



AGRARIAN SCIENCES

Floristic patterns of alluvial forests in Atlantic Forest and Pampa: Climate and geographic insertion as determining factors

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Abstract: The aims of this study were to identify floristic assemblages for alluvial forests in the Atlantic Forest and Pampa regions in Brazil, assess the level of floristic similarity between assemblages, and determine environmental gradients and indicator species for these assemblages. Surveys carried out in alluvial forests in the Atlantic Forest and Pampa regions were selected, based on which a presence/absence matrix was built for tree species. A cluster analysis was performed to verify the existence of species assemblages. Floristic similarity was determined by means of the Sorensen Distance measure, from which a dendrogram was developed. The floristic matrix was ordinated by means of NMDS. A PCA was performed with climatic data from areas to determine environmental gradients. An assessment of indicator species was carried out afterwards. Two groups of areas not related to the separation of the regions became visible from the dendrogram and were corroborated by NMDS. Temperature, rainfall and altitude gradients were synthesized by the PCA. *Gymnanthes klotzschiana* and *Andira fraxinifolia* were the most relevant species, respectively, in the Paran -Uruguay and Atlantic assemblages. Alluvial forests were gradually separated in two floristic assemblages associated with river basins and migration routes, while especially influenced by tropicality and altitude gradients.

Key words: Atlantic basin, indicator species, migratory routes, Paran -Uruguay basin.

INTRODUCTION

In the current scenario in which human activities lead to the rapid transformation of all ecosystems on the planet (Steffen et al. 2007), a better understanding of the factors that determine floristic patterns in forests on a regional scale is essential for the design of conservation strategies and the ecological restoration of remaining natural areas. Despite a growing effort of work under such approach in the neotropics, knowledge on areas subject to recurrent flooding is still scarce (e.g., Silva et al. 2007, Wittmann et al. 2017) such as alluvial forests, which represent the areas along rivers,

on plains and terraces where flood pulses and hydric saturation periodically occur (IBGE 2012).

Alluvial forests function as a protective cover for natural resources by maintaining the hydrological cycle and protecting soils (Melo et al. 2011). These environments are highly relevant in the context of climate change, especially in areas tending to savanization (i.e., the Amazon and northern areas of Atlantic Forest), considering they may function as humid refuges in a future macroclimate of increased rainfall seasonality (Wittmann et al. 2017). Regardless of their ecological relevance, alluvial areas have been highly impacted by human activities (van den Berg & Oliveira-Filho 2000).

Environmental selectivity resulting from hydric stress in areas subject to flooding require plants to adapt morphologically, anatomically and physiologically (Kosłowski 2002). The ability of plants to withstand hydric stress along with existing biotic interactions (Kraft et al. 2015) defines the floristic composition and structure of plant communities (Silva et al. 2012, Cruz & Campos 2013, Carvalho et al. 2016), while the differences in flood pulses influence species establishment and diversity (Lobo & Joly 2009). As a result, a smaller number of species is functionally able to thrive on floodplains by rivers compared to areas not subject to flooding. These species are adapted to and dependent on flood dynamics. Under this perspective, the relevance of alluvial environments is undisputable, especially considering the provision of ecosystem services such as the protection of water resources and the conservation of biodiversity and gene flows, as alluvial environments form ecological corridors for animals and for plant dispersal (Van Den Berg et al. 2007, Lima & Zakia 2009).

Notwithstanding the relevant contribution of studies already conducted on alluvial habitats (Oliveira-Filho et al. 1997, Silva et al. 2007, 2016, Carvalho et al. 2016, Rodrigues et al. 2016, Kanieski et al. 2017, Cruz et al. 2018, Gonçalves et al. 2018), there is a scarcity of large scale assessments that contemplate the identification of patterns in areas subject to periodic flooding considering their regional insertion in different vegetation types. Wittmann et al. (2017) only recently carried out a study using this approach, demonstrating that Brazilian alluvial forests have similar phytogeographic patterns to equivalent non-alluvial forests, with floristic assemblages determined by macroecological factors associated with climate and evolutionary factors related to long distance dispersal. Considering that some ecological factors are

spatially structured, complementary studies on different regional scales are relevant to increase the understanding of floristic patterns.

This study aimed to contribute to a better understanding of floristic and phytogeographic patterns of alluvial areas in the Atlantic Forest and Pampa, regions where forest fragmentation is renowned. These regions were selected because they are characterized by distinct climatic contingents, therefore allowing for a joint and complementary approach of the tropical and subtropical domains. Similar climatic conditions occur where Atlantic Forest and Pampa are geographically close, in southern Brazil, resulting in shared species of the flora due to the fact that climate is one of the most important factors in species distribution (Buriol et al. 2007). We expected that the separation of biomes were not determinant in the formation of floristic assemblages despite the floristic similarity between Atlantic Forest and Pampa, due especially to the high diversity of vegetation types in the Atlantic Forest domain. We also expected alluvial environments to be associated with temperature and rainfall gradients.

The Atlantic Forest region is known for its high proportion of endemic species and considered one of the most important biodiversity hotspots on the planet. It is therefore a priority for the conservation of several habitat types (Myers et al. 2000, Mantovani 2003, Varjabedian 2010) which result from an extensive distribution range. The Atlantic Forest is increasingly constrained and fragmented despite conservation efforts. It has currently been reduced to only 12.5% of the original cover (SOS Mata Atlântica, INPE 2018) and contains the highest number of species officially threatened with extinction in Brazil (Tabarelli et al. 2003). The Pampa, on the other hand, is limited to one Brazilian state and has been largely altered by agriculture, grazing and the introduction and spread of invasive

alien species (Echer et al. 2015). Formed by highly diverse ecosystems in terms of animals and plants, the Pampa is characterized by a peculiar floristic composition (Araujo et al. 2018, Marchi et al. 2018). This diversity is, however, threatened, while studies on its genetic heritage and conservation status are scarce (Santos & Silva 2011, Echer et al. 2015).

This paper aimed to provide answers to the following questions: i) which are the main floristic assemblages in alluvial forests in the central-southern part of the Atlantic Forest and Pampa regions, and what determines these assemblages? ii) Is there floristic similarity between alluvial forests in Atlantic Forest and Pampa? iii) Which species are indicators of the main assemblages in alluvial forests in the central-southern part of the Atlantic Forest and Pampa? iv) What are the environmental gradients associated with the main floristic assemblages of alluvial forests in Atlantic Forest and Pampa?

