Uruguay River; M-UY = Middle Uruguay River; U-DE = Upper Delta; L-DE = Lower Delta; RLP = Río de la Plata. The colours represent the three main clusters found in this study. Please see the pdf version for colour reference.

areas and *Zizaniopsis bonariensis* community is not related to anyone), these swamp grasslands have species in common like *Aspilia pascalioides*, *Cayaponia martiana*, *Cleome trachycarpa*, *Lathyrus paranensis*, and *Stigmaphyllon bonariense*, whose distributions encompass the Paraná province and most LRPB.

The distribution of animal species follows the same pattern as the plants, with a strong Paraná province connection. Many species of Aves (e.g., *Trogon surrucura*: Di Giacomo & Contreras, 2002; Nores et al., 2005), Ophidia (e.g., *Chironius bimaculatus*: Arzamendia & Giraudo, 2009), Chelonia (e.g., *Hydromedusa tectifera*, *Phrynops williamsi*: our own observations), Mammalia (e.g., *Bibimys chacoensis*, *Sooretamys angouya*: our own observations), Ephemeroptera (e.g., *Caenis uruzu*: Dos Santos, Emmerich, Molineri, Nieto, & Domínguez, 2016), and Opiliones (e.g., *Eusarcus hastatus*: Ringuelet, 1959) that inhabit the Riverine district, are also common in the Paraná province or in the whole Paraná dominion.

All these results indicate that the broad area of endemism delimited here is more strongly related with the Paraná biota.

Area taxonomy

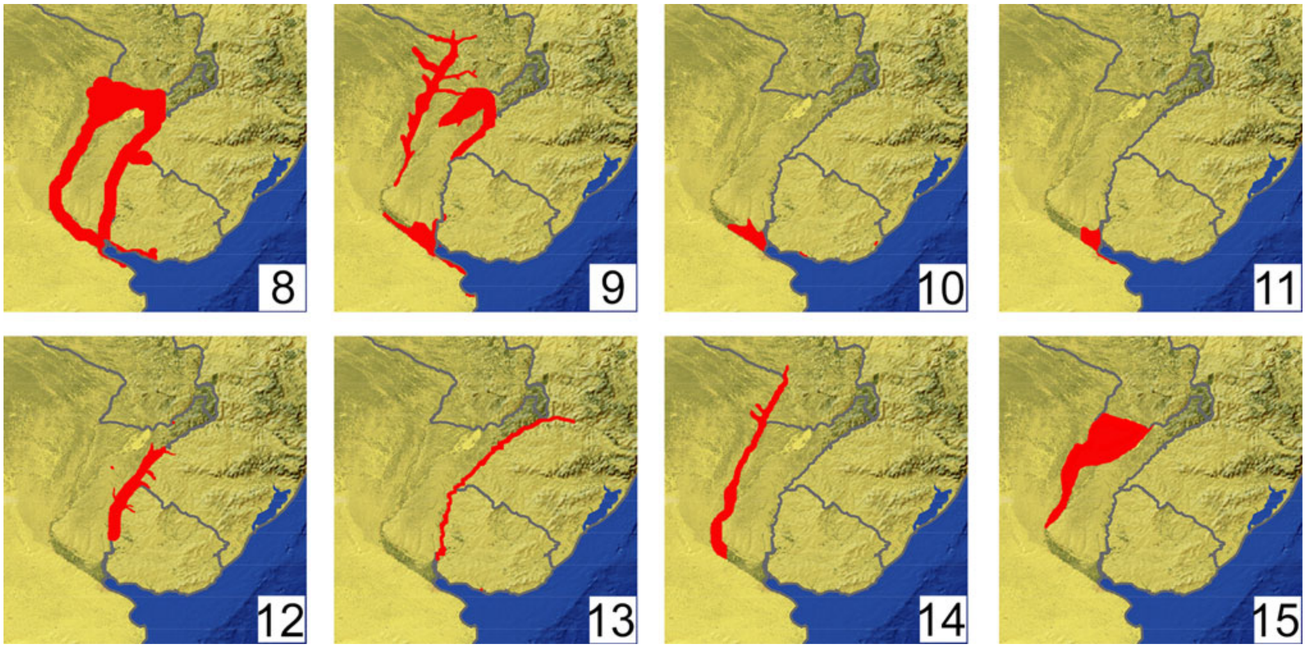
We propose adding a new district, with three new subdistricts, to Cabrera's (1951) three districts of the Paraná province. We establish new names for the district and for two subdistricts because previous names provided by other authors coincide only in part with our areas and extend to neighbourhood regions or are small and are included in our areas. These names are cited as synonyms under each new name. We also include the original names of the areas in Spanish, as established by Cabrera (1951, 1971) together with the new names proposed here.

