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Diversidade arbórea de florestas ribeirinhas na Província Pampiana no Brasil

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Resumo

A informação sobre como a diversidade é distribuída geograficamente é fundamental para a conservação da biodiversidade. Nós avaliamos a contribuição relativa das diversidades alfa e beta para a diversidade de espécies arbóreas em florestas ribeirinhas na Província Biogeográfica Pampiana no Brasil, nas escalas local e regional, e avaliamos as diferenças da diversidade alfa entre paisagens. As unidades amostrais na escala regional (paisagens) foram seis quadrados de 5 x 5 km, distribuídos em municípios distintos. Em cada uma dessas unidades regionais, amostramos três parcelas, que são as nossas unidades amostrais em escala local. Amostramos todas as árvores com diâmetros à altura do peito (DAP) maior ou igual a 5 cm. Nós utilizamos a partição multiplicativa da diversidade com "número de equivalentes" (*Hill numbers*) associada a dois modelos nulos para comparar a diversidade através das escalas espaciais. No total, 6.639 árvores foram amostradas em 4,5 ha de área amostral. As espécies nativas totalizaram 6.009 indivíduos, que foram distribuídos em 101 espécies, 74 gêneros e 37 famílias. As paisagens estudadas tiveram a riqueza padronizada de espécies arbóreas variando de 17,95 ($\pm$ 1,9) até 53,49 ($\pm$ 6,2). A partição hierárquica de diversidade com *Hill numbers* indicou um padrão de baixa diversidade alfa e alta diversidade beta de espécies arbóreas em florestas ribeirinhas na Província Biogeográfica Pampiana no Brasil, tanto na escala local como na regional. Os dois modelos nulos confirmaram esse padrão e sugerem que diferentes processos estão atuando nas escalas local e regional, de forma a reduzir a diversidade alfa e aumentar a diversidade beta. Além disso, a diversidade alfa variou consideravelmente entre as paisagens, com os maiores valores encontrados naquelas localizadas ao norte da Província Pampiana e mais próximas às rotas de migração de espécies atlânticas. Considerados juntos, esses resultados indicam que a filtragem ambiental e, principalmente, a limitação de dispersão de espécies podem estar determinando os padrões de diversidade na escala mais ampla, assim como diferentes mecanismos influenciados pelos distúrbios dos pulsos de inundação podem estar determinando os padrões na escala mais fina, dos quais destacamos a exclusão competitiva e a tolerância ao estresse. Nossos resultados foram importantes para descrever padrões de diversidade de espécies arbóreas através das escalas espaciais nas florestas Pampianas brasileiras e para fornecer importantes *insights* sobre os processos que estão determinando as diversidades alfa e beta nas escalas local e regional. O próximo passo é testar e separar os efeitos dos fatores ambientais e da limitação da dispersão de espécies como determinantes da diversidade.

Palavras-chave: diversidade alfa, diversidade beta, estrutura de comunidades, modelos nulos, florestas Pampianas, florestas ribeirinhas, florestas subtropicais estacionais semidecíduas, partição da diversidade.

Abstract

How diversity is distributed geographically within a region is a fundamental information to conserve regional biodiversity. We evaluate the relative contribution of alpha and beta diversities to tree species diversity of riverine forests within Brazilian Pampean Biogeographic Province at local and regional scales and analyzed alpha diversity differences between landscapes. The regional sampling units (landscapes) were six 5 x 5 km square, in each of which we sampled three 250 x 10 m plots, the local sampling units. We sampled all tree with diameter at breast high (DBH) more than or equal to 5 cm. We used multiplicative partitioning on Hill numbers associated to two null models to decompose diversity across spatial scales. A total of 6,639 trees were sampled in a total area of 4.5 ha. The native species added up 6,009 individuals that were distributed in 101 species, 74 genera and 37 families. The studied landscapes showed standardized tree species richness ranging from 17.95 ($\pm$ 1.9) to 53.49 ($\pm$ 6.2). Hierarchical diversity partitioning on Hill numbers indicates a pattern of low alpha diversity and high beta diversity of tree species in riverine forests in Brazilian Pampean Biogeographic Province at local and regional scales. The two null models confirm this pattern and suggest different processes acting at local and regional scales to decrease alpha diversity and increase beta diversity. Moreover, alpha diversity was considerably variable among landscapes, the highest values were found in landscapes located in the northern region of Brazilian Pampean Province, closer to the migration routes of Atlantic species. Taking together these finds suggest that environmental filtering and mainly species dispersal limitation might be shaping diversity at the broadest scale and different mechanisms influenced by flood pulse disturbances might be driving diversity at the finest scale, such as competitive exclusion and stress tolerance. Our findings were important to describe patterns of tree species diversity across spatial scales within Brazilian Pampean forests and provide useful insights about process driving diversity at each spatial scale. The next step is to testing and disentangling the effects of environmental factors and species dispersal limitation in shaping diversity at broad scaled.

Keywords: alpha diversity, beta diversity, community structure, diversity partitioning, null model approach, Pampean forests, riverine forests, subtropical seasonal semideciduous forests.

Sumário

Introdução Geral

Diversidade biológica é um conceito essencialmente hierárquico, que inclui diferentes níveis de organização, desde genes até ecossistemas, e desempenha um papel importante em processos ecológicos e evolutivos (Gaggiotti et al. 2018). Diversidade de espécies (taxonômica ou florística) representa uma das possíveis abordagens sobre diversidade biológica. Essa abordagem pode ser considerada um modo inicial e fundamental, pois estuda a unidade básica da diversidade, que são as espécies (Magurran 2004).

Whittaker (1960; 1972) definiu termos para a descrição da diversidade em relação à hierarquia de escalas. Esses termos (medidas) foram reunidos em dois grandes grupos: diversidade de inventário e diversidade de diferenciação. O primeiro agrupa as medidas de diversidade em unidades geográficas definidas: diversidade pontual (dentro da amostra), alfa (dentro do habitat), gama (dentro de uma paisagem) e épsilon (dentro de uma província biogeográfica). O segundo agrupa as medidas de diferenciação entre as unidades de uma mesma categoria: diversidade beta interna (entre amostras dentro do habitat), beta (entre habitats dentro de uma paisagem) e delta (entre paisagens). No entanto, este sistema é pouco utilizado devido à dificuldade de definir qual é a escala adequada para cada componente (Whittaker et al. 2001). Tendo em vista a praticidade e a objetividade, os pesquisadores simplificam as definições para escala local (alfa), regional (gama) e variação entre locais (beta) ou, alternativamente, a estimativa de quanto o total regional excede os valores médios locais (beta). Em trabalhos com múltiplos níveis hierárquicos, a diversidade é definida como aquela que ocorre dentro das unidades amostrais de determinado nível (alfa), na diversidade agregada dessas unidades (gama) e na diversidade de variação entre estas unidades amostrais (beta).

As florestas presentes na Província Biogeográfica Pampiana (Cabrera e Willink 1980), apesar de serem de grande interesse biogeográfico e ecológico por causa de sua localização, são pouco conhecidas em relação aos padrões e determinantes de diversidade. A Província Pampiana está inserida no Domínio Chaquenho e limita-se ao norte com as Províncias Atlântica e Paranaense, pertencentes ao Domínio Amazônico. Os limites a oeste ocorrem com a Província do Espinal, que também pertencente ao Domínio Chaquenho. O Oceano Atlântico completa a sua delimitação pelo leste. As formações campestres são predominantes na paisagem pampiana e formações arbóreas ocorrem com maior intensidade nas regiões norte da Província Pampiana, no Uruguai e no Rio Grande do Sul. É exatamente no estado mais austral do Brasil que ocorre o limite sul das florestas do Domínio Amazônico, transacionando para Província Pampiana próximo ao paralelo 30°S (Cabrera e Willink 1980).

Esta peculiaridade do Rio Grande do Sul despertou o interesse de Lindman (1909) e Rambo (1956). Ambos constataram que as condições climáticas no estado eram favoráveis ao desenvolvimento florestal, mas ca. 60% da sua área era coberta por campos. Rambo (1956) deduziu que os campos tinham origem edáfica ou climática relacionada a condições pretéritas. Dados palinológicos suportam a origem climática ao sugerirem que as formações florestais na Província Pampiana se tornaram mais amplas e diversas após as condições climáticas tornarem-se mais quentes e úmidas (Behling et al. 2005; Mourelle et al. 2017). Mourelle et al. (2017) apresentaram evidências da presença de vegetação arbórea ribeirinha com razoável adensamento durante o último período glacial. No entanto, os mesmos dados sugerem que há apenas ca. 2000 anos antes do presente é que houve um aumento gradual na abundância e na diversidade arbórea e somente há ca. 500 anos antes do presente as florestas ribeirinhas apresentaram uma composição similar à atual.

Atualmente, são descritas áreas florestais diversificadas na matriz campestre da Província Pampiana no Rio Grande do Sul, tais como, florestas mistas com *Araucaria* (Carlucci et al. 2011), mistas com *Podocarpus* (Longhi et al. 1992; Giongo 2007; Giongo e Waechter 2007), estacionais semideciduais (Jurinitz e Jarenkow 2003), matas de "pau-de-ferro" (Longhi et al. 1987) e áreas de formação arbórea aberta, como os butiazais (Marchiori et al. 1995) e os parques de espinhos (Rambo 1956; Marchiori et al. 2014). Embora as florestas de restinga na Planíce Costeira (IBGE 2004) e as florestas estacionais semideciduais na encosta leste da Serra do Sudeste entejam incluídas na Província Pampiana, elas estão floristicamente relacionadas à Mata Atlântica *lato sensu* (Oliveira-Filho e Fontes 2000), e devem ser consideradas como disjunções da Mata Atlântica.

As diferentes formações florestais citadas acima encontram-se relativamente restritas a determinadas regiões na Província Pampiana. As florestas estacionais semideciduais são as que possuem a distribuição mais ampla, e podem ser separadas nas florestas que ocorrem associadas aos cursos d'água (florestas ribeirinhas) e naquelas que ocorrem em solos razoavelmente bem drenados, principalmente, nas encostas. Com essa distinção, podemos considerar que a única formação florestal bem distribuída nas diferentes regiões da Província Pampiana é a ribeirinha. Florestas ribeirinhas podem ser consideradas como a transição entre ambientes terrestres e aquáticos em nível local, assim como corredores em escalas amplas (Malanson 1993). Desse modo, as florestas ribeirinhas são as mais antigas na Província Pampiana (Behling et al. 2005; Mourelle et al. 2017) e interconectam diferentes regiões fisiográficas e geomorfológicas através de uma rede florestal nas áreas adjacentes aos cursos d´água.