MATERIALS AND METHODS

Data collection

Studies on floristic or phytosociological surveys carried out in alluvial forests in the Atlantic Forest and Pampa were selected from searches on Google Scholar as a base for this assessment. Studies in transitional areas between these regions were included. The Atlantic Forest has a diverse physiographic composition that includes pioneer (initial colonization by plants) and forest formations: Dense Ombrophilous Forest (Atlantic coast forests), Mixed Ombrophilous Forest (Araucaria forests), Deciduous and Semideciduous Seasonal Forests (IBGE 2012). The Pampa, on the other hand, is mainly characterized by grasslands classified as Steppe or Savanna intermixed with pioneer and forest formations of Mixed Ombrophilous Forest (Araucaria forests), Deciduous Seasonal Forests

and Semideciduous Seasonal Forests (IBGE 2012). The Dense Ombrophilous Forest (DOF), also defined as Tropical Rain Forest, is associated with high temperatures and high rainfall. It is characterized by lush evergreen vegetation composed of large trees, a high number of exclusive species and diverse life forms. It is subdivided in alluvial, lowland, submontane, montane and high montane formations due to altitudinal variation, with significant decrease in richness in higher altitudes (IBGE 2012). Araucaria Forest is the common name for Mixed Ombrophilous Forests (MOF), which is marked by the occurrence of *Araucaria angustifolia* in the canopy and intense replacement of angiosperms in the undergrowth. The term “mixed” refers to the coexistence of Tropical (Afro-Brazilian) and Temperate (Austral Brazilian) forests, where elements of the ancient orders Pinales and Laurales characterize the physiognomy (Roderjan et al. 2002). These forests are subject to high rainfall (therefore Ombrophilous), but temperatures are lower because they occur in areas of higher altitudes (IBGE 2012). Seasonal Deciduous (SDF) and Semideciduous Forests (SSDF) occur in areas conditioned to climatic seasonality where a portion of the trees in the canopy drop their leaves in the unfavorable season. These forests are classified as Semideciduous when 20 to 50% of the canopy trees drop their leaves, and as Deciduous when the percentage is higher than 50%. Seasonality is associated with the dry period in the tropical area of Brazil, and with the cold period in the subtropics (IBGE 2012). Diversity in Seasonal Forests is lower than in Ombrophilous Forests even on soils of high fertility (Roderjan et al. 2002).

Given the varying nomenclature attributed to areas associated with water bodies, as clarified by Rodrigues (2009), we only selected studies in which periodic flooding or alluvial soils were characterized. Forest surveys along

structurally controlled river margins, as those set in geological faults, were not considered. The association of each area with Atlantic Forest or Pampa was derived from the IBGE vegetation map (2017).

The data was organized in a species presence/absence matrix. A total of 56 areas (Table SI- Supplementary Material) located in the states of Santa Catarina (01), Paraná (20), Rio Grande do Sul (16), São Paulo (05), Rio de Janeiro (02), Minas Gerais (08), Mato Grosso do Sul (03) and Espírito Santo (01) were selected. Species were grouped by families in accordance with the APG IV system (2016). Synonyms were refined based on the Brazilian Flora 2020 Database (2017). Non-identified taxa were excluded. Only species occurring in alluvial formations were considered from studies that covered other vegetation types.

Study areas

The areas considered in our study cover eight states in five geographic regions in Brazil, and are generally well conserved despite past disturbance in the respective biomes. The areas are mainly flat and subject to periodic flooding of variable frequency and duration. The soils on the floodplain are marked by varying levels of hydromorphy, classified as Gleysol or Fulvic Neosol. All drainage basins are inserted in the Atlantic and Paraná-Uruguay basins.

The Prata River basin is the second largest drainage basin in Brazil, formed by the rivers Paraná, Paraguay and Uruguay (Tucci 2006). The Paraná basin includes the Paraná river basin up to the mouth of the Iguaçu river. A tropical climate predominates in the area, with a subtropical variant mainly in the states of Paraná and Santa Catarina. The Uruguay basin covers the entire area of the Uruguay river, which is formed by the confluence of the Pelotas and Canoas rivers that flow into the

Prata river estuary. The Uruguay river marks the border between Brazil and Argentina, as well as between the states of Rio Grande do Sul and Santa Catarina, in Brazil. The climate in this area is subtropical. Rainfall is distributed throughout the year and more intense in the summer months (Kettelhut & Pereira 2006). The Atlantic basin is formed by a number of coastal basins that flow into the ocean, in five drainage regions: Western Northeast Atlantic, Eastern Northeast Atlantic, Eastern Atlantic, Southeastern Atlantic and Southern Atlantic. The Southeastern Atlantic drainage is formed by the water basins that flow into the Brazilian southeastern coast, including part of the eastern region and the Zona da Mata in the state of Minas Gerais. The rugged terrain favors the occurrence of orographic rains and marked climatic diversity always associated with high temperatures (MMA 2006a, ANA 2015). The Southern Atlantic drainage covers the southernmost region of the coastal mountain range. The climate is predominantly subtropical with high rainfall and no dry period, with summers varying from hot to mild depending on the altitude (MMA 2006b).

Data analysis

A Cluster analysis was performed based on the tree species presence/absence matrix to assess the existence of species assemblages (Valli 2002) between the communities considered in this study. Floristic similarity was determined by means of the Sorensen Distance measure. A dendrogram was generated with a clustering method using the UPGMA (Unweighted Pair Group Method with Arithmetic Mean) algorithm.

The floristic data matrix was ordinated by means of Non-Metric Multidimensional Scaling (NMDS) multivariate analysis using Sorensen Distance as the floristic dissimilarity measure (Minchin 1987). In this ordination method, the areas are plotted on a dispersal graph, with

distances between them proportional to the respective dissimilarities (Clarke & Warmick 1994, Babweteera & Brown 2009). The use of this method in the study of communities has advantages such as not assuming linear relations between variables, being less sensitive to distortion, and less influenced by outliers. Besides, it can be applied to several types of ecological circumstances (Clarke & Warmick 1994, Mcgarigal et al. 2000). The adequacy of NMDS ordination for data interpretation was evaluated by means of “stress” values (standardized residual sum of squares) considering values lower than 0.2 as appropriate, as established by Kruskal (1964). “Stress” refers to the distortion between the similarity or dissimilarity matrix and the ordination generated in the graphic representation of axes (Ferreira & Casatti 2006). The geographic coordinates of the different areas were plotted on a map with an indication of the floristic assemblages to which they belonged in order to spatialize the results.