A. Paraná province (provincia Paranense) (Cabrera, 1971). A1. Mixed Forest district (distrito de las Selvas Mixtas) (Cabrera, 1951); A2. Montane district (distrito Montano) (Cabrera, 1951); A3. Grasslands district (distrito de los Campos) (Cabrera, 1951); A4. Riverine district (distrito Ribereño), new district; A4. 1. Paraná Delta subdistrict (subdistrito Delta del Paraná) (Burkart, 1947), new status; A4. 2. Uruguay Basin subdistrict (subdistrito Cuenca del Uruguay), new subdistrict; A4. 3. Paraguay–Paraná Flooding Valleys subdistrict (subdistrito Valles de inundación del Paraguay–Paraná), new subdistrict.

Riverine district, distr. nov. (Fig. 16)

Other biogeographic unit names and plant communities that partly coincide or are included in the Riverine district are: Parque Mesopotámico (in part) (Hauman, Burkart, Parodi, & Cabrera, 1947); distrito Mesopotámico, Sector Meridional (in part) (Ringuelet, 1961); distrito de las selvas mixtas (in part) (Cabrera, 1951, 1953, 1971, 1976); Ecorregión Delta e Islas de los ríos Paraná y Uruguay (Matteucci, 2012a); Ecorregión Esteros del Iberá (Matteucci, 2012b). One genus, 34 species, and three infraspecific taxa are exclusive to this district (Appendix S5, see supplemental material online).

Diagnosis: The Riverine district covers the flood valleys of the Paraguay–Paraná fluvial axis, from northeastern Argentina and southern Paraguay to the Paraná Delta, and the Uruguay River from southern Brazil to the Río de la Plata. It also includes the Iberá wetlands, originated from the abandoned river beds of the Paraná



Figs. 8–15. Examples of some species distribution reflecting the different patterns found in this study. (8, 9) Main pattern: (8) *Eryngium mesopotamicum*, (9) *Scapteromys aquaticus.* (10, 11) Delta and Río de la Plata pattern: (10) *Argenteohyla siemersi siemersi*, (11) *Baccharis phyteuma*. (12, 13) Uruguay River pattern: (12) *Aeschynomene lorentziana*, (13) *Mesabolivar uruguayense*. (14, 15) Paraguay-Paraná-Iberá pattern: (14) *Baccharis albida*, (15) *Physalaemus santafesinus*.

River (Orfeo & Neiff, 2008), and the tributaries of these rivers in Paraguay, Uruguay, and south-eastern Brazil. It coincides in Argentina with the Delta and the islands of the Paraná and Uruguay rivers ecoregion and with the Iberá wetlands ecoregion. The vegetation and the climatic, geomorphological, edaphic, and hydrological characteristics are summarized in Matteucci (2012a,b). The gallery forest of *Ocotea acutifolia*, *Allophyllus edulis*, *Pouteria salicifolia*, and *Sebastiania brasiliensis* (Cabrera & Dawson, 1944), swamp grasslands of *Panicum prionitis* (Ragonese, 1941) and swamp grasslands of *Scirpus giganteus* (Cabrera, 1949), are exclusive to this district. An almost complete overlap of the following species was found: *Baccharis penningtonii*, *Eryngium mesopotamicum*, *Oxypetalum sylvestre*, *Paspalum haumanii*, *Scirpus giganteus*, *Vicia epetiolaris*, *Zizaniopsis bonariensis*, *Erythrolamprus jaegeri coralliventris*. Most of these species live in complete sympatry along the geographic range of the district, so the overlap in their distributions is considerably high.

The Riverine district is constituted by three subdistricts: the Paraná Delta, Uruguay Basin, and Paraguay–Paraná Flooding Valleys subdistricts, which are described below.

