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TOPOGRAPHY AND SEASONALITY PROMOTES TAXONOMIC BETA DIVERSITY OF SEEDLINGS IN A TROPICAL WETLAND

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Abstract: Spatial and temporal beta diversity of seedlings in tropical wetland remain poorly understood. We assessed the ecological pattern of taxonomic beta diversity of seedling assemblages along a topographic gradient, seasonally flooded disturbance, and sampling years in a tropical wetland. We tested that seasonally flooded disturbance on seedling assemblage promotes a high taxonomic beta diversity due to a high taxonomic turnover along the topographical gradient. Here we examined a large database from 200 plots (each having 0.5 × 0.5 m), across eight seasonally flooded grasslands in the Pantanal of central-west Brazil. We selected data on ponds for four years at two characteristic hydrological phases per year: post-flood (July and August), and post-dry season (October and November). We classified the topographical gradient into three levels 1) low—longer duration of flood; 2) mid—intermediate level; and 3) high—short duration of flood (dry soil). For both post-flood and post-dry seasons, we counted the number of seedlings within five plots at each topographic level. Additionally, taxonomic beta diversity was examined via novel abundance-based metrics (including both turnover and nestedness patterns). Overall, taxonomic beta diversity was consistently higher in high topographic level and post-dry season plots. We observed differences in beta diversity components between topographical levels, seasons and years. Topographical gradient and seasonally flooded promotes more variation in taxonomic turnover and beta diversity; due to these environmental filters we presume that the resulting beta diversity can be decisive in the species diversity in this tropical wetland.

Keywords: flood disturbance; nestedness-resultant component; taxonomic turnover; topographical gradient.

INTRODUCTION

Wetlands are disturbance-dependent ecosystems where flood dynamics is considered the main driver of temporal and spatial variation in plant community composition (Middleton 1999, Targhetta *et al.* 2015, Bao *et al.* 2018). Disturbances provide conditions for plant species regeneration and, compared with static stable systems, the predictable seasonally flood can promotes high species turnover across temporal and spatial scales (Middleton 1999, Tonkin *et al.* 2017, Bao *et al.* 2018). Flood dynamics in seasonal wetlands, mainly post-flood and post-dry duration usually determine which plant species will germinate, establish and develop in a given habitat, such as topographical conditions (Van der Valk 1981, Bao *et al.* 2017, 2018). This seasonal disturbance by flood dynamics is an environmental filter of these plant communities because the soil water saturation creates anaerobic conditions (Vartapetian & Jackson 1997), or dry season conditions can promote differences in species-specific requirements for germination and growth (Casanova & Brock 2000, Bao *et al.* 2014). These patterns in tropical wetlands have been addressed analyzing changes in species composition of seedlings after natural disturbance by seasonal flood (*e.g.*, Bao *et al.* 2018). However, the spatial and temporal changes in seedling species composition (β-diversity) in seasonally flood-disturbed tropical wetland remain poorly understood.

The beta diversity (β-diversity) approach has a long history in ecology and can be broadly understood as a measure of the spatial and temporal variation in species composition (Tuomisto 2010, Anderson *et al.* 2011). The simplest meaning of taxonomic β-diversity and one of the most used is the percentage of dissimilarity in species composition between two communities (Koleff *et al.* 2003). Recently, a series of papers brought key conceptual advances for the disentanglement of the patterns underlying pairwise dissimilarity in species composition (Baselga 2010, 2012, Carvalho *et al.* 2012). Thus, previous studies have shown how different types of disturbances can cause high environmental heterogeneity and promotes high temporal and spatial β-diversity (*e.g.*, Tonkin *et al.* 2017, Villa *et al.* 2018). For this reason, it is presumed that disturbance by flood dynamics can be inducing changes in β-diversity on a spatial (topographic gradient), and temporal scale (between seasons and years) in seedling communities.

On the other hand, taxonomic β-diversity can indeed be decomposed into taxonomic turnover (*i.e.*, species replacement between communities) and nestedness-resultant components, *i.e.*, those that reflect the difference in the number of species among communities (Baselga 2010, 2012). Turnover occurs when existing species are replaced by different ones at new sites, whereas nestedness patterns result when species loss or gain causes species-poor sites to resemble a strict subset of species-rich sites (Baselga *et al.* 2017). For instance, a high level of β-diversity can characterize two contrasting situations; i) first; it can result from a low proportion of shared species between two communities with a similar number of species, leading to a high contribution of the turnover component and a low value for the nestedness-resultant component. In contrast, ii) it can also result from a species richness difference between two communities, when the poorest is a subset of the richest, leading to a low value for the turnover but a high value for the nestedness-resultant component (Villéger *et al.* 2013, Baselga *et al.* 2017).