A Principal Component Analysis (PCA) was performed with climatic data from WorldClim (Hijmans et al. 2005) to determine environmental gradients. A multicollinearity analysis by means of VIF (Variance Inflation Factor) was executed to identify redundant variables. Variables with high multicollinearity ($VIF > 10$) were removed.

An analysis of indicator species was then conducted to determine which species best represented each assemblage. A significance level of $p < 0.05$ was defined as a reference. This method allows for the identification of species strongly associated with a certain dataset. Indicative values for each species are independent of the relative abundance of other species (Dufrêne & Legendre 1997).

The analyses were processed using R Statistics Software, version 3.4.1 (R Development Core Team 2017), using the *vegan* (Oksanen et al. 2017), *labdsv* (Roberts 2016), *dendextend* (Galili

2015), *maptools* (Bivand & Lewin-Koh 2017) and *USDM* (Naimi et al. 2014) packages.

RESULTS

The dissimilarity dendrogram (Figure 1) clearly showed the existence of two distinct floristic assemblages predominantly associated with the river basins in which the surveyed areas were inserted. The Atlantic basin (blue) and Paraná-Uruguay (red) basin covered eight and 48 areas, respectively. The Atlantic basin group was mainly concentrated along the Atlantic Forest coast (Figure 2), with a tendency of areas in more tropical climate. The Paraná-Uruguay group was continentally distributed in both regions (Atlantic Forest and Pampa) over a larger geographic range, predominantly in subtropical climate.

The highest floristic similarity of all the areas considered in this study (approximately 20% dissimilarity) was observed between two watersheds in the Paraná-Uruguay basin (Dani and Rodr), while areas with the highest floristic similarity in the Atlantic basin had approximately 40% dissimilarity (Rena and Sand). The areas selected for the present study with respective identification codes and complementary data are listed in (Table SI).

A list of 776 tree species in 145 botanical families was compiled from the 56 areas reviewed in this study (Table SII). The number of species varied between 8 in the area of lowest richness to 157 in the area of highest richness, with an average of 52 species. The group formed by alluvial forests in the Atlantic basin included 394 species distributed in 68 families, of which *Fabaceae* (55 species), *Myrtaceae* (52 species), *Lauraceae* (23 species) and *Rubiaceae* (20 species) were best represented. While 55 families were represented by less than 10 species, 22

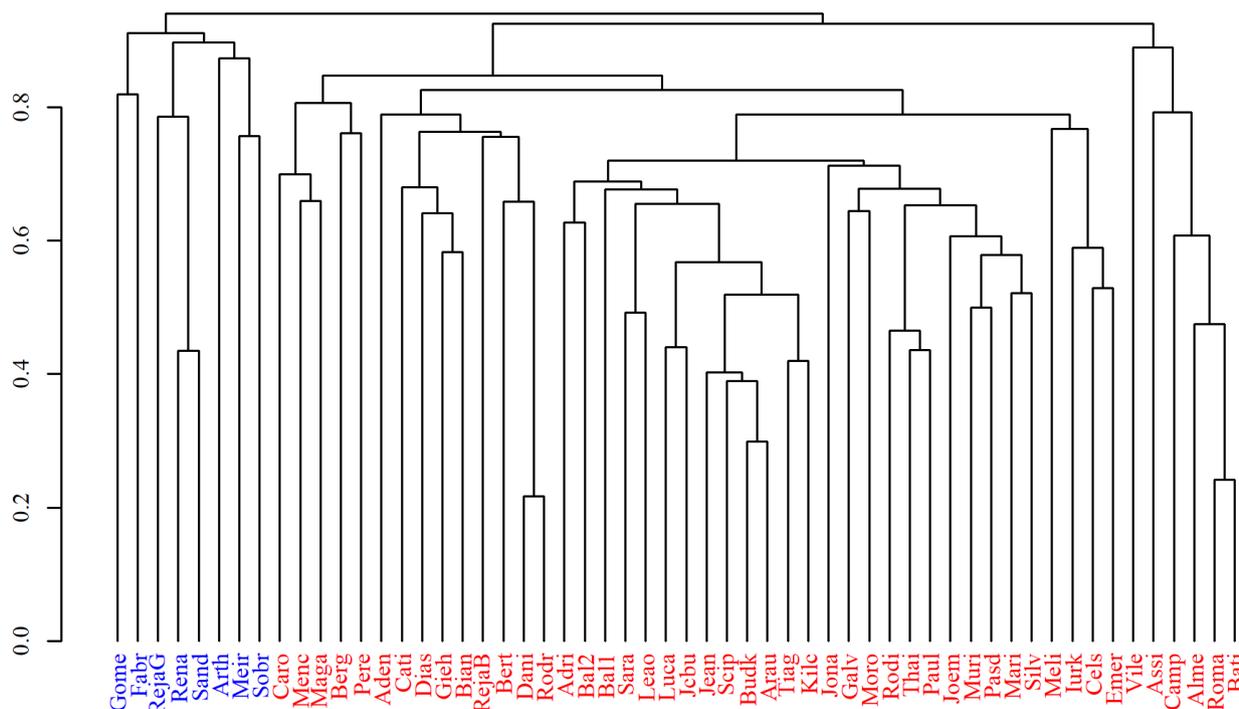


Figure 1. Dendrogram generated by means of Sorensen Distance and UPGMA for alluvial forest areas in Atlantic Forest and Pampa. Areas in the Paraná-Uruguay basin are shown in red. Areas in the Atlantic basin are shown in blue.

families were represented by only one species. The four best represented families in the group amounted to 150 species, equivalent to 38.07% of the total number of species. The group formed by alluvial forests in the Paraná-Uruguay basin included 538 species in 83 families, of which *Myrtaceae* (91 species), *Fabaceae* (72 species), *Lauraceae* (30 species) and *Rubiaceae* (29 species) were best represented. While 69 families were represented by less than 10 species, 32 families were represented by only one species. The best represented families amounted to 222 species, equivalent to 41.26% of the total number of species in the group.

The occurrence of two distinct floristic assemblages was complementarily verified from the ordination of areas by NMDS (Figure 3). This ordination showed a “stress” level of 0.15, which indicates its appropriateness for the interpretation of results. The Atlantic group was more cohesive, with areas less dispersed,

inferring higher similarity. The Paraná-Uruguay group showed higher dispersal of areas by NMDS, reflecting lower floristic similarity.