Os estudos sobre a vegetação arbórea da Província Pampiana podem ser agrupados, quanto à escala de abordagem, em dois tipos extremos: os pontuais e os regionais. Os estudos pontuais correspondem àqueles citados acima, que descrevem um tipo específico de vegetação. Embora tenham importante contribuição sobre o conhecimento florístico e estrutural destas formações, estes

trabalhos são limitados pela ausência de réplicas e extensão reduzida da área de estudo. No outro extremo, os trabalhos regionais, elaborados com metadados, são muito importantes para descrever relações florísticas em escalas mais amplas e identificar possíveis determinantes da diversidade. Os trabalhos de Oliveira-Filho et al. (2015) e Rezende et al. (2016) demonstraram que as florestas localizadas na Província Pampiana são floristicamente distintas das florestas da Mata Atlântica *lato sensu*. Os trabalhos de Giehl e Jarenkow (2012) e Oliveira-Filho et al. (2015) identificaram importantes varáveis ambientais que atuam em escalas amplas. No entanto, não há nenhum trabalho que integre as escalas locais e regionais, para descrever como a diversidade varia através das escalas espaciais.

Neste contexto, desenvolvemos nossa pesquisa com o objetivo de avaliar, através das diferentes escalas espaciais, os padrões da diversidade arbórea em florestas ribeirinhas localizadas na Província Biogeográfica Pampiana no Brasil. Para tanto, utilizamos uma metodologia padronizada e com estrutura hierárquica. Adotamos o protocolo RAPELD (https://ppbio.inpa.gov.br/instalacao; Magnusson et al. 2005; Costa e Magnusson 2010) com alterações para adequá-lo à amostragem das Florestas Pampianas. As áreas de estudo correspondem a cinco sítios estabelecidos pelo Rede de Pesquisa Campos Sulinos (http://www.ufrgs.br/redecampossulinos), acrescidas de um sítio estabelecido por nós com os mesmos critérios adotados pela Rede (Figura 1).

A estrutura hierárquica de amostragem foi composta por dois níveis espaciais: regional e local. Na escala regional, as unidades amostrais foram os seis sítios denominados unidades amostrais de paisagem (UAP), que correspondem a uma área de 2.500 ha (5 x 5 km). Dentro de cada UAP, demarcamos três parcelas de 250 x 10 m com uma distância mínima de 1 km entre si. As parcelas correspondem às unidades amostrais na escala de paisagem e foram compostas pela adição contígua de 25 unidades amostrais de 10 x 10 m. A demarcação da parcela de 250 x 10 m foi paralela à margem do rio ou arroio mantendo fixa uma distância de 10 m da margem (Figura 2). Para alcançar os objetivos, nós utilizamos a partição multiplicativa da diversidade com "número de equivalentes" (*Hill numbers*) através de hierárquicas escalas espaciais hierárquicas.
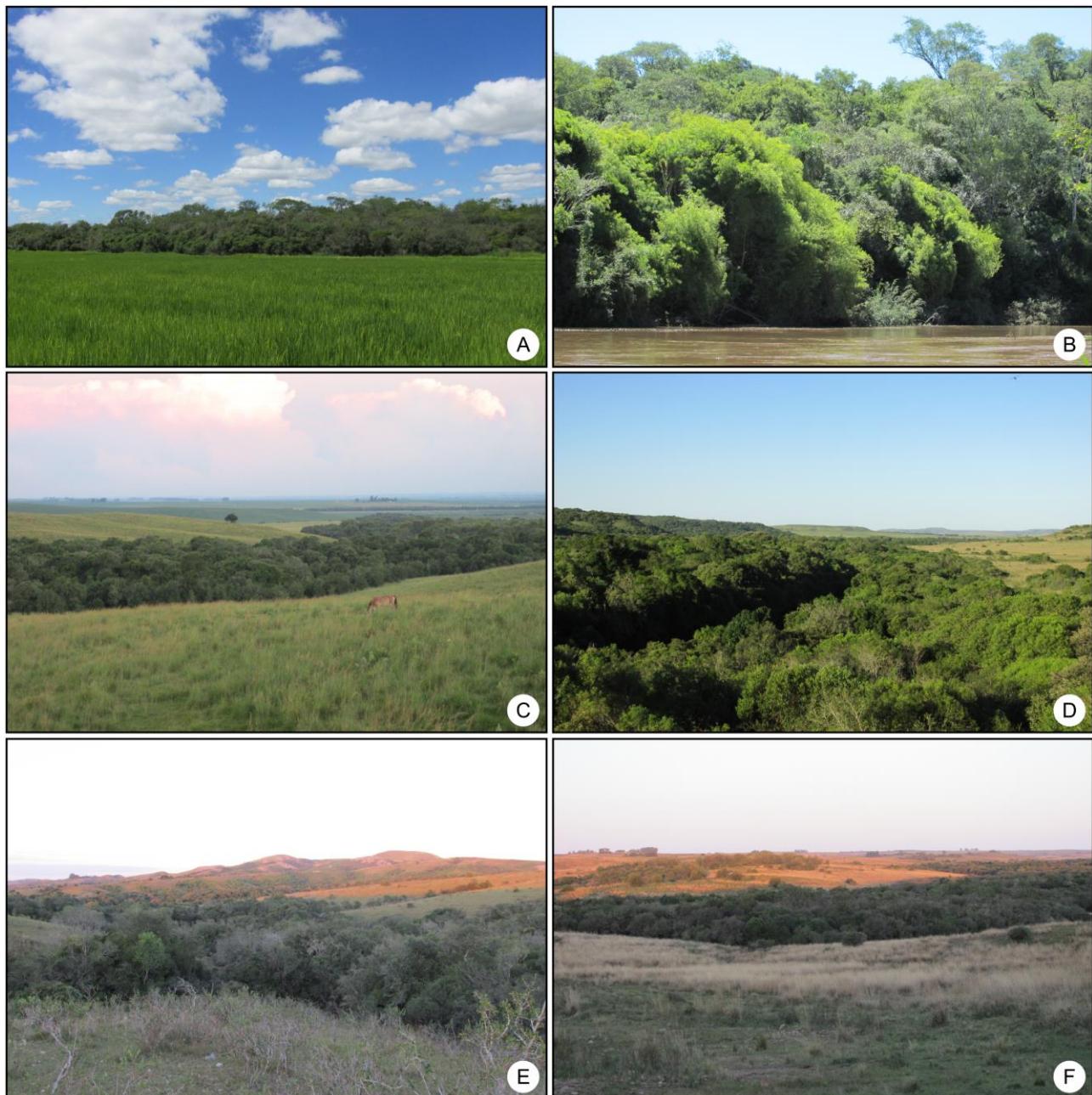
Figura 1: Florestas ribeirinhas localizadas nos cinco sítios estabelecidos pela Rede Campos Sulinos e no sítio estabelecido por nós, na Província Biogeográfica Pampiana no Brasil. Santo Antônio das Missões (A), São Francisco de Assis (B), São Gabriel (C), Quaraí (D), Santana da Boa Vista (E) e Lavras do Sul (F).
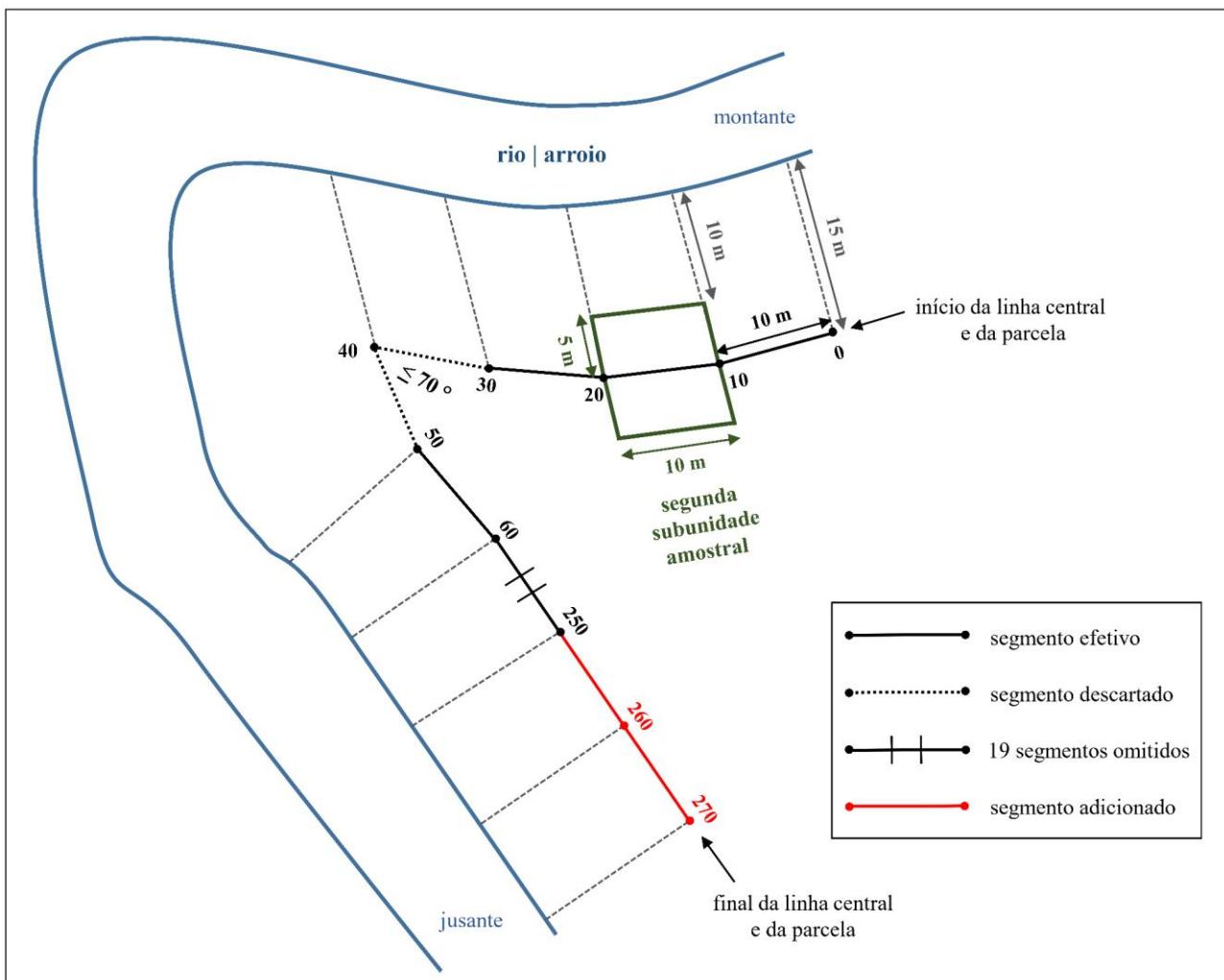
Figura 2: Demarcação da parcela de 250 x 10 m em floresta ribeirinha na Província Biogeográfica Pampiana no Brasil. A parcela foi composta por 25 unidades amostrais adicionadas continuamente ao longo de uma linha central. O início da linha central e da parcela foi na estaca de número zero, que estava 15 m distante da margem do rio ou arroio. A segunda estaca foi adicionada 10 m à frente da primeira (na direção de montante à jusante) e 15 m da margem do rio. O segmento entre as estacas formou o segmento da linha central. Este procedimento foi repetido até à estaca de número 250 (o final da linha central e da parcela) se o ângulo entre dois segmentos consecutivos fosse maior que 70°. Caso contrário, o segundo segmento foi descartado. No exemplo, os dois segmentos foram descartados, pois haveria a sobreposição entre as subunidades amostrais 4 e 5 de forma que não poderia ser compensada como os protocolos do RAPELD determinam. Os segmentos descartados foram compensados no final da parcela. A subunidade amostral correspondeu a um quadrado de 10 m de lado e distante 10 m da margem do rio. Os dois lados da subunidade amostral que eram perpendiculares ao rio foram medidos a partir da linha central com 5 m em direção ao rio e 5 m em oposição.