Paraná Delta subdistrict (Burkart, 1947), stat. nov. Other biogeographical unit name and plant communities that partly coincide with the Parana Delta subdistrict is the Subregión Ecológica Antiguo Estuario Marino (Matteucci, 2012a). The Paraná Delta subdistrict was proposed by Burkart (1947) in his work of the Argentinean vegetation, with the district category. Even though Burkart (1947) did not consider the Río de la Plata and the rivers that drain into it (e.g., Santa Lucía basin in Uruguay or Boca Cerrada creek in Argentina), we maintain Burkart's name because it mostly covers the subdistrict found here. One genus, 20 species, and four infraspecific taxon are exclusive to this subdistrict (Appendix S5, see supplemental material online).

Diagnosis: The Paraná Delta subdistrict covers the Paraná Delta and associated fluvial geoforms in the Río de la Plata coastal plains (Fig. 4). Its southern limit coincides with the Samborombón Bay, where salinity increases gradually due to the Atlantic Ocean influence. An almost complete overlap of the following taxa was found: *Baccharis phyteumoides*, *Mimosa bonplandii*, and *Argenteohyla siemersi siemersi*. The former two are characteristic species of the riverine scrublands which are usually found in sympatry.

Uruguay Basin subdistrict, subdistr. nov

Other biogeographic unit names and plant communities that partly coincide or are included in the Uruguay Basin subdistrict are: distrito Ribera del Uruguay (in part) (Burkart, 1947); Subregión Ecológica Río Uruguay (Matteucci, 2012a). Seven species and one infraspecific

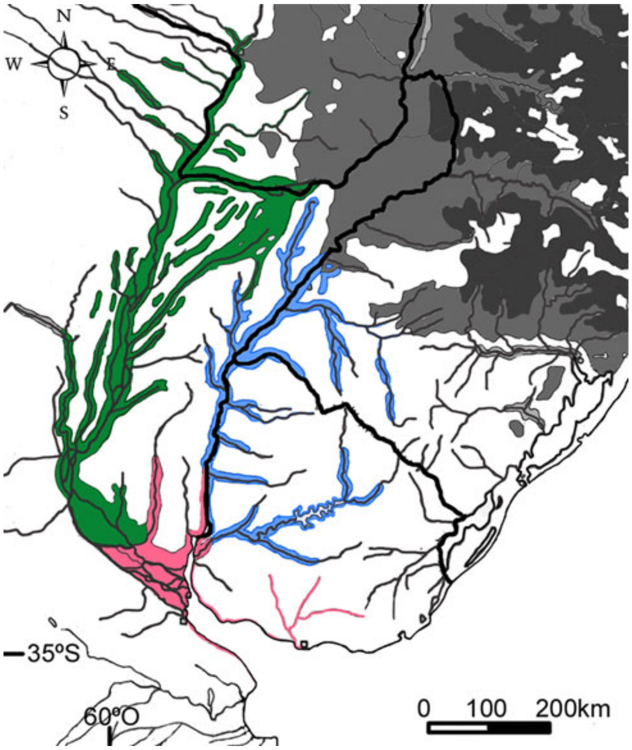


Fig. 16. Map of southern South America vegetation of Hueck (1972) showing the Riverine district of the Paraná province as defined here, with its three sub-districts: red, Paraná Delta; blue, Uruguay Basin; green, Paraguay–Paraná Flooding Valleys. The colours of the subdistricts correspond to the colours of the dendrogram of Fig. 7. Please see the pdf version for colour reference.

taxon are exclusive to this subdistrict (Appendix S5, see supplemental material online).

Diagnosis: The Uruguay Basin subdistrict includes the valleys of the Uruguay River and its tributaries, from southern Misiones (Fig. 5) in Argentina to the river's mouth at Río de la Plata. It comprises mainly gallery forests and riparian scrubs. A high degree of overlap of the following taxa was found: *Aeschynomene lorentziana*, *Commelina erecta* f. *dielsii*, *Mimosa amphigena*, *M. obstrigosa*, *Sporophila palustris*, and *Mesabolivar uruguayensis*.

Paraguay–Paraná Flooding Valleys subdistrict, subdistr. nov

Other biogeographic unit names and plant communities that partly coincide or are included in the Paraguay–Paraná Flooding valleys subdistrict are: Distrito Ribera del Paraná (in part) (Burkart, 1947); distrito Esteros y Lagunas del Iberá (Burkart, 1947); distrito Chaqueño Oriental (in part) (Cabrera, 1951, 1953, 1976); distrito Hidrofítico, sub distrito Fluvio-insular (Ragonese & Castiglioni, 1970); distrito Hidrofítico, sub distrito del Iberá (Ragonese & Castiglioni, 1970); Paraná flooded savannas ecoregion (Dinerstein et al., 1995); Subregión ecológica Hidrosistemas de Planicies de Inundación (Matteucci, 2012a); Ecorregión Esteros del Iberá (Matteucci, 2012b). One genus, nine species, and three infraspecific taxa are exclusive to this subdistrict (Appendix S5, see supplemental material online).

