UNIVERSIDADE FEDERAL DO RIO GRANDE DO SUL
INSTITUTO DE BIOCIÊNCIAS
PROGRAMA DE PÓS-GRADUAÇÃO EM BOTÂNICA

Estrutura de florestas ribeirinhas na bacia do Baixo Jacuí e aspectos funcionais de *Gymnanthes klotzschiana* Müll.Arg.

Edilvane Inês Zonta

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Dissertação apresentada ao Programa de Pós-Graduação em Botânica da Universidade Federal do Rio Grande do Sul como parte dos requisitos para obtenção do título de Mestre em Botânica.

Orientador: Prof. Dr. João André Jarenkow

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Resumo

Este estudo tem como objetivos (1) investigar variações e relações da estrutura, biomassa acima do solo e diversidade de florestas ribeirinhas com fatores abióticos em regimes distintos de inundação, e (2) verificar se atributos funcionais apresentam maior variabilidade entre do que dentro de populações de *Gymnanthes klotzschiana* e se fatores abióticos estão relacionados a atributos funcionais que diferem entre populações. Coletas de dados edáficos, florísticos, estruturais e/ou funcionais foram realizadas em florestas ribeirinhas situadas em diferentes locais no estado do Rio Grande do Sul, sul do Brasil. Biomassa total acima do solo, altura média, biomassa média individual acima do solo e diversidade foram maiores em ambientes eventualmente inundados, enquanto densidade e riqueza foram semelhantes entre os ambientes estudados. Observamos diferenças significativas nos atributos funcionais entre populações e maior variabilidade na escala de população que de parcela para conteúdo de matéria foliar seca (LDMC) e altura. Área foliar e área foliar específica apresentaram maior variação dentro do que entre populações. Área foliar específica e LDMC se correlacionaram significativamente com variáveis edáficas e climáticas. Além de distúrbios por inundação influenciarem negativamente o acúmulo de biomassa e componentes da estrutura florestal, propriedades edáficas e topográficas tiveram um efeito maior sobre a biomassa média individual acima do solo, sugerindo que estas variáveis também podem influenciar os padrões de montagem de florestas ribeirinhas e a distribuição espacial de biomassa acima do solo. Condições abióticas podem estar selecionando por características fenotípicas e estratégias ecológicas diferentes em populações de *G. klotzschiana* e influenciando na amplitude do nicho funcional desta espécie. Nossos resultados sugerem que ambientes com condições abióticas distintas dentro e/ou entre florestas ribeirinhas são críticos para a manutenção de uma porção expressiva da diversidade arbórea regional, de estoques de carbono e de populações de *G. klotzschiana* com características fenotípicas distintas frente às mudanças climáticas e de uso da terra.

Palavras-chave: Amplitude de nicho. Áreas úmidas. Distúrbios por inundação. Florestas ribeirinhas subtropicais. Variabilidade intraespecífica do atributo.

Abstract

This study aims (1) to investigate variations and relationships of the structure, aboveground biomass and diversity of riverine forests with abiotic factors in distinct flood regimes, and (2) to verify whether functional traits present greater variability among rather than within populations of *Gymnanthes klotzschiana* and whether abiotic factors are related to functional traits that differ among populations. Edaphic, floristic, structural and/or functional data collections were performed in riverine forests situated in several locations in the state of Rio Grande do Sul, southern Brazil. Total aboveground biomass, average height, average individual aboveground biomass and diversity were higher in eventually flooded environments, while density and richness were similar between both studied environments. We observed significant differences in the functional traits among populations and greater variability at the scale of populations than of plots for leaf dry matter content (LDMC) and height. Leaf area and specific leaf area presented a greater variation within rather than among populations. Specific leaf area and LDMC were significantly correlated with edaphic and climatic variables. In addition to flood disturbances negatively influencing the accumulation of biomass and components of the forest structure, edaphic and topographic properties had a major effect on the average individual aboveground biomass, which suggest that these variables can also influence the patterns of riverine forest assembly and spatial distribution of aboveground biomass. Abiotic conditions may be selecting via different phenotypic characteristics and ecological strategies in populations of *G. klotzschiana* and influencing in the functional niche breadth of this species. Our findings suggest that environments with distinct abiotic conditions within and/or among riverine forests are critical for the maintenance of an expressive portion of regional diversity, carbon stocks and populations of *G. klotzschiana* with different phenotypic characteristics in face of climate change and land use.

Keywords: Flood disturbance. Intraspecific trait variability. Niche breadth. Subtropical riverine forests. Wetlands.

Sumário

Introdução geral

Zonas úmidas são ecossistemas na interface entre ambientes aquáticos e terrestres que podem ser permanente ou periodicamente inundados por águas superficiais, ou apresentar solos saturados (Nilsson & Svedmark, 2002; Kadlec & Wallace, 2009; Junk *et al*., 2014). Estas zonas desempenham um papel importante no fornecimento de inúmeras funções e serviços ecossistêmicos (Silva *et al*., 2017), como purificação da água, controle de inundações, produção de alimentos e manutenção da diversidade biológica (Junk *et al*., 2014). No entanto, o intenso processo de desmatamento tem causado o desaparecimento de muitas florestas de planícies de inundação (Wittmann, 2012), o que tem levado esta formação a estar entre as mais ameaçadas no Brasil (Junk *et al*., 2014). Pouca informação existe sobre zonas úmidas na Mata Atlântica (Junk *et al*., 2014) e poucos estudos foram realizados em florestas ribeirinhas deste bioma, principalmente considerando regimes distintos de inundação.

Padrões na vegetação ribeirinha respondem a três principais gradientes aninhados no tempo e no espaço: gradiente climático/continental, gradiente longitudinal intrarripário, e gradiente trans-ripário. Tais gradientes atuam, respectivamente, ao nível de bacia hidrográfica, em mudanças ao longo da extensão de um curso hídrico (nascente-foz), e através de fluxos laterais de água entre o curso hídrico e a planície de inundação (Mitsch & Gosselink, 2000). Fluxos laterais de água, relacionados a eventos de inundação, mudam a dinâmica de rios e afetam a vegetação mecanica e/ou fisiologicamente em função da intensidade do evento e da depleção nos níveis de oxigênio no solo, respectivamente (Malanson, 1993). Entretanto, efeitos como estes, causados por pulsos de inundação, variam consideravelmente devido à heterogeneidade geomorfológica que ambientes ribeirinhos apresentam (Junk *et al*., 2011). Estudos demonstram que florestas ribeirinhas são distintas quanto à sua estrutura em função da alta heterogeneidade ambiental a que estão submetidas (Sanchez *et al*., 1999; Matos & Felfili, 2010). Heterogeneidade esta que pode ocorrer devido a variações edáficas e topográficas (Oliveira-Filho *et al*., 1994a), além dos regimes de inundação que determinam a diversidade e a distribuição das espécies em áreas inundáveis (Oliveira-Filho *et al*., 1994b; Damasceno-Junior *et al*., 2005; Budke *et al*., 2008).

O pulso de inundação se caracteriza por constituir o principal mecanismo que gera diferentes fases em ambientes inundáveis (Junk *et al*., 1989). Estas fases podem ser de dois tipos: *potamofase* (fase de inundação com fluxos laterais de matéria orgânica, organismos e minerais do leito do rio para as margens) e *limnofase* (fase de escoamento, a qual consiste na regressão da inundação com fluxo inverso de materiais das áreas inundadas para o leito do rio) (Neiff, 1999). Em áreas inundáveis extensas, como nas margens de grandes rios, pulsos de inundação são previsíveis, unimodais e relacionados a eventos anuais de maior precipitação. Enquanto que em rios de pequena ordem ocorrem pulsos de inundação polimodais e imprevisíveis, dependentes da precipitação local ou à montante (Junk *et al.*, 2011).

De acordo com a função *f* FITRAS, o pulso de inundação possui como atributos principais: frequência, intensidade, tensão, recorrência, amplitude e estacionalidade, os quais podem ser de dois tipos: 1) atributos espaciais (amplitude, intensidade e tensão) – definem os efeitos do pulso de inundação sobre áreas inundáveis; 2) atributos temporais (frequência, recorrência e estacionalidade) – relacionados ao comportamento histórico dos atributos espaciais (Neiff, 1990; Neiff, 1999).

Eventos de inundação se relacionam de forma direta à umidade do solo e à profundidade de águas subterrâneas (Malanson, 1993). Entretanto, diante da maior dificuldade em obter estas informações, a maioria dos estudos relaciona a estrutura de florestas ribeirinhas à frequência e duração de inundações (Malanson, 1993; Budke *et al.*, 2008). Porém, é importante ressaltar que a depleção de oxigênio no solo varia ao longo do gradiente de umidade, assim medições da umidade do solo podem constituir uma variável que descreve muito mais as condições de saturação do solo do que medidas do nível de inundação (Malanson, 1993).

A saturação hídrica do solo, relacionada a inundações, leva a transformações ambientais de duração limitada e incerta (Crawford, 1982), que podem durar de poucas horas a muitos meses (Tyree, 2007). Estas condições podem atuar como filtros na seleção de espécies com adaptações morfológicas e/ou fisiológicas a tais ambientes (Jung *et al.*, 2010). Plantas adaptadas a locais propensos à inundação incluem espécies que podem crescer ativamente sob estresse e distúrbios, bem como espécies que sobrevivem em uma condição quiescente ou dormente (Crawford, 1982; Tyree, 2007).