In this study, we assessed the ecological pattern of taxonomic β-diversity of seedling assemblages along a topographic gradient and seasonally flooded disturbance in a tropical wetland. Here we examined a large database from 200 plots (each having 0.5 × 0.5 m), across eight seasonally flooded grasslands in the Pantanal of central-west Brazil. We tested the hypothesis that seasonally flooded disturbance on seedling assemblage promotes a high taxonomic β-diversity due to a high taxonomic turnover along the topographical gradient. Our proposed hypothesis led to the following key prediction: the disturbance that follows seasonal flood can cause high environmental heterogeneity (which is an indirect indicator of niche partitioning by predictable annual floods), which in turn may promotes the local β-diversity in this wetland.

MATERIAL AND METHODS

Study area

The present study was carried out in the subregion of Abobral, Pantanal wetland, Mato Grosso do Sul, Central-West Brazil (19º18’31” S and 57º03’15” W).

The climate of the region is tropical sub-humid, with a mean annual temperature of 26ºC and an average annual rainfall of 1100 mm (Silva & Abdon 1998). The Brazilian Pantanal is regulated by the flood pulse, the seasonality in this region is marked by well-defined periods of rain/flood and drought, characterized by annual flood (October-March) and dry period (between April and August), with pluvial and fluvial fluctuations, with maximum (7.34 m) and minimum level (2.37 m) of the Miranda river (data collected at Base de Estudos do Pantanal - BEP, between 2005 and 2015, Figure 1b). The ground level can vary between 1 to 60 cm (Silva & Abdon 1998), such variation of topography added to the different sites of hydrological regime form permanent and periodically flooded zones (Pott & Silva 2015).

Experimental design and vegetation sampling

Samplings were made in eight seasonal ponds, distant 1 km between them. Samples were collected for three years during two characteristic hydrophases of the Pantanal wetland: in the post-flood and post-dry. Points were established in the first year of sampling (2011) and, at the end of the flood season, topographic levels were classified into three categories: (*i*) low – longer duration of flood (waterlogged soil); (*ii*) mid – intermediate level (wet soil) and (*iii*) high – short duration of flood (dry soil), keeping a distance between them ca. 10m horizontally and ca. 30 cm vertically (Figure 1c). The transects were established using as reference the watermark of the flood level on fence poles and taller plants (cf. Bao *et al.* 2018a).

In the field, the number of seedlings was quantified within five 0.5 × 0.5 m plots at each topographic level, in two seasons, in eight ponds, in four years, totalizing 960 plots. During each sampling year (2011, 2013, 2014, 2015), for both post-flood and post-dry seasons five plots for each topographic level (low, mid, high), the number of seedlings was quantified, totalizing 15 plots per sampling ponds, and 240 plots per year (Bao *et al.* 2018b). Only seedlings that displayed cotyledons up to the second pair of leaves were considered for identification. All individuals were identified using specialized literature, through consultation with the CGCM Herbarium of Universidade Federal de Mato Grosso do Sul, field guides were used, and assistance from taxonomists. Seeds of some species were collected and germinated in the greenhouse so that seedling characteristics of known species could be compared with seedlings in the field (Bao *et al.* 2018). Altogether, 8884 individual belonging to 41 identified seedling species were recorded. The Angiosperm Phylogeny Group IV (APG IV 2016) was used for taxonomic classification.

Data and statistical analyses

All analyses were carried out in R Environment (R Core Team 2018). We calculated the dissimilarity in species composition between three topographic levels, two seasons, and four years using the taxonomic β-diversity decomposition approach proposed by Baselga (2010, 2012). For the β-diversity decomposition three pairwise β-diversity metrics were calculated (*e.g.*, Villa *et al.* 2018). First, βsor accounts for the total compositional variation between seedling assemblages (including both turnover and nestedness patterns) using Sørensen dissimilarity index (β_{sor}). Second, βsim captures only compositional changes due to species turnover, using Simpson dissimilarity index (β_{sim}). Third, βsne represents nestedness-resultant dissimilarity, which measures how dissimilar the sites are due to a nested pattern (Baselga *et al.* 2010). βsne was calculated as the difference between βsor and βsim (*e.g.*, Baselga, 2010, 2012, Villa *et al.* 2018).