Capítulo 1[1]

Partitioning tree species diversity across hierarchical spatial scales in Brazilian Pampean

riverine forests

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[1] O manuscrito foi formatado conforme as normas da revista Acta Botanica Brasilica

Abstract

Partitioning diversity across hierarchical spatial scales can reveal at which scale diversity is higher or lower and allow to disentangling relative effects of community assembly process. We evaluated the relative contribution of alpha and beta diversity to tree species of riverine forests at local and regional scales and analyzed alpha diversity differences between landscapes within Brazilian Pampean Biogeographic Province. Regional sampling units (landscapes) comprised six 5 x 5 km squares, in each of which we sampled three 250 x 10 m plots, the local sampling units. We adapted the RAPELD protocol and sampled all trees with diameter at breast high (DBH) $\geq$ 5 cm. We used multiplicative partitioning on Hill numbers associated to two null models to decompose diversity. A total of 101 native tree species was sampled in a total area of 4.5 ha. The studied landscapes showed standardized tree species richness ranging from 17.95 ($\pm$ 1.9) to 53.49 ($\pm$ 6.2). Beta diversity was higher, and alpha diversity was lower than expected by chance at all scales. The scale of major contribution of beta diversity was the regional, so efforts in conservation of riverine forest should consider processes associated to environmental filtering and species dispersal limitation.

Key-words: alpha diversity; beta diversity; community structure; diversity partitioning; null model approach; Pampean forests; riverine forests; subtropical seasonal semideciduous forests

Introduction

How diversity is distributed geographically within a region is a fundamental information to conserve regional biodiversity (Jost *et al.* 2010). Diversity patterns and processes are scale dependent and studies across multiple spatial scales can reveal differences in diversity associated to the observational grain and extension, thus allowing to disentangle relative effects of community assembly process (Crist *et al.* 2003; Chandy *et al.* 2006; Chase & Myers 2011; Barton *et al.* 2013; Myers & LaManna 2016). Among different ways of measuring diversity proposed by Whittaker (1960; 1972; see Tuomisto 2010a; b), the diversity partitioning decomposes the regional diversity (gamma; γ) into the within- (alpha; α) and the between- (beta; β) group components. In this context, beta diversity is an important component of differentiation because it connects two types of inventory diversity, alpha and gamma, which are associated to geographic units at different levels of resolution (Whittaker 1972; Whittaker 2001; Magurran 2004). More precisely, beta diversity is the extent of change (or variation) in species composition in a set of communities (local scale) within a geographical area of interest (Whittaker 1960; Legendre & De Cáceres 2013). Thus, as a scalar that links different spatial scales, beta diversity can provide insights into processes underlying the assembly, diversity, and dynamic of communities (Myers & LaManna 2016).

Spatial scale is delimited by three components: spatial grain (the grain size of the elementary sampling unit), spatial extent (the total length or area) and sampling interval (the average distance between neighboring sampling units) (Whittaker 2001; Legendre & Legendre 2012). Analyses of spatial patterns should specify these elements in sampling design. The observational spatial window

is defined by the lower limit of detection by spatial grain and the upper limit of prediction by the spatial extension (Legendre & Legendre 2012). Barton *et al.* (2013) proposed the *sliding window* perspective, by varying both spatial grain and spatial extension, to evaluate the relative effect of factors on community assembly at different scales. The *sliding window* perspective can be used to evaluate patterns of diversity by comparing predictions from putative mechanisms operating across different spatial scales (Barton *et al.* 2013).

Community assembly processes can individually or interactively determine diversity by shaping occurrence and relative abundance of species across spatial scales (Myers & LaManna 2016). Two main categories of processes have been related to community assembly (*sensu* Chase & Myers 2011): deterministic (following the Niche Theory; Chase & Liebold 2003) and stochastic (following the Neutral Theory; Hubbell 2001) related processes. These processes are complementary and the window of observation across spatial scales influences our perception of their relative roles, as communities tend to be more habitat-structured at large scales and neutral-structured at fine scales (Chase 2014). Null models and analyses at multiple spatial scales are important to disentangle the relative roles of these processes on community assemblies (Chase & Myers 2011; Myers & LaManna 2016).

Patterns and drivers of plant species diversity of subtropical forests in South America have been studied in recent years. Giehl & Jarenkow (2012) highlighted the importance of niche conservatism and the decrease of species richness from tropical to subtropical climates. Gonçalves & Souza (2014) studied ecotonal areas of Subtropical Atlantic forests and showed a continuous floristic variation along with edaphic and climatic conditions related to topographic gradients. Oliveira-Filho *et al.* (2015) divided subtropical Pampean from Atlantic forests, which share a high proportion of species, but show gradual changes that result in floristic differentiation with no strong transition areas of species replacement. However, the proportion of species turnover among distinct forest formation within the Atlantic forests is considerable (Bergamin *et al.* 2018) and the importance of species replacement of Pampean forests, as a marginal habitat, to Atlantic Forest biome is highlighted (Neves *et al.* 2017). Despite recent advances in knowledge of subtropical forests in South America, there are no study that links local and regional scale by relative contribution of alpha and beta diversity.

In this study, we examine the relative contribution of alpha and beta diversity to tree component of riverine forests within Brazilian Pampean Biogeographic Province at local and regional scales and evaluate differences of alpha diversity among landscapes at the broad scale. We cover a great environmental heterogeneity in this Province and used a standardized sampling protocol to make comparable replicates across landscapes and spatial scales. Studied landscapes comprise distinct geological substratum, as in this region there are no strong topographic gradient, an important driver of species replacement at broad scale (Gonçalves & Souza 2014). Moreover, differences in species

dispersal limitation related to migration routes of Atlantic species (Rambo 1960; 1961) can play a role in differences on species richness among landscapes. At local scale, riverine forests are known to have high environmental heterogeneity over space and time related to flood pulse (Junk & Wandzen 2004; Budke *et al.* 2010) that can increase beta diversity among distinct sites through species sorting process. Alpha diversity can also vary, increasing or decreasing according to the duration and frequency of flood pulse (Giehl & Jarenkow 2015). Therefore, we intend to evaluate whether beta diversity plays an important role to local and regional species diversity and whether the landscapes have considerable differences in species richness. We addressed the following questions: (i) Do the landscapes have distinct alpha diversity? (ii) Is tree species beta diversity higher or lower than expected by chance at the two spatial levels (local and regional)? (iii) What is the main focal scale for conservation efforts of riverine Pampean forests?

Materials and Methods

Study Areas

We developed our research in areas within the Pampean Biogeographic Province in Rio Grande do Sul, the southernmost state of Brazil. The Pampean Province located in southeastern South America is characterized by grassland physiognomies (Cabrera & Willik 1980) and by the increasing presence of forests in its northernmost region. Presence of forests in Pampean Province is geologically recent and has been related to climatic changes that allowed an initial wood riverine vegetation development, during the late glacial period, to reach riverine forests with similar species composition to the current one at ca. 500 years before present (Mourelle *et al*. 2017). Tree species arrived mainly by plant migration routes from Atlantic forests and there was not enough time to allow new species to evolve (Rambo 1960; 1961; Behling *et al.* 2005). Forests located in Brazilian Pampean Province correspond to Subtropical Seasonal Semideciduous Forests and are namely Pampean (or Pampa) Forests (Oliveira-Filho *et al*. 2015; Rezende *et al.* 2016).

The study areas included different combinations of physiographic, hydrological and geomorphological regions and geological substratum (see Table S1) to account environmental heterogeneity required to measure beta diversity as variation in community structure (*sensu* Anderson *et al.* 2011). We selected five sites of the *Programa de Pesquisa em Biodiversidade* (PPBio) *Rede Campos Sulinos* (https://www.ufrgs.br/redecampossulinos) and added another site to include one more landscape with sandstone substratum in our sampling design. These sites cover an extensive area and were denominated landscape sampling units (LSUs) and each one was identified by the municipality name where they were allocated (Fig. 1). The geological substratum included basaltic,