Em condições de inundação, a redução na aeração do solo leva à depleção no suprimento de oxigênio para as raízes podendo afetar o crescimento das plantas. Estes efeitos ocorrem principalmente em função do desequilíbrio hormonal e de mudanças na concentração de íons potencialmente tóxicos no solo devido à inundação (Crawford, 1982). Wright (1977) sugere que o estresse causado às plantas pela falta (secas) ou excesso de água (inundações) gera sintomas relacionados ao desequilíbrio hormonal, tais como inibição do crescimento, fechamento estomático total ou parcial, epinastia peciolar, aumento na permeabilidade das raízes, entre outros. Entretanto, o estresse por inundação pode ser tolerado quando atributos funcionais, como maior área foliar específica (SLA), melhoram as trocas gasosas das plantas com a atmosfera durante a submergência (Voesenek *et al.*, 2006; Mommer *et al.*, 2006; Jung *et al.*, 2010).

Atributos funcionais consistem em características (morfológicas, fisiológicas e/ou fenológicas) que impactam indiretamente a aptidão de espécies, através de efeitos no crescimento, reprodução e sobrevivência (Violle *et al.*, 2007). Estas características representam estratégias ecológicas e determinam como as plantas respondem a condições ambientais distintas, podendo afetar outros níveis tróficos e influenciar as propriedades dos ecossistemas (Pérez-Harguindeguy *et al.*, 2013). A maioria dos estudos em ecologia funcional enfatiza variações interespecíficas com base em valores fixos de atributos (isto é, ao nível de espécie) (Cornelissen *et al.*, 2003). Esta abordagem está pautada no argumento de que 'para serem úteis à ecologia de comunidades, os atributos deveriam variar mais entre do que dentro de espécies' (McGill *et al.*, 2006). Sob este ponto de vista, a variabilidade intraespecífica acaba sendo negligenciada (de Bello *et al.*, 2011; Violle *et al.*, 2012) e as espécies são caracterizadas apenas pelos seus valores médios de atributos (Kichenin *et al.*, 2013). No entanto, estudos recentes demonstram que a variação intraespecífica em resposta a variáveis abióticas é maior do que previamente assumido (Albert *et al.*, 2010, Kichenin *et al.*, 2013).

A plasticidade fenotípica e a diversidade genética determinam a capacidade das espécies de lidarem com mudanças nas condições ambientais (Jung *et al.*, 2010) e são as principais fontes de variação intraespecífica de atributos (Violle *et al.*, 2012). A variabilidade funcional intraespecífica aumenta as chances de uma espécie ultrapassar filtros abióticos em função do ajuste dos valores de atributos aos requerimentos abióticos e aumenta a probabilidade de particionamento de nicho com espécies coocorrentes (Jung *et al.*, 2010). Portanto, toda a amplitude de variação fenotípica do atributo funcional deveria ser mensurada em populações naturais, independentemente de ser causada por fatores genéticos ou ambientais (Violle *et al.*, 2012). Diante do exposto, levantamos algumas hipóteses acerca da variação funcional intraespecífica e realizamos um estudo (Manuscrito 2) com uma abordagem ao nível de populações. Neste caso, populações da espécie *Gymnanthes klotzschiana* Müll.Arg.

A espécie *G. klotzschiana* apresenta ampla e expressiva distribuição nas planícies aluviais do sul do Brasil (Smith *et al.*, 1988). Diversos trabalhos demonstram que esta espécie está entre as mais abundantes em comunidades arbóreas ribeirinhas sul-brasileiras (Barddal *et* *al*., 2004; Budke *et al*., 2008; Giehl & Jarenkow, 2008; Carvalho *et al*., 2009). *Gymnanthes klotzschiana* apresenta características anatômicas que conferem adaptação a solos encharcados (Kolb *et al*., 1998) e cresce em habitats úmidos sob luz solar plena ou difusa (Smith *et al*., 1988), sendo abundante em áreas de floresta ribeirinha sujeitas a inundações frequentes (Zonta *et al*., Manuscrito 1).

Diante do papel fundamental das florestas ribeirinhas na provisão de serviços ecossistêmicos e na manutenção da diversidade regional de plantas, principalmente em paisagens altamente fragmentadas e com mudanças no uso da terra, além do limitado conhecimento acerca da variabilidade funcional intraespecífica e da presença proeminente de *G. klotzschiana* em florestas ribeirinhas no sul do Brasil, levantamos as seguintes questões:

(1) Comunidades arbóreas ribeirinhas submetidas a regimes distintos de inundação apresentam padrões estruturais, de acúmulo de biomassa acima do solo e de diversidade distintos? Fatores abióticos explicam possíveis diferenças?

(2) Há maior variabilidade de atributos funcionais entre do que dentro de populações de *G. klotzschiana*? Fatores abióticos estão relacionados a variações nos atributos funcionais entre populações desta espécie?

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Manuscrito 1

Aboveground biomass stocks and structural features in riverine tree communities subject to unpredictable floods[1]

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[1] Manuscrito formatado de acordo com as normas do periódico *Austral Ecology*

Aboveground biomass stocks and structural features in riverine tree communities subject to unpredictable floods

Abstract Subtropical riverine forests are subject to unpredictable and polymodal floods, which promote spatial and temporal heterogeneity in the soil moisture and nutrient availability. The role of these abiotic variables for patterns of biomass accumulation and structuring in riverine forests are not well understood. To evaluate assembly patterns of these forests, we performed a tree component survey on distinct flood regimes (often and eventually flooded) in three riverine areas in southern Brazil. Analyses of spatial generalised linear mixed models were carried out to verify whether structural parameters and biomass accumulation differ between studied environment conditions due to flood disturbances and variation in topography and edaphic properties. We sampled 73 species, of which 15 were recorded only in frequently flooded environments, 19 only in environments subject to eventual flooding, and 39 were common to both conditions. Total aboveground biomass, mean height, average individual aboveground biomass and diversity were higher in eventually flooded environments, while density and richness were similar between both studied environments. Edaphic and topographic properties had a positive and substantial effect on the average individual aboveground biomass, indicating that these variables may also influence the patterns of riverine forest assembly and spatial distribution of biomass. Our findings demonstrate that environments with distinct abiotic conditions in riverine forests are critical in maintaining an expressive part of the regional tree diversity and carbon stocks.

Keywords: Atlantic forest, environmental gradient, flood disturbance, diversity, wetlands.

INTRODUCTION

Wetlands are ecosystems at the interface between aquatic and terrestrial environments (Junk *et al*. 2014) that play an important role in the provision of ecosystem services (Silva *et al*. 2017). Nevertheless, intense deforestation has placed these formations among the most threatened in Brazil (Wittmann 2012; Junk *et al*. 2014). Little information exists about wetlands in the Atlantic Forest (Junk *et al*. 2014), and few studies have been carried out on riverine forests considering distinct flood regimes.

Riverine vegetation patterns respond to three major temporally and spatially nested environmental gradients: (1) climatic/continental gradient (acts at the watershed level), (2) intra-riparian longitudinal gradient (reflects variations along the length of a stream), and (3) transriparian gradient (generates lateral water flows) (Mitsch & Gosselink 2000). Lateral flows of water, matter and energy between the riverbed and floodplains are promoted by flood pulses that act as agents of ecological processes (Kingsford 2000). Flood events alter river dynamics and affect vegetation mechanically and/or physiologically as a function of the intensity of the flood and depletion of soil oxygen levels, respectively (Malanson 1993). In extensive flooded areas, such as on the fringes of large rivers, flood pulses are predictable, unimodal and related to annual events of higher precipitation. Otherwise, in riverine areas of small order rivers, flood pulses are polymodal and unpredictable, depending on local or upstream precipitation (Junk *et al*. 2011).

Floods vary in duration, intensity, frequency and pulse form (Junk *et al*. 2011) and are related directly to the depth of groundwater and soil moisture (Malanson 1993). However, given the greater difficulty in obtaining this information, most studies have related the structure of riverine forests to flood frequency and duration (Malanson 1993). Soil moisture may be totally or partially influenced by floods (Moeslund *et al*. 2013); however, small-scale topographic variations influence both local moisture conditions and edaphic properties (Mitsch & Gosselink 2000). Although the influence of topography on soil moisture conditions affecting drainage and flood duration is well known, the function performed by topography-soil-moisture mechanisms in controlling vegetation patterns are poorly understood (Moeslund *et al*. 2013). In addition, it is important to emphasise that oxygen depletion in the soil varies along the moisture gradient. Thus, soil moisture measurements may best describe soil water saturation conditions rather than flood level measurements (Malanson 1993).

Effects of flood pulses on organisms vary considerably depending on the geomorphological heterogeneity present in flood areas (Junk *et al*. 2011). Consequently, the spatial and temporal distribution of disturbances generated by such events is also heterogeneous; originating a mosaic of forest patches at different successional stages (Giehl & Jarenkow 2008; Luize *et al*. 2015), and promoting spatial variability in the accumulation of aboveground biomass (Rosenfield & Souza 2014). Although flood disturbances have major effects, structural and diversity patterns in riverine forests respond not only to flood regimes but also to small-scale variations in environmental conditions (topography, soil moisture, soil texture, etc.) (Oliveira-Filho *et al*. 1994). In addition, the role of these variables on patterns of biomass accumulation in flooded forests remains unclear (Assis *et al*. 2019).

The provision of ecosystem services, maintenance of an important complement of regional plant diversity and prevention of species loss due to climate change and land use require understanding of ecological patterns and processes related to freshwater wetland biodiversity including riverine forests (Silva *et al*. 2017; Wittmann *et al*. 2017). In order to investigate relationships between vegetation with abiotic characteristics in riverine forests, we formulated the following hypotheses: (1) riverine tree communities exhibit variation in structure and biomass accumulation along a flood gradient in response to both disturbance regimes and topographic and edaphic properties; (2) richness and diversity are higher in areas less prone to flood disturbances.