The PCA (Figure 4) showed that Axis 1, with total explained inertia of 39.85%, was strongly correlated with the variables temperature in the wettest quarter (bio 8) and rainfall in the coldest quarter (bio 19), with loadings of 0.46 and -0.46, respectively. Therefore, while areas with wet winters and lower temperatures in the period of highest rainfall are shown to the left side of the ordination, areas with antagonistic climatic conditions, drier winters and higher temperatures in the period of highest rainfall, are shown to the right of the ordination. Axis 2, which explained 22.44% of the total variation, was strongly correlated with the variables temperature in the warmest quarter (bio 10), temperature in driest quarter (bio 9) and isothermality (bio 3), with loadings of -0.56, 0.52 and 0.50, respectively. The lower part of the

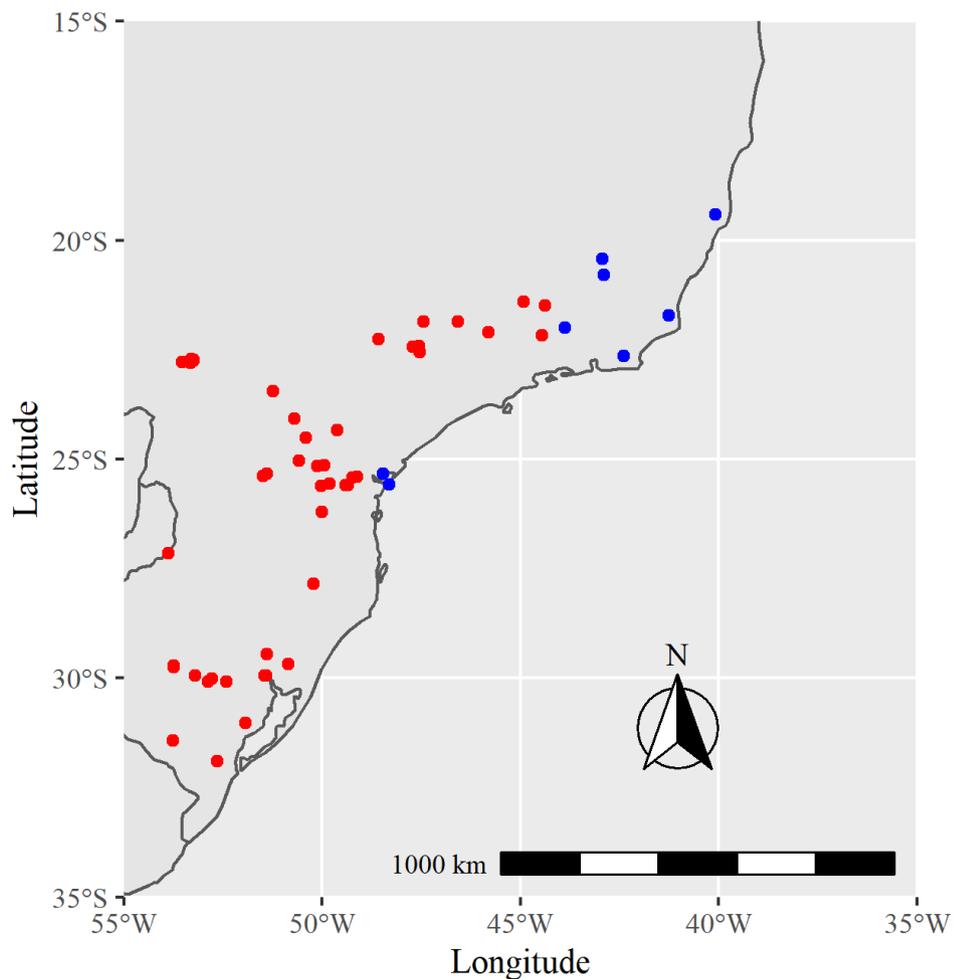


Figure 2. Geographic distribution of alluvial forests in Atlantic Forest and Pampa. Areas in the Paraná-Uruguay basin are shown in red. Areas in the Atlantic basin are shown in blue.

ordination shows areas with less warm summers and higher isothermality (diurnal temperature range rather similar to annual temperature range), while the upper part shows areas with warmer summers and lower isothermality (diurnal temperature range lower than annual temperature range). The upper right quadrat includes the areas where the driest quarters are hotter, while the lower left quadrat includes the areas with low temperature in the driest quarter.

The analysis of indicator species showed that the group formed by alluvial forests in the Paraná-Uruguay basin contained 13 species considered indicators (Table I). These species were distributed in nine families, *Euphorbiaceae* and *Myrtaceae* being dominant

with three species each. The group formed by alluvial forests in the Atlantic basin contained 69 indicator species (Table I) distributed in 31 families. *Fabaceae* and *Myrtaceae* stand out with 10 and 8 species, respectively. The highest indicator value was attributed to *Gymnanthes klotzschiana* Müll. Arg.. This is the species with the highest affinity with the first assemblage. *Allophylus edulis* (A.St.-Hil., Cambess & A. Juss.) and *Vitex megapotamica* (Spreng.) Moldenke also stand out in the same assemblage, while *Andira fraxinifolia* Benth. had the highest value in the second assemblage, followed by *Pera glabrata* (Schott) Poepp. ex Baill. and *Aniba firmula* (Nees & Mart.) Mez.