granitic and sandstone formations and there were two LSUs for each substratum type (Tab. S1). The physical soil structure in samples collected by us at each LSU had a range from 13.3 to 70.3% of sand and a range from 14 to 53% of clay (Tab. S1). The climate of the study region, according to Köppen's classifications, is predominantly humid subtropical without dry season and with hot summer (*Cfa*) (Alvares *et al.* 2013). We extracted climatic variables from *WorldClim* database (Hijmans *et al.* 2005) for the period of 1970-2000 (see in Tab. S1). The range of mean annual temperature between LSUs was from 18.4 to 20.7 °C and for the mean annual precipitation the range between LSUs was from 1,371 to 1,731 mm. The five LSUs of *Rede Campos Sulinos* were located near of headwaters, where we sampled the riverine forests along the banks of small rivers or streams. According to Junk *et al.* (2014), these areas are subjected to polymodal (frequency) and unpredictable flood pulses of short duration.
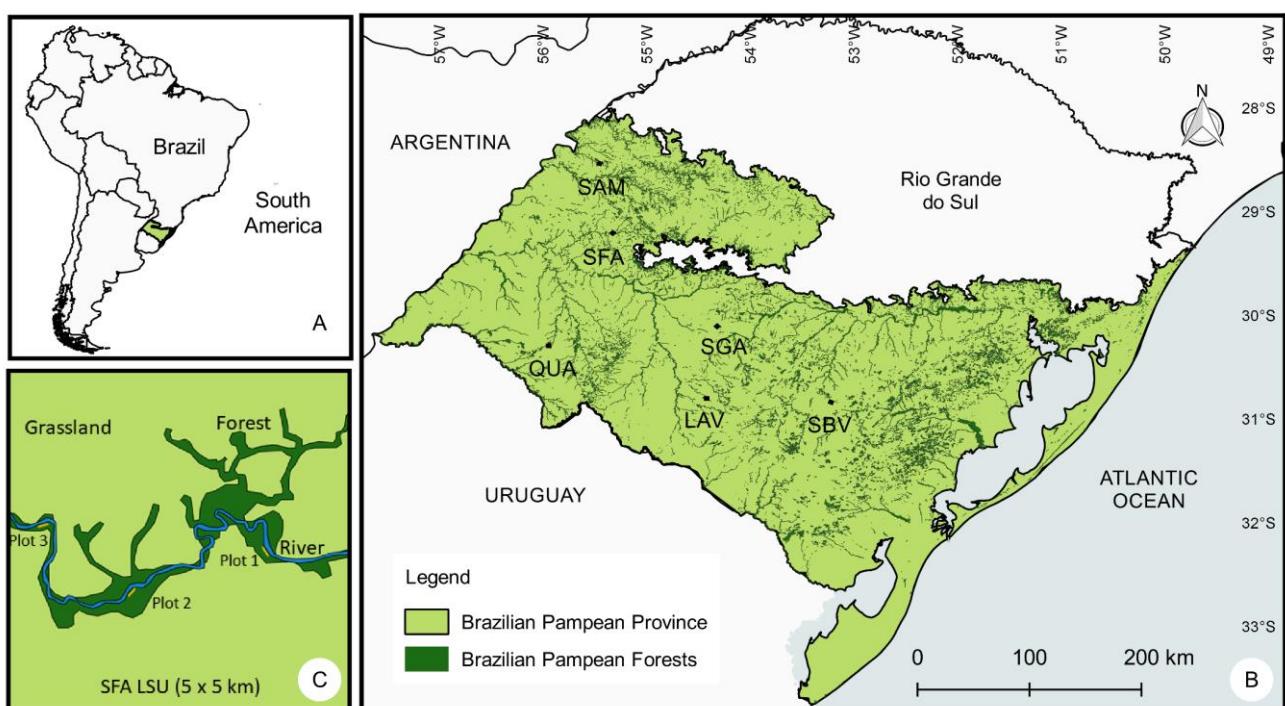
Figure 1. (A) Localization of study region in South America, (B) the remnants of Brazilian Pampean Forests (base year 2009: UFRGS-IB-Centro de Ecologia 2016) with the six landscape sampling units (LSUs) denominated by the name of the municipality and (C) the São Francisco de Assis LSU with the three sample plots in detail. The names of municipalities were abbreviated by: LAV = Lavras do Sul; QUA = Quaraí; SAM = Santo Antônio das Missões; SBV = Santana da Boa Vista; SFA = São Francisco de Assis; SGA = São Gabriel.

Sampling design

Plot demarcation and vegetation sampling followed the RAPELD protocol (https://ppbio.inpa.gov.br/instalacao; Magnusson *et al.* 2005; Costa & Magnusson 2010) developed by PPBio, with some adjustments for the Pampean forests (plot length with 250 m, width with 10 m and minimum diameter at breast high [DBH] with 5 cm). We also adjusted the number of plots to

obtain patches with enough size to allocate the plots while maintaining a minimum distance of 1 km in a grassland dominated landscape (see Fig. 1C).

At regional level, the six LSUs (Fig. 1B) were located in Lavras do Sul (LAV), Quaraí (QUA), Santo Antônio das Missões (SAM), Santana da Boa Vista (SBV), São Francisco de Assis (SFA) and São Gabriel (SGA) municipalities. Each LSU is a 5 x 5 km square, in each of which, three 250 x 10 m plots were demarcated in riverine forests apart at least 1 km each other. These plots were composed by 25 sampling units that were continuously added along a central line 15 m distant from the riverbank. The sampling unit was a square with a 10 m side and with 10 m distance of the riverbank. In each sampling units we included all trees with DBH more than or equal to 5 cm. All individuals were identified at the species level; when necessary we required identification by experts in addition to routine comparisons with exsiccates of the ICN Herbarium. The species names were standardized by valid names in *The Plant List* (2013) with the R package "Taxonstand" (Cayuela *et al.* 2017). Some species names were replaced by valid name in *Flora do Brasil 2020* (2018) to include changes of experts' recent researches. The delimitations of botanic families followed the *APG IV System* (APG IV 2016). In each plot, we collected six topsoil samples (0 to 20 cm deep) at each 50 m, which were homogenized and analyzed as a composite sample by the Laboratório de Solos da Faculdade de Agronomia of Universidade Federal do Rio Grande do Sul according to methodology of Tedesco *et al.* (1995).

Data Analyses

Hill numbers

Diversity analyses were performed with Hill numbers, which contemplate the replication principle required to measure diversity with intuitive meaning, allowing the meaningfully results to guide conservation strategies (see Jost 2006; 2007; Jost *et al.* 2010; Tuomisto 2010a; b; 2013). Hill numbers are a parametric family that unified several diversity indices in a continuum that differ only in their sensitivity to species relative abundance by parameter q (Hill 1973; Jost 2006; 2007; Chao & Chiu 2016). The order (parameter) q of a diversity indicates its sensitivity to common and rare species (Chao *et al.* 2012). When Hill numbers are estimated by order $q = 0$, species abundances are not weighted and it corresponds to species richness. When q order tends to limit of one, species weighted is equal to the proportion of species frequency and it corresponds to the exponential of Shannon entropy and denote the "typical species", without favoring rare or abundant species (Chao *et al.* 2012).

Sampling effort

The sample sufficiency was analyzed by sample coverage, a measure of sample completeness expressing the probability for a species of the community to be observed in the sample (Chao & Jost 2012). In the opposite, the coverage deficit (unity minus the sample coverage) represents the probability that a new species (unsampled) would be found when one new individual tree is added to the sampling. We also used sample coverage to standardize coverage level of LSUs and compare species diversity of samples of equal completeness according to Chao & Jost (2012). We applied this standardized criterion to integrated curves that links rarefaction (interpolation) and prediction (extrapolation) to orders $q = 0$ and $q = 1$ of Hill numbers (Chao *et al.* 2014), described originally by Colwell *et al.* (2012) to species richness. Extrapolation was estimated up to double of reference sample size (empirical value in each LSU). These analyses were performed in the R environmental (R Core Team 2018) with the R package "iNEXT" (Hsieh *et al.* 2016) to coverage-based (standardized criterion) and sample-sized-based (number of individuals are more intuitive for interpretation) curves for individual-based abundance data. The 95% confidence interval was obtained by the bootstrap method with 1000 replications.

Partitioning species diversity across hierarchical spatial structure

We defined a hierarchical structure with two spatial levels, local and regional (Fig. 2). We estimated species diversity across different levels of spatial scales with multiplicative partitioning on Hill numbers, that follow the replication principle and makes beta unrelated to alpha and gamma diversity (Jost 2007; Chao *et al.* 2012; Gaggiotti *et al.* 2018). Beta diversity should be independent of alpha diversity to makes beta comparable between different levels of spatial scale with different values of alpha, which obviously increase towards higher levels of hierarchy (Jost 2007; Gaggiotti et al. 2018). Beta diversity of multiplicative partitioning on Hill numbers is "the effective number of distinct communities or samples", that is between unity (when all communities are identical) and N, the number of communities or samples (when all communities are completely distinct) (Chao *et al.* 2012). We selected orders $q = 0$ and $q = 1$, which are concave functions (see Lande [1996] and Ricotta [2005]) that can be used to multiple hierarchical partitioning when samples have unequal weight, which is important to retain properties of distinct landscapes on estimated values of alpha and beta diversity (Jost 2007). To order $q = 0$, we weighted sample with equal weights to ensure beta independent of alpha diversity (see Jost 2007).

We decomposed species diversity in multiple hierarchical spatial scales with *PARTITION 3.0* (Veech & Crist 2009) and *iDIP* (Chao & Chiu 2017) softwares, which partition diversity according to Jost (2007). With the first software, we performed two null models, elaborated by Crist *et al.* (2003) and Veech & Crist (2009), to test if alpha and beta diversities in each spatial scale were less or more

than expected by chance. The results of hierarchical partition of species diversity to order $q = 1$ with unequal weights were the same in the two softwares, so we used the differentiation measure of *iDIP* to compare beta diversity across spatial levels. Beta diversity estimated on Hill numbers depends on the number of samples and their sizes (weights) (Gotelli & Chao 2013; Gaggiotti *et al.* 2018). To make beta component comparable across spatial levels in a hierarchical (nested) structure, where the number of samples decreases and of individuals increases towards higher levels, beta was normalized as a differentiation measure. This Shannon differentiation measure is the one complement of multiple-community overlap measure $(1 - C_{1N})$, that correspond to the mean proportion of nonshared species, which varies from 0 (all species shared) to 1 (none species shared). The Shannon differentiation measure has monotonicity and "true dissimilarity" properties (see Gaggiotti *et al.* 2018). As species richness ($q = 0$) is known to have a stronger under-sampling bias due undetected species and undetected shared species (Gotelli & Chao 2013; Chao & Jost 2015) we used only the Shannon differentiation measure ($q = 1$) that usually has less sampling bias (Gaggiotti *et al*. 2018).
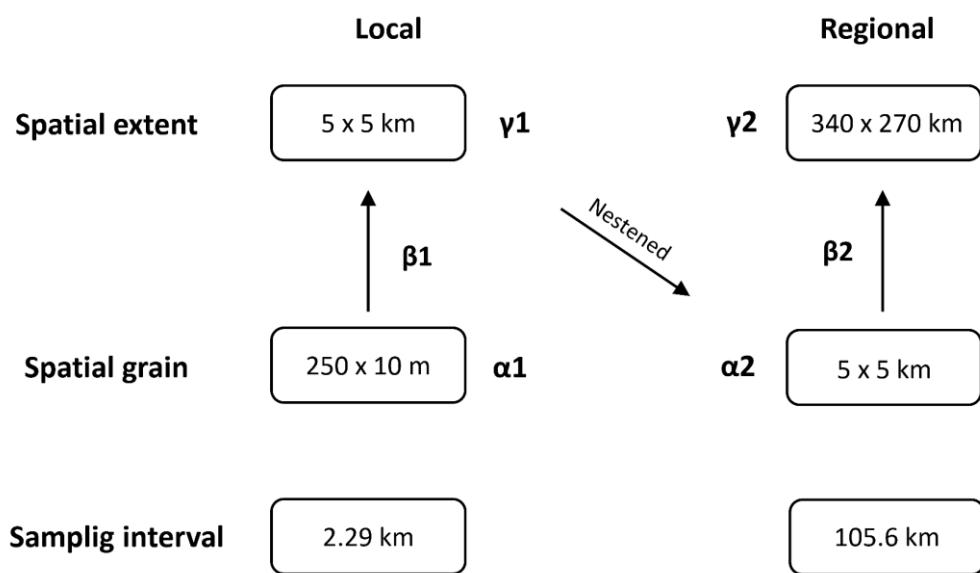
Figure 2. Hierarchical spatial scale of sampling design adopted in our research. The sampling interval was measured as the average of distance measure of each sampling unit to its nearest neighboring sampling unit.