MATERIAL AND METHODS

Study area

The tree component survey was performed in three areas within the riverine fringes of the mid sector of the Capivari, Pequiri and Ratos streams. These streams are tributaries of the right margin of the lower Jacuí river course, located in the municipalities of Rio Pardo (30°01’34.62’’S, 52°16’53.2’’W; 23 m a.s.l.), Cachoeira do Sul (30°03’16.05’’S, 52°42’8.59’’W; 30 m a.s.l.) and Eldorado do Sul (30°04’32.0’’S, 51°40’3.99’’W; 24 m a.s.l.), in the state of Rio Grande do Sul, southern Brazil, respectively. Floods in the study areas are unpredictable and polymodal, and related to lateral water flows promoted by events of great local or upstream precipitation. These events may occur at any time during the year, and there are no marked seasonal precipitation periods (Oliveira-Filho *et al*. 2015).

The riverine forests studied are included in a subtropical Atlantic semi-deciduous forests matrix (Oliveira-Filho *et al*. 2015). The regional climate is subtropical humid mesothermal (Cfa, according to Köppen’s system), with annual mean temperature between 18^{o}C and 20^{o}C, and annual rainfall between 1,600 mm and 1,900 mm (Alvares *et al*. 2014). The soils in the study areas are classified as eutrophic hydromorphic planosols (Streck *et al*. 2002).

Data collection

We performed the surveys in two contrasting conditions in each study area: frequently and eventually flooded. Frequently flooded corresponds to sites of lower topographic elevation (1.5 m above the water stream level on average) and eventually flooded sites are topographically higher (3.8 m above the water stream level on average). In each study area, we sampled two plots of 20 × 50 m (subdivided into 10 × 10 m sample units) in both flood conditions, totalling 1.2 ha. All trees with perimeter at breast height ≥ 15 cm were sampled, and the total height was estimated by comparison with a graduated rod (Durigan 2012). Identifications were performed on the study site, and collections were made when necessary. Families were delimited according to the APG IV (2016) classification system.

Soil chemical and textural variables were obtained from composite samples collected at the centre and vertices of each plot, up to 20 cm deep, after litter removal. We collected six undeformed soil samples from the plot centres, three at each depth of 0-10 cm and 10-20 cm and at a distance of 30 cm from each other at both depths, in order to evaluate the physical properties of soil bulk, volumetric moisture, gravimetric moisture, airspace, macroporosity, microporosity and total porosity. Analyses were carried out by Soil Laboratories of the UFRGS Soil Department, based on Embrapa (1997) protocols.

The average elevation for each sample unit relative to the watercourse level was obtained using the mean of the elevations measured at the extremities, measured with the use of a water-filled levelling hose and metric tapes (Cardoso & Schiavini 2002).

Data analysis

Absolute density (AD) and basal area (ABA) were estimated for all recorded species in each environmental condition. We considered the parameters of density, average height, total aboveground biomass (AGB) and average individual AGB per sample unit and per plot. The AGB (in kg) of individual trees was calculated using the allometric equation in accordance with Chave *et al*. (2014), based on tree diameter (D, cm), total height (H, m) and wood specific gravity (ρ, $g.cm^{-3}$):

$$AGB = 0.0673 \times (\rho \times D^2 \times H)^{0.976}$$

Wood specific gravity of the species was based on the mean species value or mean genus value obtained from the Global Wood Density Database (Zanne *et al*. 2009) and specialised literature (Lorenzi 1998; 2009). The mean individual AGB was calculated by dividing the total AGB per plot and per sample unit by the density of individuals.

Edaphic variables were scaled to obtain equal weights and were then subjected to principal components analysis (PCA) to reduce their dimensionality. The first three principal components (PCs) accounted for little more than 80% of the total variance (Table 1). Thus, the scores of these PCs were used as explanatory variables in subsequent analyses at the plot scale.

Spatial dependence in the data was investigated and confirmed by applying the Mantel test, constructing a variogram and inspecting its key parameters. We then performed analyses of spatial generalised linear mixed models (GLMM) for each parameter as a function of the average elevation at the sample unit scale, PC scores at the plot scale and flood regimes at both scales. The site and geographical coordinates of the sample units or plots were included in the models as a random effect to account for sample design and to model spatial dependence. The best model was selected using Akaike information criteria (AIC) according to Burnham & Anderson (2004). Assumptions of normality and homogeneity of variance for response variables were tested and met using the Shapiro-Wilk and Levene tests, respectively. The Poisson probability density function was used for density, as it included counts of individuals.

Table 1. Correlation of edaphic variables with principal component (PC) scores for riverine forests subject to different flood regimes in southern Brazil. Percentage values in parentheses indicate the variance explained by the PCs.

Variable	**PC1 (41.67%)**	**PC2 (22.24%)**	**PC3 (17.57%)**
Clay (%)	-0.91	-0.01	-0.08
Sand (%)	0.90	-0.17	0.18
Silt (%)	-0.86	0.27	-0.23
pH (in H_2O)	-0.31	0.82	-0.41
P (mg dm^{-3})	0.07	0.56	0.26
K (mg dm^{-3})	-0.21	-0.33	-0.54
Organic matter (%)	-0.45	-0.58	0.16
Al (cmol dm^{-3})	-0.43	-0.71	0.48
Ca (cmol dm^{-3})	-0.56	0.38	0.70
Mg (cmol dm^{-3})	-0.79	0.47	0.17
H + Al (cmol dm^{-3})	-0.51	-0.64	0.55
Cation Exchange Capacity (cmol dm^{-3})	-0.62	-0.45	0.61
Bases saturation (%)	0.02	0.97	0.01
Al saturation (%)	0.06	-0.94	-0.09
Ca/Mg	0.61	0.13	0.66
Ca/K	-0.34	0.41	0.75
Mg/k	-0.63	0.55	0.45
Soil bulk (g cm^{-3})	0.85	0.06	-0.15
Macroporosity (m^3 m^{-3})	0.50	0.03	0.61
Microporosity (m^3 m^{-3})	-0.93	-0.10	-0.27
Total porosity (m^3 m^{-3})	-0.90	-0.06	0.16
Gravimetric moisture (kg kg^{-1})	-0.92	-0.04	-0.07
Volumetric moisture (m^3 m^{-3})	-0.93	-0.10	-0.27
Airspace (%)	0.51	0.06	0.62

Richness estimates were performed using Jackknife 1 (Walther & Moore 2005). Diversity order parameters (species richness, exponential of Shannon’s entropy index and inverse of Simpson’s concentration index) were compared between environmental conditions through diversity profiles based on the Hill numbers (Chao *et al*. 2014). All analyses were performed using R software (R Core Team 2018).

RESULTS

We sampled 1,927 trees belonging to 73 species and 31 families (Appendix S1). Of these, 973 individuals from 54 species and 23 families were sampled in environments subject to frequent flooding, and 954 individuals, 58 species and 28 families in eventually flooded environments. Fifteen species were recorded only in frequently flooded environments, 19 only in environments subject to eventual flooding and 39 were common to both conditions. Myrtaceae was the richest family (21 species), followed by Fabaceae (five), Salicaceae, Sapotaceae and Rubiaceae (four species each). In sites with frequent flooding, the species covering the greatest absolute basal area was *Gymnanthes klotzschiana* Müll.Arg., and in eventually flooded conditions, was *Luehea divaricata* Mart. & Zucc. The total AGB estimated for frequently flooded environments was 158.55 $Mg.ha^{-1}$ and 224.58 $Mg.ha^{-1}$ for environments subject to eventual flooding.

Density did not vary as a function of the abiotic variables considered, while total AGB, average individual AGB and mean height varied at plot and sample unit scales (Table 2). Total AGB was negatively associated with frequent flood conditions at both scales analysed. Average individual AGB was positively related to mean elevation and PC 1 of the PCA and negatively correlated with the frequently flooded condition. Variations in average height were associated with PC 3 of the PCA and frequent flood conditions.

Table 2. Spatial generalised linear mixed models (GLMM) with lower Akaike information criteria (AIC) values for the density, total aboveground biomass (AGB), mean individual AGB and average height at the plot and sample unit scales. Site and geographical coordinates were considered as random effects in all models.

Variables at the plot scale	**ß coefficients**	**Estimate ± standard error**
Density (ind $plot^{-1}$)		
	Intercept	154.93 ± 1.09
Total AGB (kg $plot^{-1}$)		
	Intercept	22458 ± 1499
	Frequently flooded condition	-6605 ± 1915
Average individual AGB (kg ind^{-1} $plot^{-1}$)		
	Intercept	132.32 ± 7.51
	Frequently flooded condition	-11.63 ± 11.88
	Principal Component 1	21.41 ± 5.10
Average height (m $plot^{-1}$)		
	Intercept	10.20 ± 0.53
	Frequently flooded condition	-1.74 ± 0.28
	Principal Component 3	0.57 ± 0.22
Variables at the sample unit scale	**ß coefficients**	**Estimate ± standard error**
Density (ind UA^{-1})		
	Intercept	14.97 ± 1.09
Total AGB (kg UA^{-1})		
	Intercept	2253.7 ± 160.4

	Frequently flooded condition	-660.3 ± 198.2
Average individual AGB (kg ind^{-1} UA^{-1})		
	Intercept	78.59 ± 29.21
	Frequently flooded condition	-2.38 ± 20.86
	Average elevation	18.48 ± 7.28
Average height (m UA^{-1})		
	Intercept	10.21 ± 0.56
	Frequently flooded condition	-1.89 ± 0.32

The observed richness was similar between the two flooding conditions (Fig. 1) and the richness estimated by Jackknife 1 confirmed this finding (frequently flooded condition = 72.7 ± 5.8 species; eventually flooded condition = 68.8 ± 4.1 species). Diversity, however, differed between environmental conditions. Higher values were observed for the exponential of Shannon's entropy index, and the inverse of Simpson's concentration index observed in environments with eventual flooding.