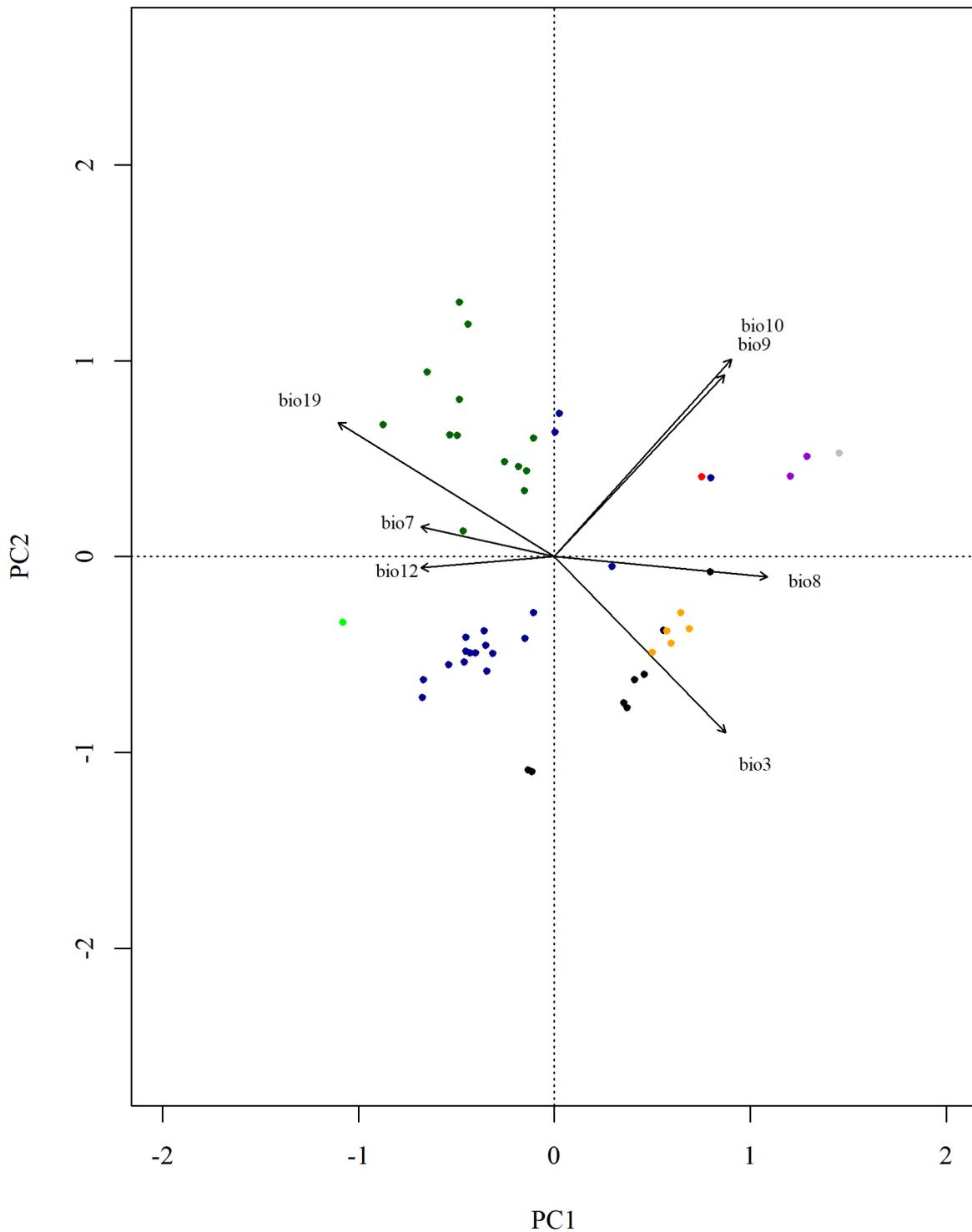


Figure 4. Climatic ordination of alluvial forests in Atlantic Forest and Pampa by means of Principal Component Analysis (PCA). (bio 3 = isothermality; bio 7 = annual temperature; bio 8 = temperature in wettest quarter no; bio 9 = temperature in driest quarter; bio 10 = temperature in hottest quarter; bio 12 = annual rainfall; bio 19 = rainfall in coldest quarter; Dark blue = Paraná; Green = Santa Catarina; Dark green = Rio Grande do Sul; Black = Minas Gerais; Orange = São Paulo; Dark violet = Rio de Janeiro; Gray = Espírito Santo; Red = Mato Grosso do Sul).

Table I. Analysis of indicator species for alluvial forests in Atlantic Forest and Pampa.

Indicator species	Family	Indicator value	p
Paraná-Uruguay basin			
<i>Gymnanthes klotzschiana</i> Müll.Arg.	<i>Euphorbiaceae</i>	0.890	0.001
<i>Allophylus edulis</i> (A.St.-Hil., Cambess & A. Juss.) Radlk.	<i>Sapindaceae</i>	0.804	0.002
<i>Vitex megapotamica</i> (Spreng.) Moldenke	<i>Lamiaceae</i>	0.777	0.005
<i>Campomanesia xanthocarpa</i> (Mart.) O.Berg	<i>Myrtaceae</i>	0.736	0.002
<i>Casearia decandra</i> Jacq.	<i>Salicaceae</i>	0.722	0.036
<i>Luehea divaricata</i> Mart.	<i>Malvaceae</i>	0.708	0.047
<i>Eugenia uniflora</i> L.	<i>Myrtaceae</i>	0.707	0.009
<i>Sebastiania brasiliensis</i> Spreng.	<i>Euphorbiaceae</i>	0.692	0.018
<i>Calyptanthes concinna</i> DC.	<i>Myrtaceae</i>	0.645	0.030
<i>Nectandra megapotamica</i> (Spreng.) Mez	<i>Lauraceae</i>	0.645	0.020
<i>Inga vera</i> Willd.	<i>Fabaceae</i>	0.629	0.026
<i>Actinostemon concolor</i> (Spreng.) Mull.Arg.	<i>Euphorbiaceae</i>	0.612	0.033
<i>Ruprechtia laxiflora</i> Meisn.	<i>Polygonaceae</i>	0.595	0.050
Atlantic basin			
<i>Andira fraxinifolia</i> Benth.	<i>Fabaceae</i>	0.783	0.001
<i>Pera glabrata</i> (Schott) Poepp. ex Baill.	<i>Peraceae</i>	0.722	0.001
<i>Aniba firmula</i> (Nees & Mart.) Mez	<i>Lauraceae</i>	0.707	0.001
<i>Cecropia glaziovii</i> Snethl.	<i>Urticaceae</i>	0.707	0.001
<i>Hyeronima alchorneoides</i> Allemão	<i>Phyllanthaceae</i>	0.707	0.001
<i>Inga edulis</i> Mart.	<i>Fabaceae</i>	0.707	0.001
<i>Nectandra oppositifolia</i> Nees	<i>Lauraceae</i>	0.707	0.001
<i>Tapirira guianensis</i> Aubl.	<i>Anacardiaceae</i>	0.640	0.002
<i>Calophyllum brasiliense</i> Cambess.	<i>Calophyllaceae</i>	0.632	0.001
<i>Guatteria australis</i> A.St.-Hil.	<i>Annonaceae</i>	0.612	0.002
<i>Inga thibaudiana</i> DC.	<i>Fabaceae</i>	0.612	0.004
<i>Lecythis pisonis</i> Cambess.	<i>Lecythidaceae</i>	0.612	0.004
<i>Myrcia racemosa</i> (O.Berg) Kiaersk.	<i>Myrtaceae</i>	0.612	0.002
<i>Pseudopiptadenia contorta</i> (DC.) G.P.Lewis & M.P.Lima	<i>Fabaceae</i>	0.612	0.001
<i>Simarouba amara</i> Aubl.	<i>Simaroubaceae</i>	0.612	0.004
<i>Tabebuia cassinoides</i> (Lam.) DC.	<i>Bignoniaceae</i>	0.612	0.002
<i>Alchornea triplinervia</i> (Spreng.) Mull.Arg.	<i>Euphorbiaceae</i>	0.559	0.004
<i>Annona dolabripetala</i> Raddi	<i>Annonaceae</i>	0.530	0.007
<i>Coussapoa microcarpa</i> (Schott) Rizzini	<i>Urticaceae</i>	0.530	0.007
<i>Euterpe edulis</i> Mart.	<i>Arecaceae</i>	0.530	0.008
<i>Garcinia gardneriana</i> (Planch. & Triana) Zappi	<i>Clusiaceae</i>	0.530	0.005
<i>Pseudobombax grandiflorum</i> (Cav.) A.Robyns	<i>Malvaceae</i>	0.530	0.009
<i>Pterocarpus rohrii</i> Vahl	<i>Fabaceae</i>	0.530	0.007
<i>Andira ormosioides</i> Benth.	<i>Fabaceae</i>	0.500	0.019
<i>Astrocaryum aculeatissimum</i> (Schott) Burret	<i>Arecaceae</i>	0.500	0.017
<i>Basiloxylon brasiliensis</i> (All.) K.Schum.	<i>Malvaceae</i>	0.500	0.017
<i>Brosimum lactescens</i> (S.Moore) C.C.Berg	<i>Moraceae</i>	0.500	0.021