In the first null model (individual-based unrestricted randomization), each individual was randomly reassigned to any lower level sample (level 1 = plot) conserving species abundance and sample sizes, after that, diversity was partitioned in multiple hierarchical spatial scales. This procedure was repeated 9,999 times and the *p*-value was obtained comparing the number of times that null distribution was equal, lower, or higher than the observed values. In this null model all individuals have the same probability to occur in any local. Although this model disregard niche-assembly and dispersal-assembly rules (Hubbell 2001; Götzenberger et al. 2012), allowing any

species to occur in any local, deviations from null model suggest mainly the effect of species aggregation and/or dispersal limitation at broad scales.

In the second null model (individual-based restricted randomization), at a certain level j of interest, each individual of level $j - 1$ was reassigned to any other sample within the same level $j + 1$ (Veech & Crist 2009). In other words, only individuals of the same LSU were reassigned within each of the three plots of that LSU. Level 2 (LSU) was not tested, because it is equivalent to results at the same spatial scale level in unrestricted randomization test (there was only one sample at level $j + 1$ to LSU, the study region, then individuals could not be unrestrictedly assigned at level $j = $ LSU). Species abundance and sample sizes were conserved in randomization procedure and the p-value was obtained by the same way that the first null model. These constraints on randomization ensure that mainly environmental and biotic factors that are expected to act on the local scale can be driven when diversity patterns deviate from null model (Götzenberger *et al.* 2012).

Results

A total of 6,639 trees were sampled in an area of 4.5 ha. The native species added up 6,009 individuals that were distributed in 101 species, 74 genera and 37 families (Table S2). The richest family was Myrtaceae with nine genera and 18 species followed by Fabaceae with 11 genera and 12 species. Euphorbiaceae was the family with the highest number of sampled individuals (2,308; ca. 35%) followed by Myrtaceae (1,849; ca. 28%). The most two abundant species were *Gymnanthes klotzschiana* (1,418 individuals) and *Eugenia uniflora* (974 individuals) which together correspond ca. 40% of total abundance. Most species were sampled only in few regions, of which 40 were restricted to one LSU, 19 species occurred only in two LSUs, 18 species in three LSUs, adding 77 species occurring in the maximum of three LSUs. Only seven species were sampled in all LSUs. The alien species and genus sampled were *Melia azedarach* and *Citrus* sp.

The sample completeness in the study region was extremely high, with coverage of 99.83% when all LSUs were taken together in a single sample. When plots were grouped by landscapes (within each LSU), the lowest coverage was 98.95% in QUA. At the plot level, the lowest value of sample completeness was found in SAM2 plot (within SAM) with 95.29%. The QUA coverage value was used in integrated curves of interpolation/extrapolation (Fig. S2) to standardize the comparison of species diversity of LSUs to the same level of sample completeness (Fig. 3).

The lowest value of standardized species richness ($q = 0$) was in LAV and the highest value was in SAM, which differed from LAV, QUA and SBV (Fig. 3A). For the Shannon diversity ($q = 1$),

the major difference was the reduction of species diversity in SFA and the separation of four distinct groups of diversity (Fig. 3B). SAM was the most diverse, followed by SGA. SBV, QUA and SFA did not differed from each other and LAV remained the least diverse landscape.
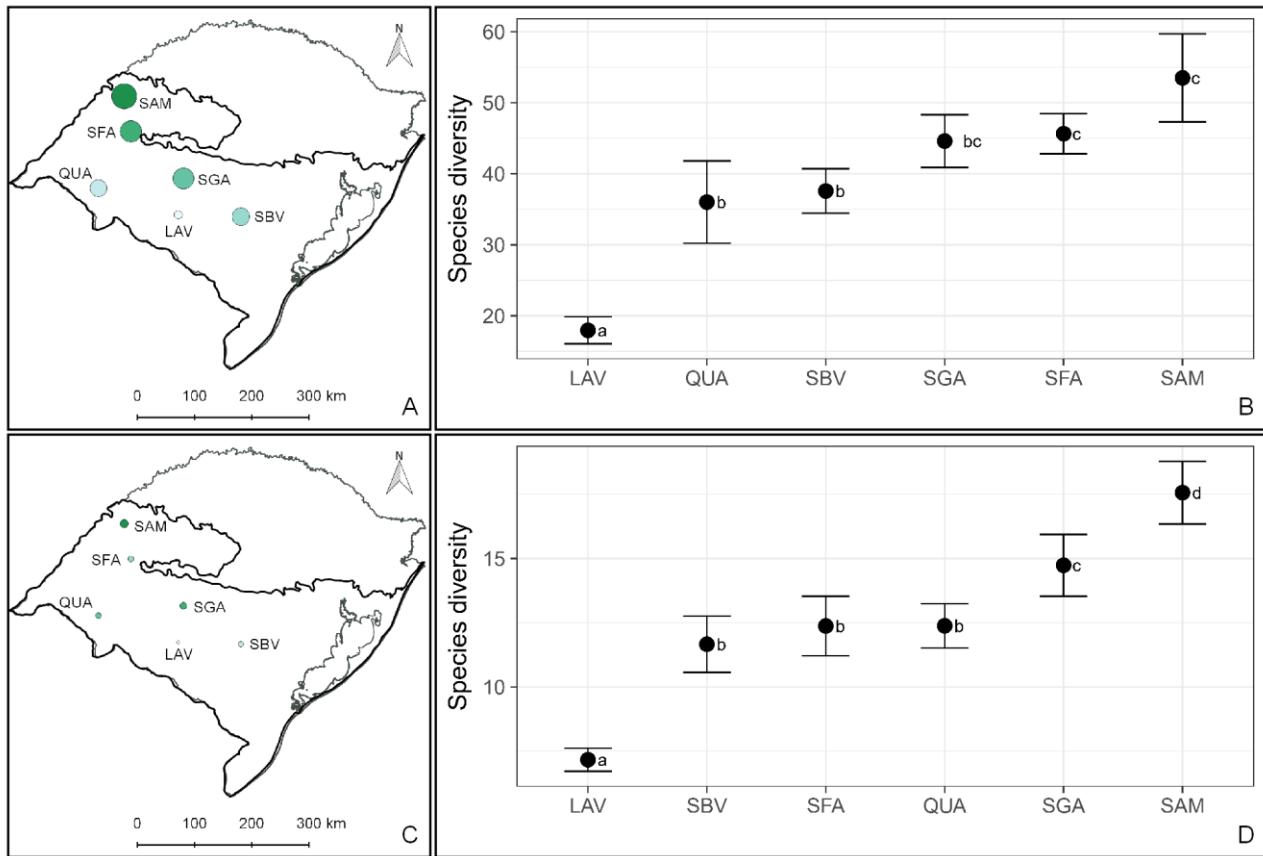
Figure 3. Standardized tree species diversity to the same level of sample coverage (98.95%) in each landscape sampling units (LSU) in riverine Brazilian Pampean forests to two q orders of Hill numbers. (A) Hill numbers of q order equal to zero corresponds to species richness. (B) When q order tends to limit of one it corresponds to the exponential of Shannon entropy. The solid dots represent the interpolated or observed (QUA) values of species diversity and the bars added to them correspond to the lower and the upper 95% confidence interval. The lowercases letters indicate if species diversity of LSU were different from each other to the same q order.

Partitioning species diversity across hierarchical spatial structure

In the hierarchical diversity partitioning on Hill numbers, the effective (equally abundant) number of species in the study region ($\gamma 2$) was 101 to order $q = 0$ and 24.71 to order $q = 1$ (Tab. 1A). Each landscape ($\alpha 2$) contained in average 41.17 and 12.64 species equivalents to orders $q = 0$ and $q = 1$, respectively. Each plot ($\alpha 1$) contained in average 26.44 ($q = 0$) and 10.04 ($q = 1$) species equivalents. Multiplicative beta diversity showed that there are 2.45 ($q = 0$) and 1.95 ($q = 1$) landscapes equivalents ($\beta 2$) and 1.56 ($q = 0$) and 1.26 ($q = 1$) plots equivalents per landscape.

The Shannon differentiation measure (the one complement of multiple-community overlap measure) of hierarchical partition of species diversity with unequally-weighted samples (Tab. 1A) were higher to regional scale (0.38) than to local scale (0.21). This means that the mean proportion

of non-shared species in a landscape is around 38% and in a plot (restricted to each landscape) is around 21%.

In the first null model (individual-based unrestricted randomization: Tab. 1A) that suggests mainly the effect of species aggregation and/or dispersal limitation at broad scales, observed alpha diversity ($\alpha 1$ and $\alpha 2$) at the two levels (plot and LSU) were lower than expected by chance. Observed beta diversity ($\beta 1$ and $\beta 2$) was higher than the expected one at the two levels. In the second null model (individual-based restricted randomization: Tab. 1B) that suggests mainly the effects of environmental and organismal factors at local scale, observed alpha diversity ($\alpha 1$) was lower than the expected by chance at the plot level (the only one tested). Observed beta diversity ($\beta 1$) was higher than expected.

Table 1. Hierarchical diversity partitioning with hierarchical randomization test (A) and non-hierarchical randomization test (B) of tree species in riverine forests in Brazilian Pampean Biogeographic Province. Multiplicative unweighted partitioning diversity to order $q = 0$ (species richness) and multiplicative weighted partitioning diversity to order $q = 1$ (exponential of Shannon index). Null models were constructed by individual-based unrestricted randomization test (the first null model) and by individual-based restricted randomization test (the second null model). In all cases observed and expected values are significantly different from each other ($p \leq 0.0001$). $1 - C_{1N}$ = the Shannon differentiation measure ($q = 1$).

Diversity level	Observed	Expected interval	Observed	Expected interval	$1 - C_{1N}$
A) 1st Null model	$q = 0$	Min - Max	$q = 1$	Min - Max	$q = 1$
Level 1 (plot)					
α1	26.44	53.72 - 57.06	10.04	21.67 - 22.3	
β1	1.56	1.3 - 1.43	1.26	1.07 - 1.09	0.21
γ1	41.17		12.64		
Level 2 (LSU)					
α2	41.17	73.17 - 78.83	12.64	23.54 - 23.91	
β2	2.45	1.28 - 1.38	1.95	1.03 - 1.05	0.38
γ2	101		24.71		
B) 2nd Null model	$q = 0$	Min - Max	$q = 1$	Min - Max	
Level 1 (plot)					
α1	27.17	31.62 - 33.96	10.04	12.03 - 12.23	
β1	1.55	1 - 1.33	1.26	1 - 1.05	
γ1	42.13		12.64		

Discussion

Our hierarchical diversity partitioning on Hill numbers indicates a pattern of low alpha diversity and high beta diversity of tree species in riverine forests in Brazilian Pampean Biogeographic Province at

local and regional scales. The two null models confirm this pattern and suggest different processes acting at local and regional scales to decrease alpha diversity and increase beta diversity. Moreover, alpha diversity was considerably variable among landscapes, the highest values were found in landscapes located in the northern region of Brazilian Pampean Province, closer to the migration routes of Atlantic species (Rambo 1960; 1961). Taking together these finds suggest that environmental filtering and mainly species dispersal limitation might be shaping diversity at the broadest scale and different coexistence mechanisms influenced by local flood pulse variation might be driving diversity at the finest scale, such as competitive exclusion and stress tolerance.