Diagnosis: The Paraguay–Paraná Flooding valleys subdistrict includes the valleys of the lower section of the Paraguay River and upper and middle sections of the Paraná River together with its tributaries. It includes the gallery forest, swamps or 'esteros' (Fig. 6) and marshes of the humid Chaco. *Physalaemus santafecinus* is present in all the river sections of the subdistrict and have a partial overlapping, in different degrees, with the rest of the species of the area, revealing this subdistrict's polythetic nature.

Discussion

A useful method for detecting hidden areas

It is noteworthy that many previous regionalization studies covering the Riverine district (e.g., Ippi & Flores, 2001; Noguera-Urbano & Escalante, 2015; Szumik et al., 2012) overlooked the high levels of endemism in this area. One possible explanation is that the rivers' associated vegetation covers a reduced surface in comparison with the neighbouring plains, and therefore the distributional patterns of the riparian biota remain obscured by the other, more widely distributed, species.

None of the grid-cell based methods could be applied to our study area for two main reasons: (a) Using a relatively small size of grid-cell (e.g., 0.5° latitude-longitude grid) would lead to artefactual results generated by under-identified distributions. This is because a large part of the study area received little attention from collectors and many grid-cells would be coded as taxa absences. As an example, Giraudo and Arzamendia (2018) recovered only one endemism area in the lower Paraguay River with 0.5° × 0.5° grid-cells; and (b) using a larger size of grid-cell (i.e., more than 1° latitude-longitude grid) would imply the inclusion of species belonging to very different communities in the same grid-cell due to the environmental heterogeneity of the area; for example typical wetland species would be associated with species inhabiting topographically higher plains. This would lead to consider as one 'natural' unit two or more areas that are in fact ecologically and historically different. For example, 1° × 1° grid-cells (e.g., Giraudo & Arzamendia, 2018) lead to the identification of large areas covering most of the Chaco province and the Paraná floodplains, with the consequent mixing of wetland-adapted species (e.g., *Eunectes notaeus*) with grassland and xerophytic forest species (e.g., *Chironius maculoventris*).

We also considered applying Geographical Interpolation of Endemism (GIE; Oliveira, Brescovit, & Santos, 2015), a method that is independent of grid-cells and is based on kernel spatial interpolation. However, the linearity of the geographic distribution of most taxa that inhabit the Riverine district, being associated with rivers, makes it impossible to use this method.

Another approach under consideration was the use of panbiogeographic tracks, which was already employed in large regions that include our study area (Arzamendia & Giraudo, 2009; del Río, Morrone, & Lanteri, 2015; Ferretti, González, & Pérez-Miles, 2012; Morrone, 2002). However, these studies didn't identify the Riverine district as an area of endemism. These authors combined wetland restricted taxa with grassland and xerophytic forest widespread species in their analysis. In this way, the wetland restricted individual tracks were embedded within larger generalized tracks. On the other hand, Morrone and Lopretto (1994), using wetland species of Decapoda (Crustacea), found support for an area of endemism in the Paraguay–Paraná River axis using panbiogeography. This reinforces the idea that distinguishing the habitat in intracontinental biogeographic studies is a fundamental step.

It could be remarked that the geographic distribution of most taxa used in this study is quite continuous along the river banks and adjacent areas, so the overlapping methods employed here, linking the linear distribution of taxa would approach the delimitation of generalized tracks of panbiogeography. The difference with previous works is that we used a taxonomically diverse set of organisms, and distinguished between floodplain species and dryer zone species.

In summary, some methods would be inappropriate for finding these small, wetland, and linear-shaped endemism areas. The overlapping of geographic distributions of taxa inhabiting ecologically similar habitats and the multivariate data analysis, on the other hand, allowed us to rescue and make evident these hidden areas that formerly remained undetected in previous regionalization schemes.

Where to place the Riverine district?

The Riverine district is located in the union of three biogeographic provinces, Pampean, Paraná, and Chacoan (Cabrera & Willink, 1973; Morrone, 2014). Our results (Appendix S3, see supplemental material online) yielded that this new district should be included in the Paraná province because of its biotic connection of shared species and communities.

