An inter-dependence of flood and drought: disentangling amphibian beta diversity in seasonal floodplains

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Abstract. Species composition in floodplains is often affected by different structuring factors. Although floods play a key ecological role, habitat selection in the dry periods may blur patterns of biodiversity distribution. Here, we employed a partitioning framework to investigate the contribution of turnover and nestedness to β-diversity patterns in non-arboreal amphibians from southern Pantanal ecoregion. We investigated whether components of β-diversity change by spatial and environmental factors. We sampled grasslands and dense arboreal savannas distributed in 12 sampling sites across rainy and dry seasons, and analysed species dissimilarities using quantitative data. In the savannas, both turnover and nestedness contributed similarly to β diversity. However, we found that β diversity is driven essentially by turnover, in the grasslands. In the rainy season, balanced variation in abundance was more related to altitude and factors that induce spatial patterns, whereas dissimilarities were not related to any explanatory variable during dry season. In the Pantanal ecoregion, amphibian assemblages are influenced by a variety of seasonal constraints on terrestrial movements and biotic interactions. Our findings highlighted the role of guild-specific patterns and indicated that mass effects are important mechanisms creating amphibian community structure in the Pantanal.

Introduction

Changes in species composition, or β diversity, in relation to spatial or temporal gradients have been addressed in different ways and for various purposes, such as effects of habitat homogenisation, long-term dynamics and geographical patterns (Tonial *et al.* 2012; Dornelas *et al.* 2014; da Cunha Bitar *et al.* 2015). Currently, there is an increasing interest in the components governing β diversity, namely, species replacement and nestedness (Baselga *et al.* 2012; da Silva *et al.* 2014). Although partitioning of β diversity may help us infer different relationships between the various processes that structure communities, there are open questions as to the best ways of computing and interpreting those components (for a review, see Legendre 2014).

Nestedness and species replacement (also called turnover) are different patterns of β diversity, and, therefore, can be the result of different processes. Species-replacement patterns (i.e. simultaneous gain and loss of species) are usually attributed to environmental filtering, limited dispersal or historical events

(Leprieur *et al.* 2011; da Silva *et al.* 2014). Differences in species composition because of nestedness (i.e. low-diversity sites are subsets of those of high diversity) may be generated by selective colonisation, selective extinction, differential habitat quality or habitat nesting (Wethered and Lawes 2005; Leprieur *et al.* 2011; Moreira and Maltchik 2015). Macroecological studies considering amphibians and other aquatic taxa have highlighted that long-term climate stability and topographic complexity would lead to high turnover-mediated dissimilarity (Dobrovolski *et al.* 2012; Baselga *et al.* 2012; da Silva *et al.* 2014). Turnover patterns should be the rule in climatically stable areas with high topographic variation, because of speciation events associated to geographic barriers. In contrast, nestedness should be higher in unstable areas, because of constraints of niche, such as drought periods or extreme temperature.

The Pantanal ecoregion is a large lowland alluvial plain in the centre of South America (Junk *et al.* 2006), with pluriannual dry and wet periods that lead to extreme and recurrent flood and drought events. Climatic conditions in the Pantanal are known to

have been unstable during the Quaternary oscillations, and the entire region may have been more dry than today (Junk *et al.* 2006). Despite the lack of detailed information on local climatic episodes, fauna and flora have faced an unstable environment in the Pantanal, both in terms of historical and current conditions. Hence, amphibian species should be able to cope with intermittent periods of large flooding and severe drought. This potentially prevents some species from colonising lowland areas, and results in reduced species richness in the floodplain, when compared with localities situated in the neighbouring plateaus (Strüssmann *et al.* 2011).

Many factors in both local and landscape scales influence amphibian distribution, including hydroperiod, vegetation, temperature and rainfall (Ficetola *et al.* 2009; Ocock *et al.* 2014). In the dry season, amphibian movement and habitat use are expected to be different, because of distinct species attributes, such as size, skin water-retention rates and water-conserving behaviours (Ocock *et al.* 2014; Watling and Braga 2015). In addition, there is evidence that flood pulses enhance landscape permeability, i.e. the so called homogenisation hypothesis (Thomaz *et al.* 2007). Thus, species sorting during dry periods would be disassembled during the flood phase, because of redistribution of organisms, which may decrease β diversity in large river–floodplain systems (Bozelli *et al.* 2015; Delatorre *et al.* 2015). Studies have indicated that post-metamorphic dispersal contributes more than adult dispersal to regional amphibian persistence and patterns of species distribution (Semlitsch 2008; Griffiths *et al.* 2010). Flooding could help departing juveniles if they can swim instead of hop, which might be more efficient than overland travel. Furthermore, high water levels would increase pond-edge area that would help amphibians avoid predators. But, it also could leave less refuge once animals are on land. However, we know little about the relative benefits and drawbacks of metamorphosing into a flooded landscape (Pittman *et al.* 2014).