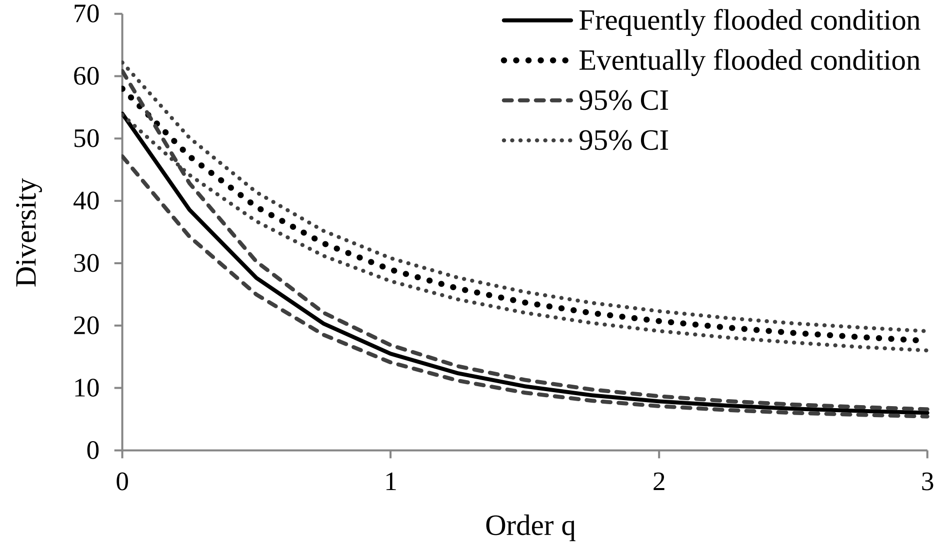

Fig. 1. Diversity profiles (based on Hill numbers) for riverine tree communities sampled in different flooding regimes in southern Brazil (species richness, q = 0; exponential of Shannon's entropy index, q = 1; inverse of Simpson's concentration index, q = 2; CI: Confidence Interval).

DISCUSSION

Our results demonstrate differences between frequently and eventually flooded contiguous sites as demonstrated by reduced total AGB, average individual AGB and average vegetation height. Although the density and richness were similar between flood conditions, AGB and diversity were higher in environments prone to eventual flood regimes. In addition, the increase in average individual AGB associated with topographically higher sites and welldrained soils indicated that the topographic and edaphic properties might also influence the structural patterns of riverine forests and the spatial AGB distribution.

The suggested negative effect of flood regimes on growth and biomass accumulation may be due to high energy water flows and sediment deposition, which are the main physical agents of disturbance (Chalmers *et al*. 2012). Ernst & Brooks (2003) found that larger trees were more sensitive to flooding, such that increased flood frequency caused higher tree mortality and led to a decrease in forest height, which accentuates structural differences. Furthermore, disturbance agents may create physiological stress that inhibits tree growth (Allen *et al*. 2019). Under hypoxic soil conditions, plant responses to limited oxygen availability manifest as damage in architecture, metabolism and growth (Pompeiano *et al*. 2017). Therefore, flood stress and disturbance may contribute to reductions in biomass stocks in the vegetation of areas subject to frequent flood disturbances.

Disturbance regimes may play a significant role in the variation of AGB and carbon stocks in the vegetation through changes in stem density and average plant biomass (Schietti *et al*. 2016). In addition to correlating negatively with the frequent flood condition, the average individual AGB was positively correlated with topographic elevation and PC 1 of the PCA. These results reflect a trend of variation in soil drainage along the flood gradient and indicate that trees at topographically higher sites may achieve greater biomass. Thus, in environments at higher topographic elevation that are eventually or not flooded, the physical properties of the soil can contribute to its enhanced drainage capacity and favour the occurrence of more robust trees with greater average individual biomass (Alves *et al*. 2010). Otherwise, physical soil properties related to greater water retention (higher microporosity and percentage of clay, for example) and lower aeration, might represent a strong abiotic filter (Oliveira *et al*. 2018) to biomass accumulation. According to Samojeden *et al*. (2018), plants in waterlogging soils may exhibit greater carbon consumption due to changes in morpho anatomical traits, which they develop in response to flood stress.

Species richness and diversity in riverine ecosystems vary on relatively small spatial scales as a result of variation in topography and flood regimes (Budke *et al*. 2008). Species richness in the present study did not corroborate with patterns of lower richness in frequently flooded sites as observed in other areas of riverine forests (Giehl & Jarenkow 2008; Budke *et al*. 2008). As riverine forests act as migratory corridors, the evolution of a specific flora adapted to floods may have been hampered by these floristic flows (Wittmann 2012). Furthermore, high species overlap between flood conditions may indicate that many are habitat generalists (Ferreira & Stohlgren 1999).

Frequent flooding sites tend to have lower tree species diversity compared to eventually flooded sites (Giehl & Jarenkow 2008), probably due to disturbances and soil waterlogging stress (Junk *et al*. 2011). Topographically higher sites and generally greater distance from the watercourse have harboured most of the tree diversity, which suggests that for the effective conservation of riverine forests, it is not enough to protect only narrow bands at the edges of water courses as predicted by Brazilian legislation (Brancalion *et al*. 2016). In addition, by aggregating both conditions, the total richness may be greater than that of the surrounding matrix. This finding demonstrates that the protection of areas with large bands and distinct abiotic conditions in riverine forests would allow the maintenance of an extensive part of the regional species pool (Wittmann *et al*. 2017) and provision of ecosystem services (Brancalion *et al*. 2016).

In conclusion, our results indicate that flooding regimes play a vital role in the process of biomass accumulation and structuring of riverine tree communities. However, small-scale topographic and edaphic variables can also influence riverine forest assembly along the flood gradient, resulting in forest patches with unique structural features. Although richness did not differ between the studied environmental conditions, when abundance and richness were considered, the diversity was greater in eventually flooded sites. Inclusion of flood-free interfluvial areas and a greater sampling effort are necessary to better understand the assembly patterns of riverine tree communities, especially those subject to unpredictable floods.

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SUPPORTING INFORMATION

Appendix S1. Parameter estimates for species sampled in riverine forests subject to distinct flood regimes.

Species†	**Family**	**AD (ind ha^{-1})‡**		**ABA (m^{2} ha^{-1})§**	
		FF††	**EF‡‡**	**FF**	**EF**
Gymnanthes klotzschiana Müll.Arg.	Euphorbiaceae	413	112	6.143	0.769
Luehea divaricata Mart. & Zucc.	Malvaceae	28	95	5.138	7.317
Terminalia australis Cambess.	Combretaceae	70	-	4.744	-
Pouteria gardneriana (A.DC.) Radlk.	Sapotaceae	35	-	2.908	-
Allophylus edulis (A.St.-Hil. *et al.*) Hieron. ex Niederl.	Sapindaceae	50	120	1.609	2.685
Actinostemon concolor (Spreng.) Müll.Arg.	Euphorbiaceae	357	153	1.258	0.582
Ruprechtia laxiflora Meisn.	Polygonaceae	47	25	1.068	0.239
Eugenia uruguayensis Cambess.	Myrtaceae	73	22	0.888	0.094
Chrysophyllum marginatum (Hook. & Arn.) Radlk.	Sapotaceae	38	68	0.764	1.644
Campomanesia rhombea O.Berg	Myrtaceae	35	60	0.740	0.886
Nectandra megapotamica (Spreng.) Mez	Lauraceae	5	-	0.567	-
Matayba elaeagnoides Radlk.	Sapindaceae	12	85	0.514	3.503
Lonchocarpus nitidus (Vogel) Benth	Fabaceae	10	-	0.490	-
Cupania vernalis Cambess.	Sapindaceae	28	23	0.445	0.752
Eugenia verticillata (Vell.) Angely	Myrtaceae	60	15	0.438	0.077
Eugenia uniflora L.	Myrtaceae	43	38	0.388	0.233
Myrsine laetevirens (Mez) Arechav.	Primulaceae	2	5	0.374	0.683
Vitex megapotamica (Spreng.) Moldenke	Lamiaceae	10	10	0.356	0.163
Casearia sylvestris Sw.	Salicaceae	43	35	0.346	0.338
Casearia decandra Jacq.	Salicaceae	38	65	0.326	0.453
Machaerium paraguariense Hassl.	Fabaceae	7	50	0.315	1.345
Inga vera Willd.	Fabaceae	2	-	0.283	-
Sorocea bonplandii (Baill.) W.C.Burger *et al.*	Moraceae	48	22	0.263	0.168
Roupala montana Aubl.	Proteaceae	3	-	0.242	-
Myrciaria tenella (DC.) O.Berg	Myrtaceae	52	142	0.214	0.530
Eugenia involucrata DC.	Myrtaceae	2	-	0.182	-
Myrcianthes gigantea (D.Legrand) D.Legrand	Myrtaceae	2	3	0.178	0.063
Myrcia multiflora (Lam.) DC.	Myrtaceae	17	25	0.170	0.352
Lithraea brasiliensis Marchand	Anacardiaceae	3	15	0.124	0.988
Myrciaria cuspidata O.Berg	Myrtaceae	8	62	0.116	0.406
Diospyros inconstans Jacq.	Ebenaceae	5	5	0.114	0.042
Sebastiania brasiliensis Spreng.	Euphorbiaceae	12	8	0.113	0.069
Eugenia mansoi O.Berg	Myrtaceae	2	-	0.077	-