Table I. Continuation

Indicator species	Family	Indicator value	p
<i>Calyptanthus rubella</i> (O.Berg) D.Legrand	Myrtaceae	0.500	0.025
<i>Carpotroche brasiliensis</i> (Raddi) A Gray	Achariaceae	0.500	0.017
<i>Chrysophyllum lucentifolium</i> Cronquist	Sapotaceae	0.500	0.017
<i>Clusia criuva</i> Cambess.	Clusiaceae	0.500	0.025
<i>Cupania racemosa</i> (Vell.) Radlk.	Sapindaceae	0.500	0.015
<i>Dalbergia nigra</i> (Vell.) Allemão ex Benth.	Fabaceae	0.500	0.016
<i>Ecclinusa ramiflora</i> Mart.	Sapotaceae	0.500	0.026
<i>Erythroxylum cuspidifolium</i> Mart.	Erythroxylaceae	0.500	0.015
<i>Eugenia expansa</i> Spring ex Mart.	Myrtaceae	0.500	0.024
<i>Eugenia macahensis</i> O.Berg	Myrtaceae	0.500	0.015
<i>Ficus gomelleira</i> Kunth	Moraceae	0.500	0.012
<i>Ilex pseudobuxus</i> Reissek	Aquifoliaceae	0.500	0.025
<i>Inga flagelliformis</i> (Vell.) Mart.	Fabaceae	0.500	0.016
<i>Joannesia princeps</i> Vell.	Euphorbiaceae	0.500	0.017
<i>Manilkara subsericea</i> (Mart.) Dubard	Sapotaceae	0.500	0.025
<i>Miconia cinerascens</i> Miq.	Melastomataceae	0.500	0.024
<i>Mollinedia schottiana</i> (Spreng.) Perkins	Monimiaceae	0.500	0.022
<i>Myrcia brasiliensis</i> Kiaersk.	Myrtaceae	0.500	0.025
<i>Myrcia insularis</i> Gardner	Myrtaceae	0.500	0.025
<i>Myrcia pubipetala</i> Miq.	Myrtaceae	0.500	0.025
<i>Myrcia strigipes</i> Mart.	Myrtaceae	0.500	0.025
<i>Naucleopsis oblongifolia</i> (Kuhlm.) Carauta	Moraceae	0.500	0.016
<i>Neoraputia alba</i> (Nees & Mart.) Emmerich ex Kallunki	Rutaceae	0.500	0.017
<i>Ocotea odorifera</i> (Vell.) Rohwer	Lauraceae	0.500	0.022
<i>Piptadenia gonoacantha</i> (Mart.) J.F.Macbr.	Fabaceae	0.500	0.021
<i>Platymiscium floribundum</i> Vogel	Fabaceae	0.500	0.024
<i>Pleroma trichopoda</i> DC.	Melastomataceae	0.500	0.025
<i>Pourouma guianensis</i> Aubl.	Urticaceae	0.500	0.024
<i>Schefflera angustissima</i> (Marchal) Frodin	Araliaceae	0.500	0.025
<i>Seguiera langsdorffii</i> Moq.	Phytolaccaceae	0.500	0.014
<i>Senefeldera verticillata</i> (Vell.) Croizat	Euphorbiaceae	0.500	0.017
<i>Solanum cernuum</i> Vell.	Solanaceae	0.500	0.021
<i>Sorocea guilleminiana</i> Gaudich.	Moraceae	0.500	0.017
<i>Tabernaemontana laeta</i> Mart.	Apocynaceae	0.500	0.022
<i>Tibouchina estrellensis</i> (Raddi) Cogn.	Melastomataceae	0.500	0.016
<i>Xylopia sericea</i> A.St.-Hil.	Annonaceae	0.500	0.019
<i>Guapira opposita</i> (Vell.) Reitz	Nyctaginaceae	0.474	0.019
<i>Matayba guianensis</i> Aubl.	Sapindaceae	0.474	0.022
<i>Cordia sellowiana</i> Cham.	Boraginaceae	0.433	0.042
<i>Guapira graciliflora</i> (Mart. Ex Schmidt) Lundell	Nyctaginaceae	0.408	0.042
<i>Handroanthus umbellatus</i> (Sond.) Mattos	Bignoniaceae	0.408	0.046
<i>Pouteria beaurepairei</i> (Glaz. & Raunk.) Baehni	Sapotaceae	0.408	0.050