Our sampling design and sampling efforts were adequate to describe diversity patterns and provide important useful information for management and conservation actions of Pampean forests. At local and regional scales, sample completeness was extremely high with values of sample coverage always above 95% (Tab. S1, Figs. S1B, S2B). This sampling adequacy can be easily visualized in the asymptotic trends of sample-size-based rarefaction and extrapolation curves of species richness (Fig. S1A) and mostly of Shannon diversity (Fig. S2A), indicating that sampled tree species are highly representative of the tree flora in riverine forests of the study region. Sobral *et al.* (2013) recorded the occurrence of 533 tree and arborescent species in all habitats in Rio Grande do Sul state, including the high diverse Atlantic forests of the northeastern portion. In Uruguay, Grela (2004) recorded the presence of 114 tree species, but he recognized the possibility of occurrence of 170 tree species in this country and Paz & Bassagoda (2002) indicated the occurrence of 70 tree species in riverine forests in Uruguay. As Brazilian Pampean forests are located between Uruguay and the Atlantic Domain in Rio Grande do Sul state and as we sampled only riverine habitats, the real gamma diversity of all riverine forests of the study region should not be much larger than our observed gamma diversity.

Alpha diversity in landscapes was variable, the highest values of standardized tree species diversity were found in LSUs (SAM, SFA, SGA) located in the north of the study region, near to the Atlantic Domain. This pattern may be related to changes in environmental conditions along latitudinal gradient and species dispersal limitation. Mean annual temperature and precipitation are higher in LSUs with higher alpha diversity (Hijmans *et al.* 2005; Alvares *et al.* 2013). According to Giehl & Jarenkow (2012), the climatic niche conservatism of tropical species explains the richness disparities between tropical and subtropical riverine forests in South America due to the inability of most tropical species to colonize the subtropics. As many species that occur in the Brazilian Pampean Forests have their center of origin or distribution in Atlantic Domain (Rambo 1960; 1961), the northern landscapes of our study region are closer to niche requirements of Atlantic species. As pointed by Oliveira-Filho *et al.* (2006) and Gonçalves & Souza (2014), the southern limit of Atlantic forests contains an impoverished subset of species tolerant to climatic variation and lower temperatures. However, Rambo (1960) had already noted the absence of strong environmental changes in south of Rio Grande

do Sul state and north of Uruguay, suggesting the importance of colonization processes of tree species from Atlantic into Pampean Domains to explain differences in species richness along the north-south gradient. According to Rambo (1960; 1961), tree species arrived in Brazilian Pampean Province mainly by two migration routes from Atlantic Domain, the oldest and most important route arrived from Paranense Province (*sensu* Cabrera & Willink 1980) by the Upper Uruguay River in the west and the later route arrived from Atlantic Province by the corridor between Atlantic Ocean and slopes of Serra Geral in the east. Therefore, the dispersal limitation of Atlantic species, which is stronger in the most distant landscapes from the Atlantic Domain, might be the most plausible process that can explain the observed pattern of alpha diversity at the regional scale, with a secondary role of environmental filtering mediated processes.

The hierarchical diversity partitioning on Hill numbers and the null models indicate a pattern of low alpha diversity and high beta diversity at both local and regional scales, suggesting different processes shaping the distribution and abundance of species in each scale. At regional scale, the variation of sampled alpha diversity in each LSU had a great influence on low value of averaged species diversity ($\alpha2$). As a consequence, the two processes discussed above can be evocated to explain the high value of beta diversity at this broader scale. The occurrence of many species restricted to few LSUs might be contributing to the low values of alpha diversity and high values beta diversity. The same mechanisms, species dispersal limitation and environmental filtering, are the most plausible to explain this restriction. Whether there were no species dispersal limitation and environmental filtering, species would be free to occur in any LSU following the first null model. Then, alpha diversity ($\alpha2$) would be between 73.17 and 78.83 ($q = 0$) and between 23.54 and 23.91 ($q = 1$) and not 41.17 ($q = 0$) and 14.67 ($q = 1$) as the observed alpha diversity, thus beta diversity ($\beta2$) would be extremally low as expected beta diversity in the first null model (Tab. 1A).

At local scale, the pattern of low alpha diversity ($\alpha1$) in plots and high beta diversity ($\beta1$) among plots was confirmed by the two null models. Constraints on randomization in the second null model ensures that mainly environmental and biotic factors that are expected to act on the local scale can be the drivers of this diversity pattern (Götzenberger *et al*. 2012). Species interactions (competitive exclusion or facilitation), species sorting by microhabitat variability, small-scale local dispersal/establishment limitation, disturbance regime, and ecological drift are possible drivers at this spatial scale (Hubbell 2001; Chase 2011; Götzenberger *et al.* 2012; Myers & LaManna 2016). In riverine communities, the flood pulse is pointed out as the main driving force controlling biota occurrence and abundance (Junk *et al.* 1989; Junk & Wantzen 2004), thus others mechanisms should be considered in interaction with this disturbing factor. An important characteristic of flood pulse is that in low-order streams it is short and unpredictable (Junk *et al*. 1989), and the polymodal frequency creates a constant removal and deposition of sediments that affects the seed bank and seedlings

(Budke *et al.* 2008). Therefore, local dispersal limitation can be reduced by stochastic redistribution of propagules. Stochastic processes are expected to be higher at smaller spatial scales, but when species pool is restricted and the sites are under disturbances regimes or stressful environmental conditions, community assembly tends to be less affected by random stochastic process than by strong niche-selective forces (Chase 2011; 2014). Although riverine forests of the studied area have high environmental heterogeneity, within-plot heterogeneity and differences in species ability regarding the use of resources under distinct environmental conditions were not enough to increase alpha diversity or their effects were reduced because of competition interactions and stress tolerance (Grime & Pierce 2012), which may restrict the local occurrence of some species and then decreasing alpha diversity.

Our results suggest that conservation efforts of riverine Pampean forests should be focused on broad scales due to the highest beta diversity at this scale and the difference of alpha diversity among landscapes related to the dispersal limitation of Atlantic species. The spatial planning of conservation efforts should consider the restricted regional tree species pool in Brazilian Pampean Forests (Oliveira-Filho *et al.* 2015; Rezende *et al.* 2016), the effect of dispersal limitation of Atlantic species from Atlantic Domain and the importance of Brazilian Pampean Province in regional context, that encompass important tree migration routes of Uruguayan flora (Grela 2004; Brussa and Grela 2007; Mourelle *et al.* 2017). Of the total (101) tree species sampled in our study, 21 species are present in the lists of vascular plants priority for conservation and of vascular plants threatened in Uruguay (Marchesi *et al.* 2013).

We also stress the importance of knowing the relative contribution of alpha and beta diversity across hierarchical spatial scale because contribution of beta diversity at the broadest scale is not always the focal scale of conservation in all studied system. Clarke *et al.* (2010), by partitioning diversity of aquatic macroinvertebrate in headwater streams in Australia, found high alpha diversity at the finest scale (in reaches) and low contribution of beta diversity in both scales (among reaches and among catchments), thus they considered a low irreplaceability in the system. Chandy *et al.* (2006) analyzed tree species diversity of temperate forests in eastern North America. They also found beta diversity higher than expected by chance in all spatial scales, but the values of beta diversity of their study cannot be directly compared with ours because they did not remove the dependence of number of samples according to Chao *et al.* (2012).

Our findings were important to describe patterns of tree species diversity across spatial scales within the Brazilian Pampean forests and provide useful insights about process driving diversity at each spatial scale. This study is pioneer in describe how tree species diversity of riverine forests varies among landscapes within Brazilian Pampean Province across multiple hierarchical spatial scales. The

next step is to test and disentangle effects of environmental factors and species dispersal limitation in shaping diversity at broad scales.

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Supplementary Material

Table S1. Characteristics of landscape sampling units (LSU) allocated in Brazilian Pampean Phytogeographic Province and some partial results. Characterization of Physiographic, Geomorphological and Hydrological Regions and geological substratum following IBGE (1986; 2010). The climatic variables are average for the period of 1970 - 2000 extracted from WorldClim (Hijmans *et al*. 2005). Soils parameters are means from top soil (0 – 20 cm) collected in the three plots for each LSU. Sample coverage was evaluated by sample-coverage rarefaction and extrapolation curves for 1000 replications. The species richness, their 95% confidence interval and the number of individuals for each LSU was estimated by the same value of standardized sample coverage (the minimal value of 98.95% found in QUA).

	SAM	SFA	QUA	SGA	SBV	LAV
Municipality	Santo Antônio das Missões	São Francisco de Assis	Quaraí	São Gabriel	Santana da Boa Vista	Lavras do Sul
Geographical coordinates	28°32'07"S 55°27'14"W	29°13'23"S 55°19'37"W	30°17'35"S 55°56'47"W	30°06'22"S 54°19'13"W	30°50'15"S 53°13'17"W	30°48'07"S 54°25'19"W
Physiographic region	Missões	Missões	Campanha	Campanha	Serra do Sudeste	Serra do Sudeste
Geomorphological region	Planalto das Missões	Planalto das Missões	Planalto da Campanha	Depressão Central Gaúcha	Planalto Sul-rio-grandense	Planalto Sul-rio-grandense
River Basin	Icamaquã - Piratinim	Itu	Ibirapuitã	Vacacaí	Camaquã	Santa Maria
Hydrological Region	Uruguay River	Uruguay River	Uruguay River	South Atlantic	South Atlantic	Uruguay River
Mean annual temperature (°C)	20.7	19.5	18.8	19.1	18.5	18.4
Mean annual precipitation (mm)	1,724	1,731	1,463	1,573	1,435	1,371
Altitude asl (m)	86	121	173	143	241	168
Geological substratum	Basaltic	Sandstone	Basaltic	Sandstone	Granitic	Granitic
Soil: pH	5.4	5.0	6.0	4.9	5.1	5.9
Soil: clay (%)	53	14	33	22	16	23
Soil: sand (%)	11.3	70.3	21.7	52.3	59.3	58.7
Sampled Richness	54	48	36	47	40	22

Sampled Individuals	1,360	1,072	1,046	1,179	973	979
Sample coverage (%)	98.97	99.63	98.95	99.15	99.38	99.49
Standardized Richness (95% CI)	53.49 (47.29 - 59.69)	45.63 (42.82 – 48.45)	36.00 (30.22 - 41.78)	44.60 (40.91 - 48.29)	37.56 (34.44 - 40.69)	17.95 (16.05 – 19.86)
Standardized Individuals	1311	715	1046	925	668	389

Table S2. The tree species and their abundance of individual sampled in riverine Brazilian Pampean forests. The species names were standardized by valid names in *The Plant List* (2013). Some species names were replaced by valid name in *Flora do Brasil 2020* (2018) to include changes of experts' recent researches. The delimitations of botanic families followed the *APG IV System* (APG IV 2016).