Chrysophyllum gonocarpum (Mart. & Eichler ex Miq.) Engl.	Sapotaceae	5	8	0.064	0.058
Syagrus romanzoffiana (Cham.) Glassman	Arecaceae	2	2	0.063	0.060
Coccoloba cordata Cham.	Polygonaceae	8	2	0.041	0.005
Eugenia hiemalis Cambess.	Myrtaceae	7	17	0.039	0.069
Ocotea pulchella (Nees & Mart.) Mez	Lauraceae	2	33	0.026	1.374
Calyptranthes concinna DC.	Myrtaceae	2	-	0.026	-
Myrsine lorentziana (Mez) Arechav.	Primulaceae	3	-	0.025	-
Strychnos brasiliensis Mart.	Loganiaceae	3	12	0.019	0.070
Myrrhinium atropurpureum Schott	Myrtaceae	2	18	0.014	0.206
Chomelia obtusa Cham. & Schltdl.	Rubiaceae	5	13	0.014	0.040
Scutia buxifolia Reissek	Rhamnaceae	2	18	0.010	0.394
Calliandra tweedii Benth.	Fabaceae	5	3	0.010	0.006
Eugenia speciosa Cambess.	Myrtaceae	2	-	0.009	-
Blepharocalyx salicifolius (Kunth) O.Berg	Myrtaceae	3	-	0.009	-
Celtis iguanaea (Jacq.) Sarg.	Cannabaceae	2	-	0.008	-
Randia ferox (Cham. & Schltdl.) DC.	Rubiaceae	2	5	0.006	0.034
Maytenus cassineformis Reissek	Celastraceae	2	2	0.005	0.005
Pouteria salicifolia (Spreng.) Radlk.	Sapotaceae	2	-	0.004	-
Faramea montevidensis (Cham. & Schltdl.) DC.	Rubiaceae	2	-	0.003	-
Myrcia glabra (O.Berg) D.Legrand	Myrtaceae	2	7	0.003	0.067
Trichilia elegans A.Juss.	Meliaceae	2	15	0.003	0.046
Cordia americana (L.) Gottschling & J.S.Mill.	Boraginaceae	-	83	-	6.477
Eugenia ramboi D.Legrand	Myrtaceae	-	12	-	0.366
Annona neosalicifolia H.Rainer	Annonaceae	-	17	-	0.364
Banara parviflora (A.Gray) Benth.	Salicaceae	-	7	-	0.330
Helietta apiculata Benth.	Rutaceae	-	2	-	0.298
Parapiptadenia rigida (Benth.) Brenan	Fabaceae	-	7	-	0.238
Citharexylum montevidense (Spreng.) Moldenke	Verbenaceae	-	5	-	0.214
Handroanthus heptaphyllus (Vell.) Mattos	Bignoniaceae	-	3	-	0.103
Myrcia selloi (Spreng.) N.Silveira	Myrtaceae	-	10	-	0.072
Myrcia palustris DC.	Myrtaceae	-	3	-	0.069
Campomanesia xanthocarpa (Mart.) O.Berg	Myrtaceae	-	3	-	0.062
Cordia ecalyculata Vell.	Boraginaceae	-	2	-	0.056
Myrcianthes pungens (O.Berg) D.Legrand	Myrtaceae	-	3	-	0.053
Banara tomentosa Clos	Salicaceae	-	5	-	0.048
Erythroxylum deciduum A.St.-Hil.	Erythroxylaceae	-	2	-	0.019
Prunus myrtifolia (L.) Urb.	Rosaceae	-	2	-	0.017
Machaonia acuminata Bonpl.	Rubiaceae	-	3	-	0.016
Maytenus dasyclada Mart.	Celastraceae	-	2	-	0.008
Solanum sanctae-catharinae Dunal	Solanaceae	-	2	-	0.008

†Species ordered according to decreasing values of absolute basal area; ‡Absolute density; §Absolute basal area; ††Frequently flooded condition; ‡‡Eventually flooded condition.

Manuscrito 2

Intraspecific variability and niche breadth of a typical tree of riverine forests in southern Brazil[2]

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[2] Manuscrito formatado de acordo com as normas do periódico *Acta Oecologica*

Intraspecific variability and niche breadth of a typical tree of riverine forests in southern Brazil

Abstract Intraspecific functional variability can play an important role in the responses of species to abiotic factors and allow a better understanding of these responses to environmental gradients. We determined whether functional traits exhibit greater variability among than within populations of *Gymnanthes klotzschiana* and whether abiotic factors are related to functional traits that differ among populations. Samplings were performed in four populations located in three different geomorphological regions in the state of Rio Grande do Sul, southern Brazil. Data of leaf area (LA), specific leaf area (SLA), leaf dry matter content (LDMC) and total height were collected from seven adult individuals per plot, with three plots per site. We observed significant differences in functional traits among populations and greater variability at the scale of populations than of plots for LDMC and height. Leaf area and SLA exhibited greater variation within than among populations. Specific leaf area and LDMC were significantly correlated with edaphic and climatic variables. Our findings indicate that environmental conditions are selecting for different phenotypic characteristics and strategies of resource use in populations of *G. klotzschiana*, and imply a tendency for increased functional niche breadth for this species.

Keywords: Ecological strategy. Functional traits. Gradients. *Gymnanthes klotzschiana*. Populations.

1. Introduction

Ecological studies are increasingly using functional trait-based approaches to better understand the responses of species to environmental gradients, disturbances and biotic interactions (Siefert, 2012; Mouillot et al., 2013; Carvajal et al., 2017). Most of these studies emphasize interspecific variation based on the argument that the variability among species is greater than variability within species (McGill et al., 2006). Thus, intraspecific trait variation (ITV) would be negligible in data sets on a global scale, but it is unclear whether ITV is also negligible for constrained geographic areas, where interspecific variation is likely much lower (Hulshof and Swenson, 2010). Recent studies have demonstrated that ITV in response to environmental gradients is greater than previously assumed (Jung et al., 2010; Carvajal et al., 2017). Therefore, ITV can be critical to a better understanding of species responses to abiotic factors in local communities and along environmental gradients (Hulshof and Swenson, 2010), especially for species with broad geographical distributions that are likely to be more variable in their traits (Richardson et al., 2013).

The Hutchinsonian niche concept assumes that a species can persist at any point within the boundaries of the multidimensional hypervolume defining its niche (Hutchinson, 1957). Based on this concept, niche overlap among environmental axes can indicate the range of conditions in which species co-occur (Mouillot et al., 2005). Functional traits have been used to quantify the niche of species (Violle and Jiang, 2009), and Rosenfeld (2002) proposed an extension to Hutchinson's concept of the niche – the 'functional niche'. According to this concept, axes of hyperspace are functions defined from functional traits (Rosenfeld, 2002). Although ITV can be used to assess the functional niche breadth of a given species based on data from different geographic areas (Violle and Jiang, 2009), little is known about intraspecific functional variability (Sánches-Gómez et al., 2013).

Differential selection along environmental gradients can promote greater degrees of population differentiation (Akman et al., 2016; Carvajal et al., 2017). Phenotypic plasticity and genetic diversity are the main sources of ITV (Violle et al., 2012) and determine the ability of species to cope with changes in environmental conditions (Jung et al., 2010), allowing the expression of traits that vary among sites in response to abiotic and biotic filters (Siefert, 2012). Intraspecific trait variation increases the chances of a species overcoming environmental filters by adjusting its trait values (Jung et al., 2010) and, if the species is sufficiently plastic, will allow it to occupy a broad range of environments (Andrade et al., 2014). Intraspecific functional variability can be approached at different ecological scales, such as among individuals in a plot, among plots of a population and among populations (Messier et al., 2010; Salazar et al., 2018).

According to Reich (2014), uniformly fast, medium or slow strategies for resource acquisition comprise general species characteristics that result from strong selective pressures on trait trade-offs. However, since species are not uniform entities (Valladares et al., 2014), their traits are not fixed (Siefert, 2012), and individuals of the same species can express different trait values in distinct environments (Lajoie and Vellend, 2015). At the intraspecific level, leaf traits can vary among populations through modifications in the strategy of resource use in order to adjust to environmental conditions (Salazar et al., 2018). Therefore, traits related to resource use are expected to become adaptively differentiated in habitats that vary in resource availability (Brouillette et al., 2014).

The species *Gymnanthes klotzschiana* Müll.Arg., an euphorbiaceous tree, has a wide distribution in alluvial plains (Smith et al., 1988) and is among the most abundant tree species in riverine forests of southern Brazil (Budke et al., 2008; Carvalho et al., 2009), particularly in environments subject to frequent flooding (Budke et al., 2008; Zonta et al. Manuscrito 1). *Gymnanthes klotzschiana* has anatomical characteristics adapted to waterlogged soils (Kolb et al., 1998, as *Sebastiania commersoniana* (Baill.) L.B.Sm. & Downs, a synonymous name), and grows in habitats under full or diffuse sunlight (Smith et al., 1988).

Based on the assumptions that plants can exhibit considerable ITV in response to the environment (Jung et al., 2010; Carvajal et al., 2017), and that this variability increases the likelihood of a species tolerating changes in environmental conditions (Jung et al., 2010; Lajoie and Vellend, 2015) and having a greater niche breadth (Violle and Jiang, 2009), as well as the relevance of considering ITV for a better understanding of the processes leading to phenotypic variation along environmental gradients (Carvajal et al., 2017), we formulated the following hypotheses: (1) there is a greater variability of functional traits among populations of *G. klotzschiana* than within; and (2) abiotic factors are related to variation in functional traits among populations of *G. klotzschiana*.