p: significance of indicator species analysis

DISCUSSION

An average of 52 tree species (between 8 and 157 species, with a standard deviation of 30) occur in alluvial forests considered in this study. However, higher numbers have been observed in non-alluvial forests in the Atlantic Forest region, corroborating the fact that flood pulses create selective conditions that reduce the number of species capable of establishing in this environment. Higuchi et al. (2018), for example, registered 84 tree species in Mixed Ombrophilous Forest, while Cagliani et al. (2018) registered 183 species in Dense Ombrophilous Forest, both of them forest types inserted in the Atlantic Forest region. The number of tree species was also higher in transitional areas between the Atlantic Forest and Pampa regions not subject to flooding than in alluvial environments, with species numbers varying between 53 (Costa et al. 2018) and 107 (Possebom et al. 2017). It is important to stress the relevance of ecosystem services provided by alluvial forests, which extend beyond floristic differences: regulation of drainage flow, reduction of siltation in rivers, streams and wetlands, maintenance of water quality and the hydrological cycle, conservation of biodiversity, and climate regulation (Aguiar Junior & Parron 2015, Marenzi & Longarete 2018). The possibility of occupation of wetlands as climate refuges in a scenario of global climate change and changes in rainfall patterns (Viadana & Cavalcanti 2006, Sobral-Souza & Lima-Ribeiro 2017) along with the increased vulnerability of endemic species established in biologically impoverished communities in fragmented habitats (Medeiros et al. 2013) stress the importance of conservation of alluvial areas in the Atlantic Forest and Pampa biomes, essential for the maintenance of ecosystem services (Ferraz et al. 2014) and the conservation of biological diversity (Sobral-Souza & Lima-Ribeiro 2017).

The total number of species found in all the studies assessed, 776, is close to estimates derived from other studies in areas subject to flooding. Silva et al. (2007) registered 510 species in 23 alluvial areas in the southern and southeastern regions in Brazil. Giehl et al. (2011) found higher numbers, 1,093 species in 58 areas subject to flooding, but in this case the study area was larger than the one in the present study, involving the southern, southeastern and central-western regions in Brazil as well as Argentina and Uruguay. Rodrigues & Nave (2009) recorded the occurrence of 947 species in 43 areas in a study that compared riparian forests in Brazil outside the Amazon region, covering flooding and non-flooding environments in the states of São Paulo, Minas Gerais, Paraná, Mato Grosso do Sul, Mato Grosso and the Federal District. Wittmann et al. (2017) registered 904 species in 58 areas in Atlantic Forest and 183 in 13 areas in Pampa in a study on areas subject to different levels of flooding. Variations in species richness may be explained by the differences in the extent and approach of these studies, and most of all because areas not subject to flooding were included in some of them. In these cases, it was not possible to compare results or draw further conclusions. Alluvial forests imply the existence of floodplains, but this condition is not always taken into consideration in studies on these environments. The floristic results obtained corroborate the conclusions by Forzza et al. (2010) that indicate *Fabaceae*, *Myrtaceae* and *Rubiaceae* as part of the group of ten most diverse families in Brazil in terms of numbers of species.

The studies in the Atlantic basin included areas in Dense Ombrophilous Forest and Semideciduous Seasonal Forest, with more areas in the first type. The Paraná-Uruguay studies included areas in Atlantic Forest and Pampa of all vegetation types with higher representativity

of Deciduous and Semideciduous Seasonal Forests followed by Mixed Ombrophilous Forest.

The highest floristic similarity in the Atlantic basin was observed between geographically proximate areas (Guaraqueçaba and Paranaguá, both in Paraná state) in Dense Ombrophilous Forest. The highest similarity in the Paraná-Uruguay basin was between Semideciduous Seasonal Forests in the Atlantic Forest in the same municipality (Ipeúna, São Paulo state). The Atlantic basin included six of the seven *stricto sensu* areas in the Atlantic Forest region, suggesting a lower level of shared species between Dense Ombrophilous Forest and the other forest types in the region, Mixed Ombrophilous Forest and Seasonal Forests. Higuchi et al. (2013) reviewed studies on forest formations in southern Brazil in which they noted higher similarity between Mixed Ombrophilous Forest and Deciduous Seasonal Forest, which are therefore more dissimilar from Dense Ombrophilous Forest, corroborating the results of this study. Although the areas of highest similarity in both basins were geographically close, geography does not fully explain the groups formed, as shown in the distribution map of the areas considered in this study (Figure 2).

The floristic organization of tree species derived by means of NMDS corroborated the results shown in the dendrogram. They indicate the existence of two separate groups of areas and denote that alluvial environments are not homogeneous, although they may occur in the same region or be geographically proximate. Fiaschi & Pirani (2009) noted the existence of distinct groups in the Atlantic Forest domain, represented by southern and northern areas, upon a review of biogeographic studies. As a smaller number of studies was available for the Atlantic basin, mainly in Dense Ombrophilous Forest, this may have influenced the formation of a more cohesive, denser group. The Paraná-Uruguay group, which included more areas

and higher phytogeographic heterogeneity, is more dispersed in terms of NMDS and more broadly distributed in Brazil, with more diverse environmental conditions in terms of climate, geology, geomorphology and soils.

The floristic assemblages determined in the present study may be explained in part by the concept of migratory dispersal routes which give emphasis to fluvial canals for species dispersal from tropical areas in the North-South direction and vice-versa. Under this perspective, the floristic profile of areas in the Paraná-Uruguay watersheds is more influenced by an interior dispersal route in the West. Diversely, the Atlantic basin is more influenced by a dispersal route along the Brazilian coast in the East, with elements typical of Dense Ombrophilous Forest covering the coastal plains and slopes of the coast range (Rambo 1961). Jarenkow & Waechter (2001) indicated the transposition of these migratory events in the high plains in Southern Brazil. Rambo (1951) suggested that the “door of Torres” (“Porta de Torres”), a coastal strip between the municipalities of Torres and Osório, allowed the entry of species of the Atlantic domain into the state of Rio Grande do Sul. Although the Atlantic corridor reaches the state of Rio Grande do Sul at the “door of Torres”, some species of the Atlantic contingent spread West, while others extended to the South and mixed with deciduous forests that reach the coast of Rio Grande do Sul due to the absence of geographical barriers, forming a gradient of specific richness (Jarenkow & Waechter 2001, Higuchi et al. 2013). Although distributed on the coastal plain, the alluvial areas closer to the coast in Rio Grande do Sul differed from other coastal areas in Brazil and were included in the Paraná-Uruguay group. The absence of the Atlantic component along the Rio Grande do Sul coastline south of Osório occurs due to different climatic conditions marked by subtropical characteristics of the

state and the absence of geographic barriers, an essential element for the formation of orographic precipitation. As explained by Roldão et al. (2012), the frequent orographic rains in the coast range (Serra do Mar) and general range (Serra Geral) are formed due to geographic isolation, a particular condition of mountain ranges.