Family	Species	Abundance
	NATIVE SPECIES	
Achatocarpaceae	*Achatocarpus praecox* Griseb.	11
Anacardiaceae	*Lithraea brasiliensis* Marchand	16
	Lithraea molleoides (Vell.) Engl.	19
	Schinus longifolia (Lindl.) Speg.	6
	Schinus terebinthifolia Raddi	1
Annonaceae	*Annona neosalicifolia* H.Rainer	49
Apocynaceae	*Tabernaemontana catharinensis* A.DC.	2
Arecaceae	*Syagrus romanzoffiana* (Cham.) Glassman	1
Asteraceae	*Dasyphyllum spinescens* (Less.) Cabrera	17
Bignoniaceae	*Handroanthus heptaphyllus* (Vell.) Mattos	1
Boraginaceae	*Cordia americana* (L.) Gottschling & J.S.Mill.	54
	Cordia trichotoma (Vell.) Arráb. ex Steud.	2
Cannabaceae	*Celtis ehrenbergiana* (Klotzsch) Liebm.*	65
	Celtis iguanaea (Jacq.) Sarg.	72
Cardiopteridaceae	*Citronella gongonha* (Mart.) R.A.Howard	1
Celastraceae	*Schaefferia argentinensis* Speg.	3
Ebenaceae	*Diospyros inconstans* Jacq.	12
Euphorbiaceae	*Actinostemon concolor* (Spreng.) Müll.Arg.	457
	Gymnanthes klotzschiana Müll.Arg.**	1418
	Gymnanthes schottiana Müll.Arg.**	1
	Sebastiania brasiliensis Spreng.	432
Lamiaceae	*Vitex megapotamica* (Spreng.) Moldenke	11

Lauraceae	*Nectandra megapotamica* (Spreng.) Mez	76
	Ocotea acutifolia (Nees) Mez	63
	Ocotea pulchella (Nees & Mart.) Mez	20
Fabaceae	*Apuleia leiocarpa* (Vogel) J.F.Macbr.	34
	Calliandra brevipes Benth.	1
	Calliandra tweedii Benth.	37
	Erythrina crista-galli L.	12
	Gleditsia amorphoides (Griseb.) Taub.	10
	Holocalyx balansae Micheli	3
	Lonchocarpus nitidus (Vogel) Benth.	9
	Machaerium paraguariense Hassl.	4
	Mimosa bimucronata (DC.) Kuntze	3
	Myrocarpus frondosus Allemao	12
	Parapiptadenia rigida (Benth.) Brenan	112
	Vachellia caven (Molina) Seigler & Ebinger	1
Loganiaceae	*Strychnos brasiliensis* (Spreng.) Mart.	69
Malvaceae	*Luehea divaricata* Mart.	47
Meliaceae	*Trichilia catigua* A.Juss.	34
	Trichilia elegans A.Juss.	11
Moraceae	*Ficus luschnathiana* (Miq.) Miq.	2
	Sorocea bonplandii (Baill.) W.C.Burger, Lanj. & de Boer	10
Myrtaceae	*Blepharocalyx salicifolius* (Kunth) O.Berg	60
	Calyptranthes concinna DC.	16
	Campomanesia guazumifolia (Cambess.) O.Berg	1
	Campomanesia xanthocarpa (Mart.) O.Berg	11
	Eugenia hiemalis Cambess.	3
	Eugenia involucrata DC.	9
	Eugenia subterminalis DC.	144
	Eugenia uniflora L.	974
	Eugenia uruguayensis Cambess.	86
	Myrcia oblongata DC.	1
	Myrcia palustris DC.	25
	Myrcia selloi (Spreng.) N.Silveira	45
	Myrcianthes cisplatensis (Cambess.) O.Berg	19
	Myrcianthes gigantea (D.Legrand) D.Legrand	18
	Myrcianthes pungens (O.Berg) D.Legrand	114
	Myrciaria tenella (DC.) O.Berg	15
	Myrrhinium atropurpureum Schott	39
	Plinia rivularis (Cambess.) Rotman	269
Petiveriaceae	*Seguieria aculeata* Jacq.**	6
Phytolaccaceae	*Phytolacca dioica* L.	1

Polygonaceae	*Coccoloba argentinensis* Speg.	4
	Coccoloba cordata Cham.	5
	Ruprechtia laxiflora Meisn.	81
Primulaceae	*Myrsine coriacea* (Sw.) R.Br. ex Roem. & Schult.	6
	Myrsine laetevirens (Mez) Arechav.	13
	Myrsine loefgrenii (Mez) Imkhan.	20
Quillajaceae	*Quillaja brasiliensis* (A.St.-Hil. & Tul.) Mart.	6
Rhamnaceae	*Scutia buxifolia* Reissek	199
Rosaceae	*Prunus myrtifolia* (L.) Urb.	5
Rubiaceae	*Chomelia obtusa* Cham. & Schltdl.	53
	Guettarda uruguensis Cham. & Schltdl.	109
	Machaonia acuminata Bonpl.[b]	2
	Randia ferox (Cham. & Schltdl.) DC.	3
Rutaceae	*Helietta apiculata* Benth.	31
	Zanthoxylum fagara (L.) Sarg.	3
	Zanthoxylum rhoifolium Lam.	11
Salicaceae	*Banara tomentosa* Clos	24
	Casearia decandra Jacq.	46
	Casearia sylvestris Sw.	14
	Salix humboldtiana Willd.	5
	Xylosma schroederi Sleumer ex Herter	5
	Xylosma pseudosalzmanii Sleumer	4
	Xylosma tweediana (Clos) Eichlam	14
Santalaceae	*Acanthosyris spinescens* Griseb.	12
Sapindaceae	*Allophylus edulis* (A.St.-Hil., A.Juss. & Cambess.) Radlk.	142
	Allophylus guaraniticus (A.St.-Hil.) Radlk.	75
	Cupania vernalis Cambess.	67
	Matayba elaeagnoides Radlk.	50
Sapotaceae	*Chrysophyllum gonocarpum* (Mart. & Eichler ex Miq.) Engl.	2
	Chrysophyllum marginatum (Hook. & Arn.) Radlk.	23
	Pouteria gardneriana (A.DC.) Radlk.	2
	Pouteria salicifolia (Spreng.) Radlk.	395
	Sideroxylon obtusifolium (Roem. & Schult.) T.D.Penn.	4
Solanaceae	*Brunfelsia australis* Benth.	11
	Cestrum intermedium Sendtn.	1
Styracaceae	*Styrax leprosus* Hook. & Arn.	33
Symplocaceae	*Symplocos uniflora* (Pohl) Benth.	5
Verbenaceae	*Citharexylum montevidense* (Spreng.) Moldenke	47
Total		**6609**

ALIEN SPECIES

Meliaceae	*Melia azedarach* L.	1

Rutaceae	*Citrus* sp.	29
Total		**30**
	NATIVE AND ALIEN SPECIES	
Total		**6639**

[*] We considered *Celtis ehrenbergiana* a distinct species of *Celtis iguanaea* according to *Flora do Brasil 2020* (2018), although they are synonymous in *The Plant List* (2013)