2. Material and methods

2.1. Study sites

The studied *Gymnanthes klotzschiana* populations were located in riverine forests of three geomorphological regions in the state of Rio Grande do Sul, southern Brazil: Central Depression, Campanha Plateau and Sul-Rio-Grandense Plateau (IBGE, 1986a). The study was performed at four sampling sites: Santana da Boa Vista - SBV (Sul-Rio-Grandense Plateau; 30°50’16.87”S, 53°13’17.46’’W; 235 m.s.m.), Santo Antônio das Missões - SAM (Campanha Plateau; 28°32’7.92’’S, 55°27’14.25”W; 87 m.s.m.), São Gabriel - SGA (West Central Depression; 30°06’23.09”S, 54°19’14.20”W; 120 m.s.m.) and Rio Pardo - RPA (East Central Depression; 30°01’34.62’’S, 52°16’53.2’’W; 23 m.s.m.) (Fig. 1). The climate of the sampling sites is humid subtropical (Cfa), with a mean annual temperature of 16ºC to 18ºC for SBV and SGA and of 18ºC to 20ºC for RPA and SAM. The annual precipitation ranges from 1,300 to 1,600 mm for SBV, from 1,600 to 1,900 mm for RPA and SGA, and from 1,900 to 2,200 mm for SAM (Alvares et al., 2014). The soils are derived from sandstones and conglomerates at SBV, siltstones and fine sandstones at SGA, basalts and phenobasalts at SAM and alluvial deposits at RPA (IBGE, 1986b). Subtropical semi-deciduous forests occur in riverine environments of all the sampling sites (Oliveira-Filho et al. 2015).

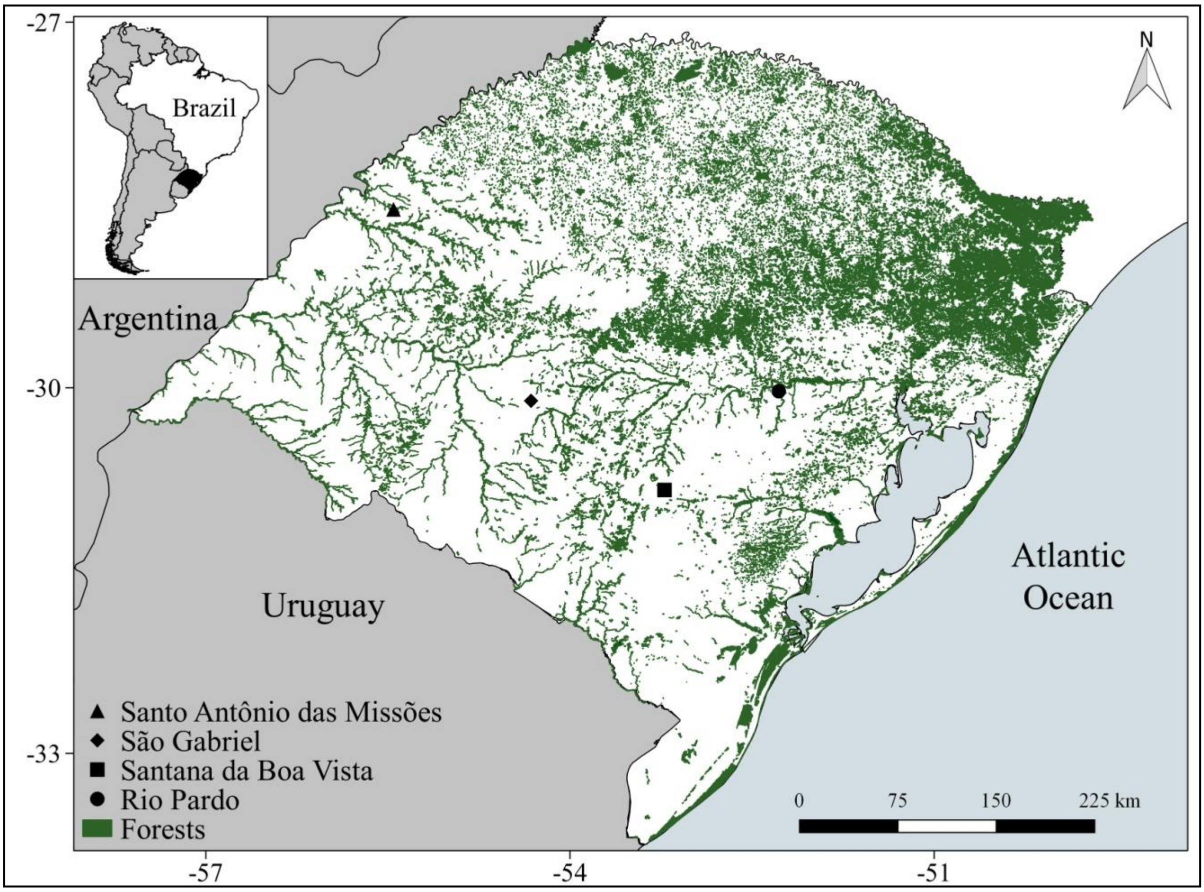

Fig. 1. Location of the state of Rio Grande do Sul and sampling sites in southern Brazil. The sampling sites are named according to the municipality in which they occur.

2.2. Data collection

The delimitation of three of the four sampling sites, one per geomophological region, followed the definitions of the PPBio Campos Sulinos project, which established landscape sampling units of 5 × 5 km at several locations in the state of Rio Grande do Sul. A fourth sampling site, located in the East Central Depression, was added. Data were collected in three 20 × 50 m plots, of each site, for a total of 12 plots. The plots were located approximately 10 m from and parallel to stream margins, and are subject to periodic flooding. The distance between plots of the same sampling site ranged 2.71 km on average, and between sites 223 km on average.

In order to characterize the sampling sites (Table 1) and to relate abiotic factors to functional traits, composite soil samples were collected at the center and vertices of each of three plots per sampling site. The samples were collected at a depth of 20-30 cm due to sand deposition caused by flood events. Soil analyses were carried out by the Soil Laboratory of the Federal University of Rio Grande do Sul following the protocols of Embrapa (1997). Data for temperature and precipitation were obtained from *WorldClim Global Climate* (Fick and Hijmans, 2017), while data on potential evapotranspiration were acquired from the Global Aridity and PET database (Trabucco and Zomer, 2009).

Table 1. Abiotic variables (means ± standard deviation) of the sampling sites in different geomorphological regions in the state of Rio Grande do Sul, southern Brazil.

Variable	**SBV**[1]	**SGA**[2]	**SAM**[3]	**RPA**[4]
Clay (%)	24.3 ± 4.0	25.3± 3.5	53.0± 2.0	41.3± 2.3
Sand (%)	58.0± 15.6	58.7± 16.6	4.0 ± 1.7	34.3± 11.6
Silt (%)	17.7± 11.6	16.0 ± 13.1	43.0 ± 2.6	24.3± 9.5
P (mg dm^{-3})	4.1 ± 1.9	6.1 ± 0.8	6.4 ± 4.6	5.4 ± 1.2
K (mg dm^{-3})	40.7 ± 12.1	64.7 ± 18.8	83.7 ± 13.3	47.0 ± 7.0
Ca (cmol dm^{-3})	3.8 ± 1.1	8.3 ± 3.2	26.8 ± 5.5	3.6 ± 0.6
Mg (cmol dm^{-3})	1.2 ± 0.3	1.9 ± 0.5	12.8 ± 1.0	1.2 ± 0.3
Base saturation (%)	42.0 ± 14.4	68.0 ± 4.6	78.3 ± 5.7	20.3 ± 3.1
CEC (cmol dm^{-3})[5]	13.1 ± 3.5	15.1 ± 4.8	50.7 ± 5.1	23.9 ± 3.7
OM (%)[6]	1.5 ± 0.4	1.2 ± 0.4	3.2 ± 0.7	2.1 ± 0.2
S (mg dm^{-3})	6.7 ± 1.1	9.3 ± 1.01	16.0 ± 5.3	18.7 ± 0.6
Zn (mg dm^{-3})	1.6 ± 0.5	1.1 ± 0.1	3.1 ± 0.5	2.4 ± 0.4
Cu (mg dm^{-3})	1.1 ± 0.7	0.4 ± 0.1	6.5 ± 2.6	1.5 ± 0.3
B (mg dm^{-3})	0.2 ± 0.0	0.2 ± 0.1	0.2 ± 0.0	0.3 ± 0.1
Mn (mg dm^{-3})	27.3 ± 11.0	34.3 ± 5.5	90.7 ± 31.3	48.3 ± 22.7
MAT (°C)[7]	18.4 ± 1.7	19.1 ± 0	20.6 ± 0	19.4 ± 0
AP (mm)[8]	1,434.7 ± 8.1	1,578 ± 0	1,742 ± 0	1,333 ± 0
PET (mm yr^{-1})[9]	1,293 ± 7	1,384 ± 0	1,529 ± 3	1,299 ± 0.6

[1]Santana da Boa Vista; [2]São Gabriel; [3]Santo Antônio das Missões; [4]Rio Pardo; [5]Cation exchange capacity; [6]Organic matter; [7]Mean annual temperature; [8]Annual precipitation; [9]Potential evapotranspiration.