Despite the fact that many authors (Acosta, 2002; Arzamendia & Giraudo, 2009; Burkart, 1957; Cabrera, 1951; Cabrera & Dawson, 1944; Di Giacomo & Contreras, 2002; Dos Santos et al., 2016; Guerrero et al., 2018; Nores et al., 2005; Ringuelet, 1955, 1959) established relationships of the biota of the Riverine district, its subdistricts, or of parts of its subdistricts, with that of the Paraná province, this relationship was not displayed in regionalization maps (e.g., Cabrera & Willink, 1973; Morrone, 2014). Furthermore, Burkart (1957) and Guerrero et al. (2018) noted that the vegetation of the Paraná Delta subdistrict lacks elements of the other surrounding provinces, such as the Pampean and Chacoan, but it is strongly connected to the Paraná elements.

We found that the Riverine district is composed by geographically restricted plant communities. The swamp grasslands of *Panicum prionitis* or *Scirpus giganteus* are connected to the Paraná province by some taxa, but are dominated by endemic species. The gallery forests and riverine scrubs extend from the streams of the Paraná province along the Paraná and Uruguay rivers and their tributaries to the Río de la Plata coast (Cabrera & Dawson, 1944; Cardoso Marchiori, 2004). These communities are conformed by endemic species of the river margins adapted to the periodical floods (e.g., *Nectandra angustifolia*, *Ocotea angustifolia*, *Inga uraguensis*, *Terminalia australis*, *Citharexylum montevidense*, *Poecilanthe parviflora*, *Cephalanthus glabratus*, *Phyllanthus sellowianus*) and by widespread species. The richness of widespread and Paraná dominion species declines towards the south (Oliveira-Filho, Budke, Jarenkow, Eisenlohr, & Neves, 2013; our own observations), and therefore the southernmost gallery forests are almost exclusively dominated by river margin endemics (cf. Burkart, 1957; Cabrera & Dawson, 1944).

The gallery forests of the Lagoa dos Patos Basin, in Southern Brazil, should probably be included in the Riverine district. They were not analysed in this study since they are no longer connected with any of the rivers of the LRPB. However, they were connected with the Uruguay River at the beginning of the Quaternary period, which is reflected in snakes' patterns of distribution (Arzamendia & Giraudo, 2009). They also share many species and communities with the Riverine district, such as the swamp grasslands of *Scirpus giganteus* and *Zizaniopsis bonariensis* and the gallery forest trees and shrubs (cf. Budke, Giehl, Athayde, Eisinger, & Záchia, 2004; Closs de Marchi & Jarenkow, 2008). Further studies must focus in this area.

Conclusions

Detecting areas of endemism, with particular ecological conditions such as low wetland areas linked to rivers, proved to be more complex than anticipated. Most regionalization schemes have until now failed to reveal these areas, which remained hidden within bigger units. The combination of the geographic location with the ecology of each species to delineate their distributions together with overlapping methods, proved to be the most effective for discovering this type of area.

Overlapping in biogeography is widely employed in many approaches searching for patterns or coincident biogeographic processes. Cladistic biogeography, comparative phylogeography, comparative dispersal-vicariance analysis, and panbiogeography are based on the overlapping of cladograms, tracks, etc. The traditional main world phytogeographic and zoogeographic regions that are currently used, established for example by Sclater (1858), Wallace (1876), or Takhtajan (1986), consist of the overlapping of endemic species. Also, cluster analysis and parsimony analysis of endemicity (PAE) consist of the display of the taxa overlapping in a nested pattern represented graphically by a dendrogram and a cladogram, respectively.

The Riverine district proposed here, with its three subdistricts, is distinguished by many endemic riparian taxa, and the particular ecological conditions that predominate in water-related environments such as gallery forests, swamps, and bogs. With the addition of this new district, the Paraná province which traditionally reached ~28° south latitude (Cabrera & Willink, 1973; Morrone, 2014), extends now until ~34° south latitude.

The search of unapparent areas with the further establishment of biogeographic units, as proposed here, might provide a framework for future studies in other ecologically unique areas embedded (and probably hidden) in bigger regions, such as high mountain tops, tabletops, endorheic basins, caves, cenotes, halophytic, thermophilic, and serpentine soil communities, and other island-like habitats.

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