For β-diversity components (βsor, βsim, βsne), we tested normal distribution with the Shapiro-Wilk test and by evaluating the Q-Q plot (Crawley 2013). To compare pairwise total beta diversity, and turnover and nestedness components between topographic levels, seasons and sampling periods, we used a permutational multivariate analysis of variance (PerMANOVA) on Bray–Curtis dissimilarity matrices, followed by a post hoc test pairwise PerMANOVA (Hervé & Hervé 2018). All these basic statistical analyses were performed using the 'vegan' package in software R (Oksanen *et al.* 2017).

To explain the main effects of topographic level, seasons, and years on β-diversity components we constructed linear mixed effect models (LMM) with Gaussian error distribution. Predictor variables were grouped into three categories, i.e., topography included three levels, seasons have two levels (*i.e.*, post-flood and post-dry), and sampling years. Two fixed effect variables (topographic levels and flood levels) and one random variable (one temporal variable - years) were used in the models. We also tested the interaction between topography and season. All models were calculated using the packages 'lme4' and 'nlme' (Bates *et al.* 2014) in the platform R (R-Core-Team 2018).

RESULTS

Beta diversity components were significantly different between topographic levels, seasons and sampling years (Figure 1). The taxonomic turnover

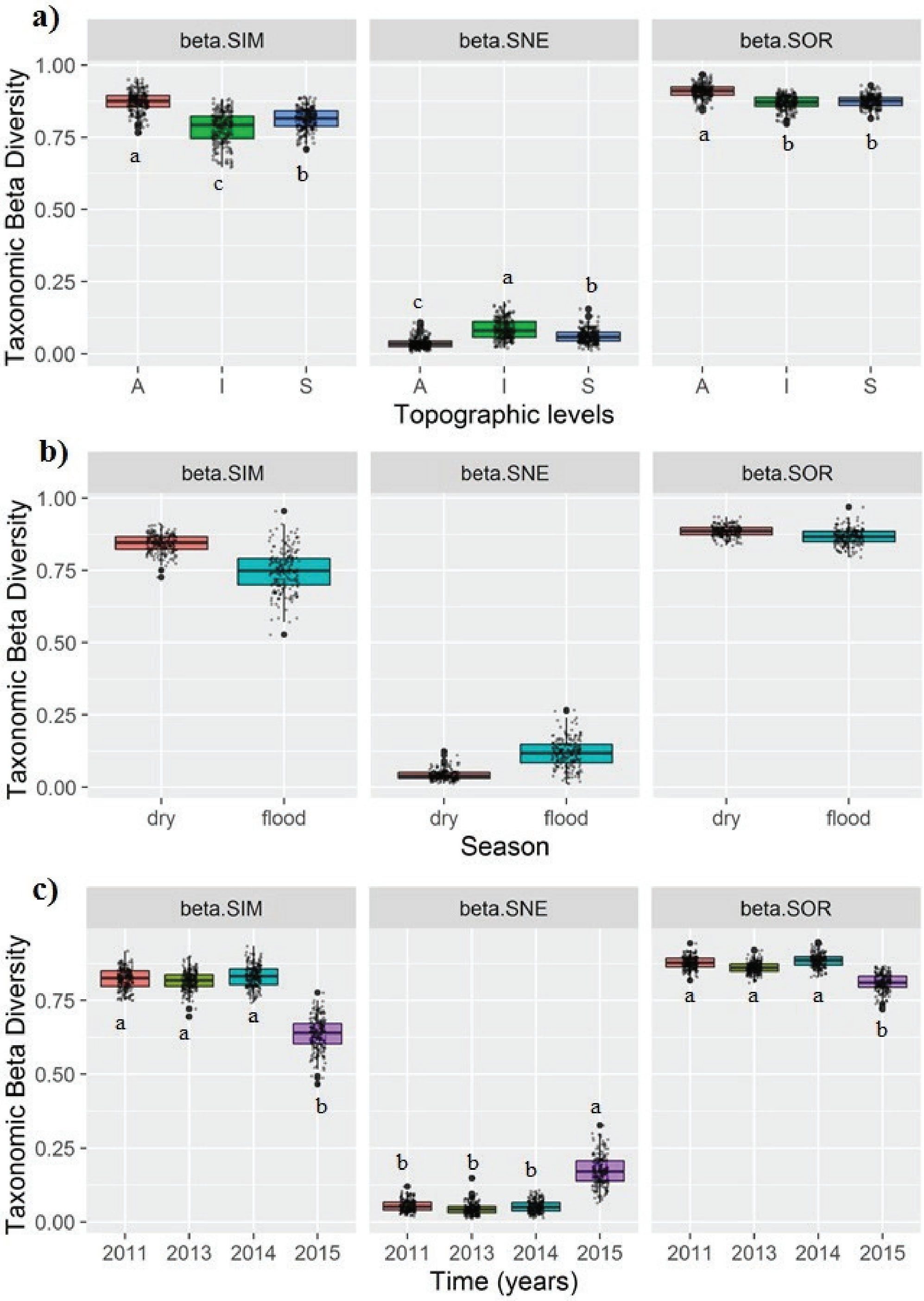

Figure 1. Differences in the taxonomic beta diversity components of seedling species assemblages at different topographic levels (waterlogged soil - A, wet soil - I, dry soil - S) (a), dry and flood seasons (b), and sampling periods (c) in the subregion of Abobral, Pantanal wetland, Mato Grosso do Sul, Central-West Brazil. Taxonomic beta-diversity (beta.SOR) and its two components, turnover (beta.SIM) and nestedness-resultant (beta.SNE) are indicated. Different letters indicate significant differences at posteriori analyses (P < 0.05).

(βsim) showed differences with the highest values at high topographic level, dry season, and the first three sampling years (Figure 1). Taxonomic β-diversity ranged from 0.90 at the high topographic level to 0.75 at intermediate and low levels. The taxonomic turnover and β-diversity were higher than the nestedness-resultant component (βsne). The nestedness component was greater during the flood season and last sampling year (Figure 1). This decline in taxonomic β-diversity (Bsor) and turnover (βsim) in the last year was driven by nestedness, which was higher over time and comprised only a minor contribution to the total beta diversity.