The Campos dos Goytacazes gap (Oliveira-Filho & Fontes 2000) produces an area of discontinuity of Dense Ombrophilous Forest between the states of Rio de Janeiro and Espírito Santo. The seasonal component reaches the coast in this area, highlighting the irregularity of rainfall throughout the year (Prata et al. 2018). This is justified by the absence of the coast range (Serra do Mar) and aggravated by the texture of soils derived of Barreiras sandstone, which creates more intense drainage. The floristic profile of forests in the region, however, is somewhat similar to Dense Ombrophilous Forests in southern Bahia (called "Hileia Baiana") (Saiter et al. 2016). It is therefore plausible that species physiologically incompatible with climatic seasonality have survived, especially in areas where soils retain more humidity throughout the entire year, as in the case of river margins. It can therefore be inferred that, even in periods of restricted rainfall in the months when the Intertropical Convergence Zone does not affect the Southern Hemisphere, species of the Atlantic contingent may use alluvial plains as dispersal corridors to the interior of the continent because there is more water available, as was also suggested by Saiter et al. (2016). In this line of reasoning, as exemplified by the "door of Torres" in southern Brazil, it is viable to consider that this region can also function as entry point for tropical humid species to integrate the flora of continental high plain forests.

Axis 1 of the PCA explained 39.85% of the data and showed that nearly all the areas to the left of the ordination were located in southern Brazil.

Dense Ombrophilous Forest areas were clustered in the lower quadrat, while Deciduous Seasonal Forest areas were clustered in the upper quadrat. These forests occur in subtropical conditions with no dry season in winter (bio 19) and lowest temperatures in the period of higher rainfall (bio8). Contrarily, part of the areas to the right of the ordination, mostly in Dense Ombrophilous Forest and some in Deciduous Seasonal Forest, in the lower quadrat, are subject to higher rainfall seasonality. On this side of the ordination, the areas in Espírito Santo (ES) and Rio de Janeiro (RJ) were more highly dispersed from the others and more densely clustered among themselves, which may be attributed to drier winters in the absence of orographic precipitation that supports the occurrence of Semideciduous Seasonal Forest. The vectors representing the variables temperature (b8, b9 and b10) point in the opposite direction of the vectors representing rainfall (bio 12 and bio 19), showing a negative correlation between these variables. Axis 1 therefore synthesized a gradient of tropicality, as the variables that best explain the data are related with temperature (bio 8) and rainfall (bio 19).

The interpretation of Axis 2 showed that the areas in the states of Minas Gerais (MG) and São Paulo (SP) are clustered in the lower part of the right quadrat, while the areas in Rio Grande do Sul (RS) are in the upper part of the left quadrat. The seasonal domain is therefore present above and below Axis 2 as a result of differences in seasonality due to the unfavorable dry season in the tropical region (lower right quadrat) and cold season in the subtropical region (upper left quadrat) (Athayde et al. 2013). The areas in MG occur at lower latitudes but at higher altitudes, as they are mostly located in the southern part of the state. The areas in RS, in Pampa, occur at higher latitudes and lower altitudes and are associated with the regularity of rainfall (bio 19) originated by cold fronts uniformly distributed

throughout the year. Axis 2 of the PCA therefore synthesized a gradient of altitude, as the variables that best explain the data are related with temperature (bio 10 and bio 9) and isothermality (bio 3). The altitudinal gradient is in fact evident from top to bottom when evaluating all areas in the graph, with areas closer to sea level in the upper part of the graph and to higher altitudes in the lower part. Isothermality may be related to altitude, between other factors, as lower areas closer to the sea level are usually subject to smaller diurnal amplitude (lower isothermality) than higher altitude areas (higher isothermality). Besides, isothermality is inversely proportional to latitude, also indicating a gradient of tropicality, as areas at higher latitudes undergo higher variation in annual temperature and are subject to lower isothermality (e.g. RS), while areas at lower latitudes are subject to higher isothermality (e.g. MG).

The analysis of indicator species corroborated the existence of floristic-structural differences between the assemblages formed. The Atlantic coast assemblage included more indicator species, which is probably due to the predominance of areas in Dense Ombrophilous Forest in the group. This forest formation contains a higher number of exclusive species than the other forest types considered in the present study, therefore resulting in higher dissimilarity (Mattei et al. 2007). None of the three species of highest value in the Paraná-Uruguay group - *G. klotzschiana*, *A. edulis* e *V. megapotamica* - are endemic in Brazil. These are species of wide distribution that occur in different vegetation types practically in all regions in Brazil. *A. edulis* is indicated as the second species with widest geographic distribution in the country (Flora do Brasil 2020). These species occur throughout the subtropical domain, especially in habitats associated with water in different forest types. Nevertheless, two of the three species of

highest association with the Atlantic group are endemic to Brazil (*Andira fraxinifolia* and *Aniba firmula*). These species are widely distributed both in terms of biome and geographic region. Considering all states, *Pera glabrata*, for example, does not occur only in Piauí state. Despite the wide distribution range, these species are mainly present in tropical (Flora do Brasil 2020). Eight of the 13 indicator species in the Paraná-Uruguay group were considered as preferring alluvial forests by Silva et al. (2007), a result coherent with the evaluation conducted in this study. Species in the families *Euphorbiaceae*, *Fabaceae*, *Lauraceae*, *Malvaceae*, *Myrtaceae* and *Sapindaceae* were present in both floristic assemblages, which suggests a stronger affinity of these families with alluvial environments than the other families.

CONCLUSION

Alluvial forests in Atlantic Forest and Pampa were divided in two floristic assemblages mainly associated with river basins and migratory routes. The separation of ecological regions (Atlantic Forest and Pampa) was not a determinant in the formation of these assemblages. *Andira fraxinifolia* was the main indicator species in the Atlantic basin, which had a higher number of indicator species than the Paraná-Uruguay basin, where the main indicator species was *Gymnanthes klotzschiana*. The main gradients associated with the habitat types considered were temperature, precipitation and altitude.

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SUPPLEMENTARY MATERIAL

Tables SI, SII.

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