Seven adult individuals of *G. klotzschiana* with a minimum perimeter at breast height of 31 cm were selected in each plot for the measurement of functional traits. Ten fully-expanded leaves that were totally exposed to sunlight and without evidence of herbivory were collected from each individual (Pérez-Harguindeguy et al., 2013). The four vegetative traits of (1) total height, (2) leaf area (LA), (3) specific leaf area (SLA) and (4) leaf dry matter content (LDMC) were selected for study because they are functional traits that reflect ecological strategies of resource use (Jung et al., 2010; Siefert, 2012; Pérez-Harguindeguy et al., 2013) and are related to water balance, competitive ability, plasticity and tolerance to stress and disturbance (Weiher et al., 1999; Westoby et al., 2002; Pérez-Harguindeguy et al., 2013). Procedures for measuring leaf traits were standardized according to Pérez-Harguindeguy et al. (2013), with all measurements being taken during the summer (February and March). After weighing the fresh mass of the leaves and scanning them, the samples were oven dried at 60°C for 72 h and weighed again to obtain the dry mass. Leaf area was calculated from the scanned images of leaves using Image J software. These data were then used to calculate SLA and LDMC per individual, following Pérez-Harguindeguy et al.

(2013). Data for total height were obtained from field estimates using a graduated rod (Durigan, 2012).

2.3. Data analysis

Assumptions of normality and homogeneity of variance for functional trait data were tested using the Shapiro-Wilk and Levene tests, respectively. Since the assumptions were not met, the data were normalized by logarithmic transformation. Linear mixed-effects (LME) models were used to partition the variance of each trait per plot and per population, with plot (nested in population) and population as random factors (Messier et al., 2010). The significance of ITV per plot and population was evaluated by including plot in the model as a fixed factor (population as random factor) and population in the model as a fixed factor (plot as random factor), respectively (Moreira et al., 2012). Analyses of variance (ANOVA) were used to investigate differences in functional traits among populations. Variables with significant differences among populations were submitted to the Tukey post hoc test. Distribution curves were constructed according to Taudiere and Violle (2015) to represent the distribution of density values for each trait and for each population.

Edaphic and climatic variables were standardized and then subjected to Principal Component Analysis (PCA) to reduce their dimensionality. The first three principal components (PCs) accounted more than 90% of the total variance (Appendix S1). We performed Pearson correlation analyses to evaluate the relationship between the PCA axes and functional traits. All statistical analyses were performed in R software (R Core Team, 2018) using the packages *car* (Fox and Weisberg, 2011), *cati* (Taudiere and Violle, 2015) and *pacman* (Rinker and Kurkiewicz, 2017).

3. Results

The decomposition of the variance for each of the traits demonstrated greater variability among than within populations for LDMC and total height, while LA and SLA had greater variation among plots than among populations (Table 2). The populations of *G. klotzschiana* from different geomorphological regions were clearly differentiated for LDMC and height (Fig. 2).

Table 2. Decomposition of the variance at plot and population scales for LA (leaf area), SLA (specific leaf area), LDMC (leaf dry matter content) and total height.

Trait	Variance (%)			Significance	
	Population	Plot	Residuals	Population	Plot
LA (cm^2)	~ 0	30.11	69.89	ns	0.002
SLA (mm^2 mg^{-1})	~ 0	35.45	64.55	ns	< 0.001
LDMC (mg g^{-1})	28.05	12.63	59.32	0.031	0.022
Total height (m)	25.82	15.35	58.83	0.045	0.012

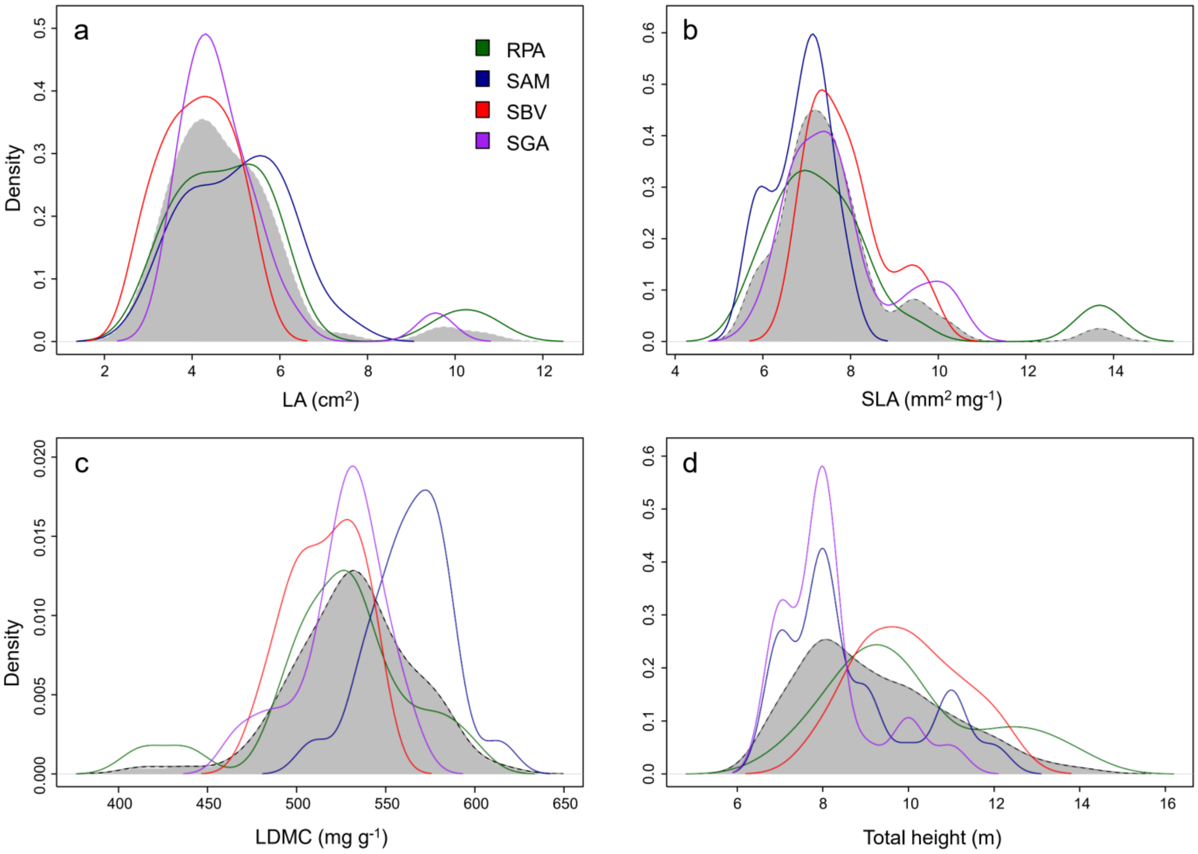

Fig. 2. Distribution of density values for each functional trait and for each population of *Gymnanthes klotzschiana* in different geomorphological regions in the state of Rio Grande do Sul, southern Brazil. a) Leaf area (LA); b) Specific leaf area (SLA); c) Leaf dry matter content (LDMC); d) Total height. The gray-filled curve indicates the mean distribution of the trait. RPA: Rio Pardo; SAM: Santo Antônio das Missões; SBV: Santana da Boa Vista; SGA: São Gabriel.

Functional traits differed significantly among populations (Table 3), with lower values for LA in SBV than in RPA, higher values for SLA in SBV than in SAM, higher values for LDMC in SAM than in the other populations, and greater height in SBV and RPA than in the other two populations. The traits SLA and LDMC were significantly inversely and directly correlated with PC1, respectively (Table 4). This PCA axis was significantly correlated with edaphic and climatic variables (Appendix S1).

Table 3. Mean ± standard deviation of functional traits of populations of *Gymnanthes klotszchiana* in different geomorphological regions in the state of Rio Grande do Sul, southern Brazil. Different letters indicate significant differences among populations obtained according to Tukey's post hoc test (***** $p < 0.05$; ******* $p < 0.001$).

Population	**LA (cm^2)**[1]	**SLA (mm^2 mg^{-1})**[2]	**LDMC (mg g^{-1})**[3]	**Height (m)**
SBV[4]	4.13 ± 0.80^{a}	7.89 ± 0.87^{a}	511.96 ± 20.15^{b}	10.00 ± 1.22^{a}
SGA[5]	4.79 ± 1.28^{ab}	7.71 ± 1.21^{ab}	521.25 ± 24.85^{b}	8.10 ± 1.09^{b}
SAM[6]	5.03 ± 1.13^{ab}	6.85 ± 0.66^{b}	559.83 ± 22.78^{a}	8.62 ± 1.53^{b}
RPA[7]	5.20 ± 1.88^{b}	7.83 ± 2.14^{ab}	518.30 ± 42.51^{b}	10.00 ± 1.87^{a}
***p* value**	*	*	***	***

[1]Leaf area; [2]Specific leaf area; [3]Leaf dry matter content; [4]Santana da Boa Vista; [5]São Gabriel; [6]Santo Antônio das Missões; [7]Rio Pardo.

Table 4. Pearson correlations between functional traits and principal components (PCs) for populations of *Gymnanthes klotzschiana* in different geomorphological regions in the state of Rio Grande do Sul, southern Brazil. Symbols indicate significant correlations (****** $p < 0.01$).

Population scale	**PC1 (65.9%)**	**PC2 (28.4%)**	**PC3 (5.6%)**
LA (cm^2)[1]	0.47	-0.57	-0.67
SLA (mm^2 mg^{-1})[2]	**-0.99****	-0.10	0.01
LDMC (mg g^{-1})[3]	**0.99****	0.04	-0.05
Height (m)	-0.43	-0.63	0.64

[1]Leaf area; [2]Specific leaf area; [3]Leaf dry matter content.

4. Discussion

The studied functional traits of *G. klotzschiana* exhibited a distinct pattern of variation at plot and population scales. The greater variability of LDMC and height among than within populations signals a trend of increasing functional niche breadth of *G. klotzschiana* and indicates that environmental conditions are selecting for different phenotypic characteristics in populations of this species. The significant differences observed among populations for SLA and LDMC, and the correlation of these traits with abiotic factors, suggest that edaphic and climatic conditions are selecting for different strategies of resource use.