The linear mixed-effects models showed that taxonomic β-diversity components were explained by topographic levels, seasons and sampling years through eight potential models (Table 1). The linear mixed-effects models revealed that shifts in β-diversity components are significantly influenced by topography and seasons. However, the topography is the main predictor that has significant effects on β-diversity components (Table 1). Differences in the components of diversity were less significant when we considered season and topography interactions.

DISCUSSION

Our results show ecological patterns of taxonomic β-diversity along a topographic gradient and seasonally flood disturbance in a tropical wetland in the Pantanal of central-west Brazil. Furthermore, analyzing taxonomic β-diversity and its respective components offers a unique opportunity to test the ecological processes in this dynamic seasonally flooded ecosystem. Likewise, we demonstrated how taxonomic β-diversity showed marked changes through the topographic gradient and seasonally flood disturbance, indicating that probably the species turnover can be the main driver for maintenance of species diversity at a local scale. Our results can represent an important contribution to the establishment of criteria for wetland management and conservation in landscapes under increasing human modification of the Pantanal of central-west Brazil.

Our results indicate that seasonal flooding has a transient effect on the spatial variation of β-diversity, indicating that climate seasonality and predictability are clearly related to diversity patterns. The high β-diversity of seedling assemblages along the topographical gradient present in this study is likely reflecting higher habitat heterogeneity

Table 1. Candidate mixed effect models predicting the effect of topographic levels (topography), seasons (season), and sampling years (time) on different components of beta diversitiy of seedling species assemblages, with Gaussian error distribution (linear mixed effects model - lmer), in the subregion of Abobral, Pantanal wetland, Mato Grosso do Sul, Central-West Brazil. The response variables are taxonomic beta-diversity (Bsor) and its two components, turnover (Bsim) and nestedness-resultant (Bsne). Sampling years (time) it was considered a random factor in all models. Interaction between topography and season it was tested. The *p*-value of each predictor are given as: (.) $p < 0.1$; * $p < 0.05$; ** $p > 0.01$; *** $p < 0.001$.