[**] The species name valid in *Flora do Brasil 2020* (2018) that replaced the species name valid in *The Plant List* (2018)
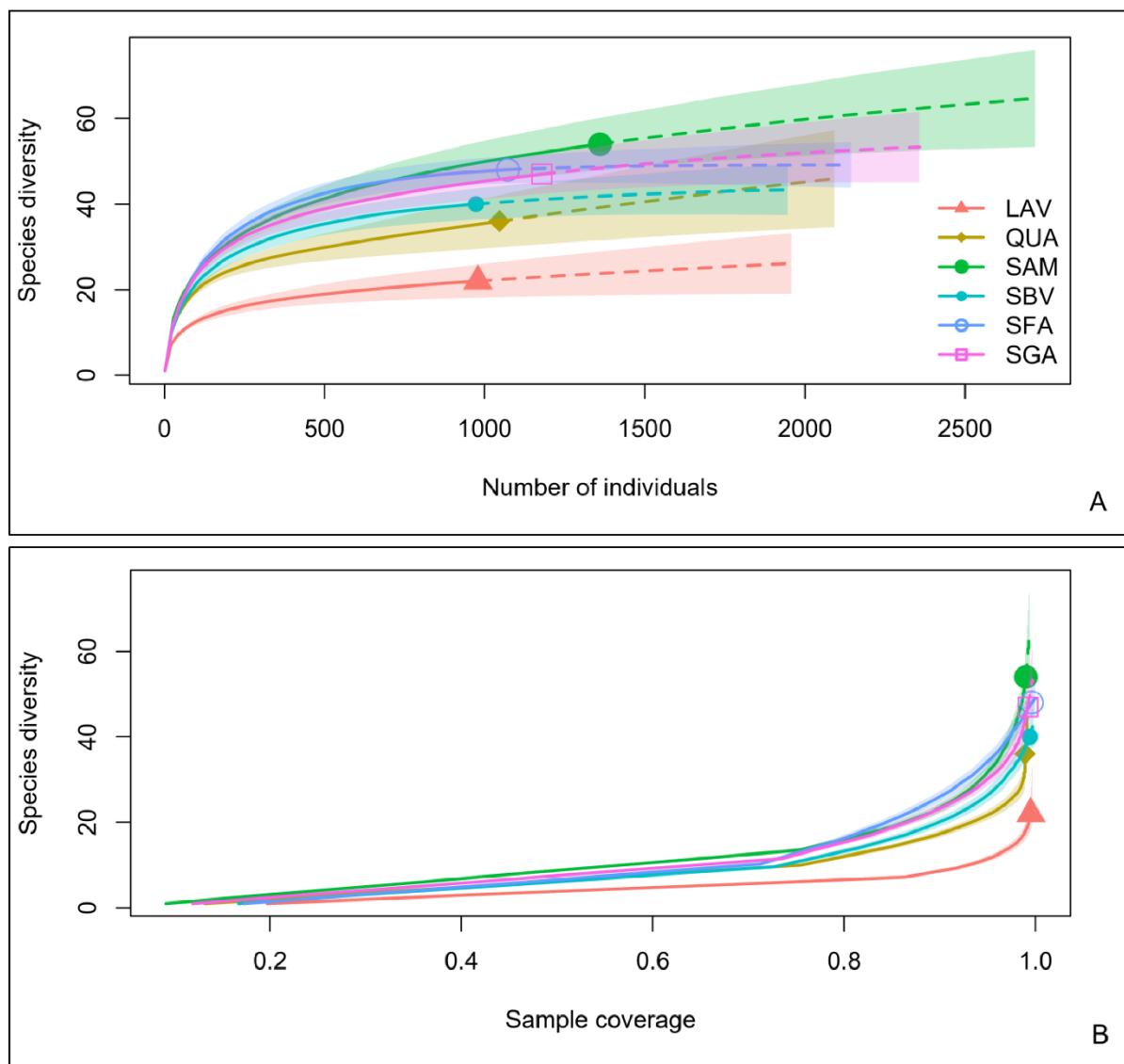
Fig. S1. Sample-size-based (A) and coverage-based (B) rarefaction (solid lines) and extrapolation (dashed lines) curves for individual-based abundance data of tree species for each landscape sampling unit (LSU) allocated in riverine Brazilian Pampean forests for order $q = 0$ of Hill numbers (species richness). Extrapolation was estimate up to double of reference sample size (empirical value in each LSU) that was denoted by geometric figures. The 95% confidence interval was obtained by the bootstrap method with 1000 replications.
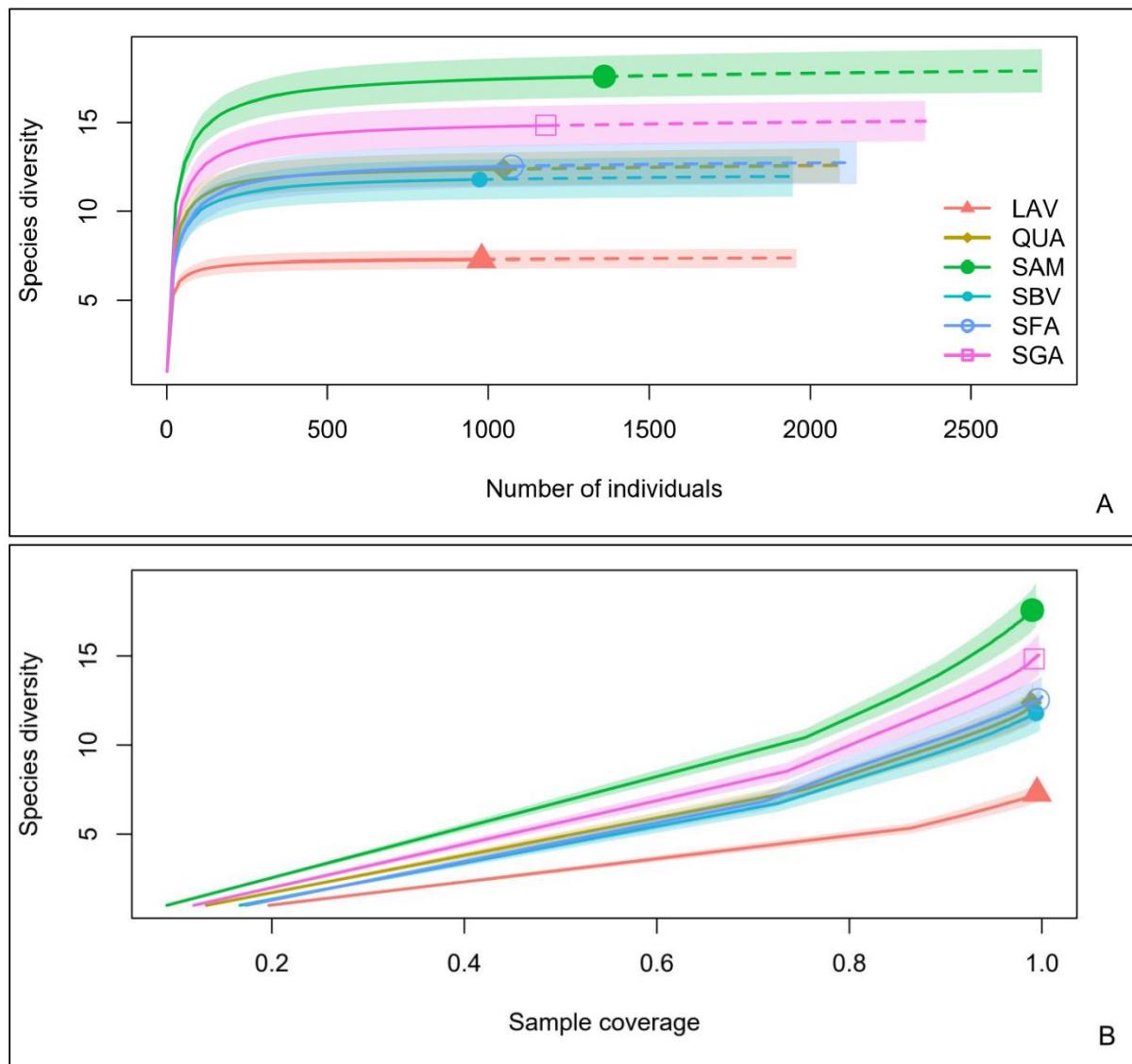
Fig. S2. Sample-size-based (A) and coverage-based (B) rarefaction (solid lines) and extrapolation (dashed lines) curves for individual-based abundance data of tree species for each landscape sampling unit (LSU) allocated in riverine Brazilian Pampean forests for order $q = 1$ of Hill numbers (Shannon diversity). Extrapolation was estimate up to double of reference sample size (empirical value in each LSU) that was denoted by geometric figures. The 95% confidence interval was obtained by the bootstrap method with 1000 replications.

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Considerações Finais

O presente trabalho foi o primeiro a descrever como a diversidade de espécies arbóreas de florestas ribeirinhas varia entre diferentes regiões e nas escalas espaciais (local e regional) na Província Biogeográfica Pampiana no Brasil. Nossos resultados sugerem um padrão de maior diversidade de espécies nas regiões localizadas ao norte da Província Pampiana, próximas à Floresta Atlântica *lato sensu*. Os resultados da partição hierárquica da diversidade e dos modelos nulos sugerem um padrão congruente, entre as escalas local e regional, de baixa diversidade alfa e alta diversidade beta. No entanto, a escala regional é a que contribui mais para a diversidade total (gama), e assim, os esforços de conservação de florestas ribeirinhas Pampianas devem ser direcionados aos processos que geram os padrões de diversidade na escala mais ampla. O uso de dois modelos nulos, um sem restrição e outro com restrição de permutações, possibilitaram a avaliação de processos relacionados a cada escala espacial e forneceram importantes contribuições sobre os processos que podem estar gerando os padrões observados. Na escala regional, a considerável diferença de diversidade de espécies entre as regiões e a redução desta com o aumento da distância das regiões às áreas de Mata Atlântica *lato sensu* sugerem um papel importante da limitação de dispersão de espécies atlânticas. Devido à ausência de um forte gradiente ambiental na região estudada, a redução da diversidade de espécies por restrições ambientais associadas ao nicho ecológico das espécies atlânticas pode ser um mecanismo menos intenso que a limitação de dispersão. Na escala local, diferentes mecanismos relacionados aos distúrbios dos pulsos de inundação parecem contribuir para os padrões encontrados. Nós reconhecemos as limitações de inferir processos a partir de padrões e, por isso, pretendemos testar os efeitos dos fatores ambientais e da limitação da dispersão de espécies na diversidade no nosso próximo artigo.

A metodologia de amostragem utilizada neste trabalho foi importante para a otimização de esforços amostrais na geração de dados em escalas amplas e a longo prazo, mas também gerou limitações no delineamento amostral do projeto de pesquisa e dificuldades na seleção de áreas e na demarcação de parcelas. Ao adotarmos o protocolo RAPELD, asseguramos que os dados amostrados em nosso trabalho poderão ser integrados aos levantados em outras regiões do país com o mesmo procedimento. No entanto, o protocolo gerou algumas restrições práticas, como o reduzido número de unidades amostrais nas escalas local (parcelas) e regional (os sítios de amostragens da Rede Campos Sulinos). Parte desta dificuldade parece estar relacionada às características do nosso objeto de estudo, as florestas na Província Pampiana no Brasil. Em uma paisagem dominada pela vegetação campestre, a seleção de áreas florestais com dimensões adequadas para a demarcação de parcelas dentro dos sítios de amostragem criou dificuldades nos trabalhos a campo e também restringiu o

número de parcelas e de sítios da Rede com condições mínimas para a amostragem da vegetação arbórea. Além disso, a inclusão de novos sítios de amostragem, como São Francisco de Assis, exige elevado esforço amostral e alta demanda de recursos financeiros.

Por fim, destacamos a importância que algumas espécies podem ter em projetos de recuperação de áreas de gradadas, principalmente nas áreas de preservação permanente nas margens de cursos d'água, e a influência da presença do gado sobre a regeneração das florestas Pampianas. Branquilho (*Gymnanthes klotzschiana* Müll.Arg.) e pitangueira (*Eugenia uniflora* L.) foram amplamente abundantes e presentes em todos os sítios de amostragem. Em locais onde os efeitos dos distúrbios dos pulsos de inundações pareciam ser mais intensos, o branquilho era uma das poucas espécies presentes e, geralmente, muito abundante. Conforme Reitz et al. (1988), o branquilho é uma espécie heliófila com grande capacidade de se desenvolver sobre os campos situados em solos úmidos, sendo muito indicada para o reflorestamento nas margens ao longo dos rios. Além disso, sua madeira é uma alternativa para o uso energético como lenha em uma região pouco florestada. A pitangueira, como uma espécie zoocórica, pode atrair a fauna e exercer o efeito poleiro, contribuindo para a introdução de propágulos de outras espécies no local. Em relação à presença do gado nas áreas florestais na Província Pampiana no Brasil, não foi possível incluí-la como uma variável nas nossas análises pela ausência de dados precisos sobre o histórico de ocupação/uso das áreas, mas certamente tem uma implicação importante para a conservação das florestas. Em muitas áreas onde as marcas da presença intensa do gado eram visíveis, o estrato regenerante estava seriamente comprometido. Nós reconhecemos a importância da pecuária para a conservação das áreas de pastagens naturais (Pillar et al. 2009), mas parece ser necessário haver algum tipo de manejo, como o cercamento de alguns fragmentos florestais, para reduzir o impacto do gado sobre o estrato regenerante. Também destacamos a necessidade da realização de estudos que avaliem os impactos da presença (e intensidade/carga) do gado sobre o estrato regenerante das florestas Pampianas e forneça informações sobre alternativas de manejo.

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