The greater variation of LA and SLA at the plot scale than at the population scale may be related to abiotic factors at local scales, and responses to heterogeneous conditions of resource availability (Moreira et al., 2012). In addition to local environmental conditions, the significant inverse correlation between SLA and the edaphic and climatic gradient expressed by axis 1 of the PCA indicates that abiotic changes at the regional scale may also be influencing the performance of this trait. The greater variation of LDMC and height at the population scale than at the plot scale suggests that these traits respond to variation in climatic and edaphic factors (Salazar et al., 2018). Similar results were observed by Salazar et al. (2018) for LDMC of populations of *Prosopis pallida* along a climatic gradient in northern

Peru, which reinforces the association between climatic factors and investment in leaf matter (Wright et al., 2005).

Selective pressures can promote a degree of population differentiation often related to the influence of abiotic filters on the expression of traits at distinct sites (Lajoie and Vellend, 2015; Carvajal et al., 2017). Variations in the optimal niche of *G. klotzschiana* may be related to the particular environmental conditions of the sites, since the population of SAM clearly has a different optimal niche than that of the other populations for LDMC. The higher values of LDMC in SAM, and its positive correlation with the abiotic gradient, suggest that the more fertile soils and more humid and hot climate of this site favor maximizing the capture of resources and their investment in structural tissues (Messier et al., 2010; Mason et al., 2011). Besides the selection imposed by abiotic conditions, the optimum niche of a species can also vary among populations due to species interactions at the local scale (Moreira et al., 2012). The observed differentiation of the optimum niche of the SAM and SGA populations compared to the other two populations for total height may be related to intra- and/or interspecific competition for light energy (Weiher et al., 1999; Pérez-Harguindeguy et al., 2013).

Leaf area was not significantly correlated with the studied abiotic variables, but significant differences were observed between SBV and RPA for this trait. Leaf area can influence thermal conductance, energy balance and leaf hydraulic architecture, and tends to be lower at sites with more limiting environmental conditions (Ackerly and Cornwell, 2007; Cornwell and Ackerly, 2009). The traits SLA and LDMC were inversely correlated (Wilson et al., 1999; Mason et al., 2011), and are related to strategies of resource use (Siefert, 2012). Lower SLA was recorded in SAM than in SBV, and higher LDMC in SAM than in the other populations. Axis 1 of the PCA was inversely correlated with SLA and directly correlated with LDMC. This finding indicates that conservative resource use strategies (lower SLA and higher LDMC) (Siefert, 2012; Lange et al., 2017) are being favored in the population with conditions of greater potential evapotranspiration and soil fertility (SAM), while acquisitive strategies (higher SLA and lower LDMC) are being maximized in the population where soils are less fertile and climatic conditions are less favorable (SBV). These results may represent evidence of differential selection (Akman et al., 2016) on distinct ecological strategies in populations of *G. klotzschiana*, related to climatic and edaphic variation among the different geomorphological regions. Our results differ from those of other studies (Ordoñez et al., 2009; Siefert, 2012), which found SLA to respond positively to increased soil fertility. Studies with an intraspecific approach at community and population scales are necessary to determine whether resource acquisition/conservation patterns are consistent with those observed in the present study, particularly for riverine forest species that are subjected to flood disturbance.

Gymnanthes klotzschiana possesses an autochoric dispersal syndrome, which can partially explain the differences observed among populations for the functional traits, since this syndrome produces shorter dispersion distances compared to zoochory and anemochory (Carrión et al., 2017). Shorter dispersion can reduce gene flow and accentuate differences among populations, especially those located in different regions (Salazar et al., 2018). Studies on population genetics and/or greenhouse experiments are needed to determine if the responses of populations of *G. klotzschiana* to environmental variation occur as a result of phenotypic plasticity and/or genetic and ecotypic variation (Ackman et al., 2016; Carvajal et al., 2017). Such information could aid the design of riverine forest restoration projects and the conservation of the genetic structure of the species.

Edaphic and climatic factors may be promoting greater intraspecific functional variability in *G. klotzschiana* and selecting for distinct ecological strategies at the population scale. Studies that consider a greater number of populations, chemical and physiological leaf traits, variation in flood regimes and genetic aspects of species occurring in riverine forests are necessary for a better understanding of the role of ITV responses to environmental gradients at different ecological scales.

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Supporting information

Appendix S1: Correlation of edaphic and climatic variables with scores of principal components (PCs). Percentage values in parentheses indicate the variance explained by the PCs. Symbols indicate significant correlations among ordination axes and variables (***** *p* < 0.05; ****** *p* < 0.01).

Variable	**PC1 (65.9%)**	**PC2 (28.4%)**	**PC3 (5.6%)**
Clay (%)	0.86	-0.51	-0.03
Sand (%)	-0.92	0.39	-0.04
Silt (%)	**0.96***	-0.25	0.13
pH (in H_2O)	0.55	0.77	0.33
P (mg dm^{-3})	0.70	-0.03	-0.71
K (mg dm^{-3})	0.89	0.27	-0.35
OM (%)[1]	0.91	-0.39	0.16
Al (cmol dm^{-3})	-0.41	-0.88	-0.21
Ca (cmol dm^{-3})	**0.98***	0.18	-0.01
Mg (cmol dm^{-3})	**0.99****	0.08	0.09
H + Al (cmol dm^{-3})	0.05	**-0.99****	0.02
CEC (cmol dm^{-3})[2]	**0.98***	-0.21	0.03
Bases saturation (%)	0.66	0.72	-0.18
Al saturation (%)	-0.49	-0.86	-0.10
Ca/Mg	-0.81	0.40	-0.43
Ca/K	**0.97***	0.21	0.08
Mg/K	**0.98***	0.08	0.15
S (mg dm^{-3})	0.48	-0.82	-0.30
Zn (mg dm^{-3})	0.79	-0.57	0.22
Cu (mg dm^{-3})	**0.98***	-0.10	0.20
B (mg dm^{-3})	-0.12	**-0.99****	0.08
Mn (mg dm^{-3})	**0.97***	-0.22	-0.03
MAT (ºC)[3]	0.93	-0.23	-0.28
AP (mm)[4]	0.83	0.55	-0.13
PET (mm yr^{-1})[5]	**0.95***	0.27	-0.17

[1] Organic matter; [2] Cation exchange capacity; [3] Mean annual temperature; [4] Annual precipitation; [5] Potential evapotranspiration.

Considerações finais

Este trabalho consiste em um dos poucos estudos sobre a diversidade e a estrutura de comunidades arbóreas ribeirinhas na margem direita do baixo curso do rio Jacuí e aborda pela primeira vez aspectos funcionais intraespecíficos de *Gymnanthes klotzschiana* em diferentes regiões geomorfológicas no Rio Grande do Sul.

Além de distúrbios por inundação influenciarem negativamente o acúmulo de biomassa e componentes da estrutura florestal, fatores edáficos e topográficos tiveram um efeito maior sobre a biomassa média individual acima do solo. Estes resultados sugerem que estas variáveis também podem influenciar nos padrões de montagem de florestas ribeirinhas e na distribuição espacial de biomassa acima do solo. Entretanto, para uma melhor compreensão dos padrões de organização de comunidades arbóreas ribeirinhas, a realização de estudos que considerem também áreas de interflúvio isentas de inundação e com uma amostragem mais ampla se faz necessária. Isso permitiria levantar questões relacionadas à densidade, distúrbio intermediário e estratégias ecológicas de estabelecimento e de uso de recursos em ambientes sujeitos ou não a regimes de distúrbio por inundação.

Embora a riqueza tenha sido semelhante entre as condições ambientais, quando a abundância foi considerada em conjunto com a riqueza, observamos que a diversidade foi maior em locais topograficamente mais altos, sujeitos a inundações eventuais e geralmente mais distantes do curso hídrico. Apesar de a legislação brasileira prever a proteção da vegetação em ambientes ribeirinhos, faixas mais estreitas de vegetação ao longo de cursos hídricos como previsto pela lei vigente (Lei de Proteção da Vegetação Nativa – 12.651/2012) pode não ser suficiente para a conservação de uma porção expressiva desta diversidade. Da mesma forma, maiores quantidades de biomassa acima do solo e, consequentemente, maiores estoques de carbono na vegetação em áreas eventualmente inundadas são imprescindíveis para a manutenção de serviços ecossistêmicos e mitigação de mudanças climáticas em escala regional.

Apesar de as áreas de estudo não apresentarem variações climáticas drásticas, observamos diferenças significativas nos atributos funcionais entre populações de *G. klotzschiana* e relações destes atributos com fatores abióticos. Tais resultados indicam que variáveis abióticas podem estar promovendo maior variabilidade funcional intraespecífica e contribuindo para o aumento na amplitude do nicho funcional de *G. klotzschiana*. Como a variabilidade intraespecífica pode ser importante na resposta de espécies a condições ambientais, ressaltamos que estudos com abordagens funcionais deveriam considerar, além da variabilidade entre espécies, aquela dentro de espécies. Estudos sobre aspectos funcionais em diferentes escalas ecológicas, com um número maior de populações e variações genéticas se fazem necessários para uma melhor compreensão do papel da variabilidade intraespecífica na resposta de espécies a gradientes ambientais e a distúrbios. Isso também permitiria avaliar se fatores ambientais exercem pressões seletivas mais fortes na variabilidade de atributos funcionais (plasticidade fenotípica) e/ou se polimorfismos genéticos estão promovendo maior variação entre populações (diferenciação ecotípica) ao longo de gradientes ambientais.