Response variable	Fixed effects	Estimate	SE	t	
Bsor	~Topography	-0.90	0.08	-6.50	***
	~Season	0.40	0.22	0.61	**
	~ Topograph*Season	-0.30	0.16	-2.83	
Bsim	~Topography	-0.81	0.27	3.78	***
	~Season	0.94	0.20	1.98	**
	~ Topograph*Season	-0.28	0.12	-1.40	*
Bsne	~Topography	-0.26	0.19	-6.97	***
	~Season	0.56	0.18	1.23	**
	~ Topograph*Season	-0.70	0.25	-2.10	*

induced by seasonally flood disturbance, where the species will establish themselves according to their tolerance; such as soil water saturation (Pott & Silva 2015). The habitat heterogeneity can allow to increase the number of coexisting species and therefore shapes the community assembly (Brown *et al.* 2013, Rodrigues *et al.* 2019a,b). Alternatively, disturbance can cause divergence in community composition (high β-diversity) by increasing habitat filtering across environmental gradients (Myers *et al.* 2015, Bao *et al.* 2017, Villa *et al.* 2018); for instance, the seasonal flooding in the Pantanal wetland regulates the seedlings richness and abundance of the seed bank (Bao *et al.* 2014, 2017). Possibly biological cycle is an important mechanism that allows maintaining this pattern; for example, the annual species tend to maintain persistent seed bank in the soil (Girard *et al.* 2010). The expected condition in environments subject to seasonal floodings, such as the Pantanal, the annual Bet-Hedging strategy maintains a seed bank more or less continuous in time (Schupp 1995, Villa *et al.* 2019). In wetlands with different plant communities, the disturbance represents the main driver of β-diversity (*e.g.*, Arieira *et al.* 2016, Bao *et al.* 2017, Tonkin *et al.* 2017). For instance, flooding has been considered the main filtering of plant species distribution in tropical floodplains (Wittmann & Junk 2003), and flood depth explained differences in species composition of colonizing young trees (Arieira *et al.* 2016).

In this context, we presumed that beyond topographical gradient, both post-flood and post-dry seasons, and their temporal (annual and interannual) variability are the main drivers of β-diversity at a local scale. The differences in seedlings germination and mainly establishment along topographical gradient associated with flooding are restricted to narrower areas where conditions are favorable (regeneration zone) (Middleton 1999). Thus, temporal and spatial heterogeneity of β-diversity under predictable dynamics of flooding is also generally associated with post-flood and post-dry duration (e.g., Girard *et al.* 2010, Bao *et al.* 2018), and organic debris deposition, which decreased incident light levels (Bao *et al.* 2018). In the Pantanal wetland, organic debris and anaerobic conditions may limit seedling abundance and species richness at low lying topographies (Bao *et al.* 2018). However, within the three-year period examined, some researchers found stability in metacommunity assembly, although the importance of habitat and spatial variables did fluctuate for different taxonomic groups (Tonkin *et al.* 2017).

This study showed differences in β-diversity components (high turnover and low nestedness) between topographic levels, seasons, and sampling years. Wetlands present many perennial species that show strong regeneration traits due to evolutionary adaptation (Capon & Brock 2006). However, although we did not evaluate density-dependent processes at the species level, and alternatively functional diversity, we presume that a short life cycle is an important driver for intra-annual temporal species turnover and high β-diversity. Wetland annual plants are mainly dependent on within-year variability under seasonal flooding, and communities are typically divided into post-flood and post-dry seedling assemblages, which persist spatially but have little temporal overlap because their active growth and reproductive stages occur during different seasons (Bao *et al.* 2017, 2018). This clear temporal segregation of post-flood and post-dry is common in different types of species assemblages, through the partitioning of limiting resource, i.e., water for life cycle processes (*e.g.*, Villa *et al.* 2019), maintains and promotes high temporal β-diversity. However, the relative importance of local- and regional-scale of multiple drivers, and the relationship between environmental heterogeneity and β-diversity is highly scale-dependent (Heino *et al.* 2015, Tonkin *et al.* 2017).

We concluded that topographic levels, seasons and sampling years affect different components of taxonomic β-diversity of seedlings in the studied wetland. Finally, for future studies, we suggest to evaluate if the variation in taxonomic β-diversity of seedlings is not solely determined by species-specific responses to habitat conditions (*i.e.*, flooding heterogeneity), but also by random selection of equivalent species with limited dispersal (dispersal assembly), creating a random distribution pattern with regard to environmental gradients (Hubbell 2001). Furthermore, with this approach, we can know about the relative contribution of different processes that can emerge through habitat filtering, dispersal limitation or a combination of assembly mechanisms.

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