Positive association between environmental heterogeneity and species richness is a recurrent pattern in amphibian assemblages (Moreira *et al.* 2010; de Almeida *et al.* 2015). Although this pattern is frequently attributed to niche-based processes (intraspecific competition, resource partitioning and predator–prey relationships), amphibians are a group with remarkable differences in life-history strategies (Wells 2007). Competitive effects are commonly overlooked, because few studies consider the presences of guilds (Both *et al.* 2011; Melo *et al.* 2014). Additionally, approaches to understanding β diversity have often utilised binary dissimilarity coefficients, which may not capture the more subtle signals of rules governing local community assemblage (Ulrich and Gotelli 2010). Quantitative indices are more appropriate within small spatial scales, because species composition should differ mostly in terms of species abundance (Legendre 2014). Abundance-based dissimilarities can be derived from balanced variation in abundance (turnover) or abundance gradients (nestedness; Legendre 2014).

In the present study, we examined patterns of β diversity in non-arboreal amphibian assemblages from the southern part of the Pantanal ecoregion. First, we partitioned β diversity into two distinct components, namely, turnover and nestedness. Then, we explored whether components of β-diversity change by spatial and environmental factors. We predicted that the relative portion of β diversity owing to nestedness would be higher than that owing to turnover because of the instability associated with the flood pulse. Furthermore, on the basis of physiological constraints associated with water balance, we expected that variations in altitude and landscape diversity would be major factors influencing similarities in amphibian species composition. Our predictions are derived from the scenario where all species are favoured by moist soil, but different species are differently desiccation tolerant. By changing microhabitat moisture, the altitude and landscape diversity may result in amphibian species losses and generate community dissimilarity by nestedness.

Materials and methods

Study area and sampling procedures

The study area was located in the Nhumirim Ranch experimental station of the Empresa Brasileira de Pesquisa Agropecuária–Embrapa, Corumbá, Brazil (18°58′59.88″S, 56°39′00″W), which has an area of 43 km^2 and includes a variety of environments, including brackish and freshwater ponds, extensive flooded grasslands, savannas and dry forests. Nhumirim Ranch is located in the Negro–Taquari interfluve, in a region known as Nhecolândia. Most of the Pantanal regions are flooded by water overflow from rivers and by rainfall runoff; however, a peculiarity of the Nhecolândia is that floods are a result mainly of rainfall runoff and the riverine flood pulse has limited influence. Annual rainfall varies from 950 to 1250 mm, and it is concentrated (~70%) from December to March.

At the experimental station, we sampled areas within grasslands and dense arboreal savannas (Fig. 1). The minimum distance between each of the 12 sampling sites was 600 m to minimise spatial autocorrelation. We sampled each site four times in the dry season (May, June, August and October 2005) and four times in the rainy season (February and March 2005, January and March 2006). Grasslands comprise a mosaic of native and exotic grasses, such as *Axonopus purpusii*, *Elyonurus muticus* and *Urochloa humidicola*. Dense arboreal savannas comprise a mix of dry forests and closed woodlands where there is little grass cover. These areas are characterised by species such as the shrubs *Byrsonima cydoniifolia* and *Annona dioica*, and the trees *Alibertia sessilis*, *Scheelea phalerata* and *Zanthoxylum rigidum* (Salis *et al.* 2006). During the rainy season, the area is almost completely covered by surface water, except for patches with a higher elevation. These remnants of paleo-levees, which rise 1 m above the mean flood level, are normally covered with woody plant species.

To sample amphibian richness and abundance, we installed a set of pitfall traps with drift fences at each site. We selected only trap locations surrounded by similar vegetation (up to 100 m). Each pitfall trap set was composed of four plastic buckets (100 L), 10 m apart from each other and arranged in 'Y'. During each sampling period, all buckets remained open for nine consecutive days. Daily, all collected amphibians were identified, marked by toe clipping and released. Voucher specimens were anesthetised and killed with an overdose of thiopental, and fixed in 10% formalin. They are housed in the zoological collections of the Universidade Federal de Mato Grosso do Sul (ZUFMS, Campo Grande, Brazil) and Universidade Federal de Mato Grosso (UFMT, Cuiabá, Brazil).
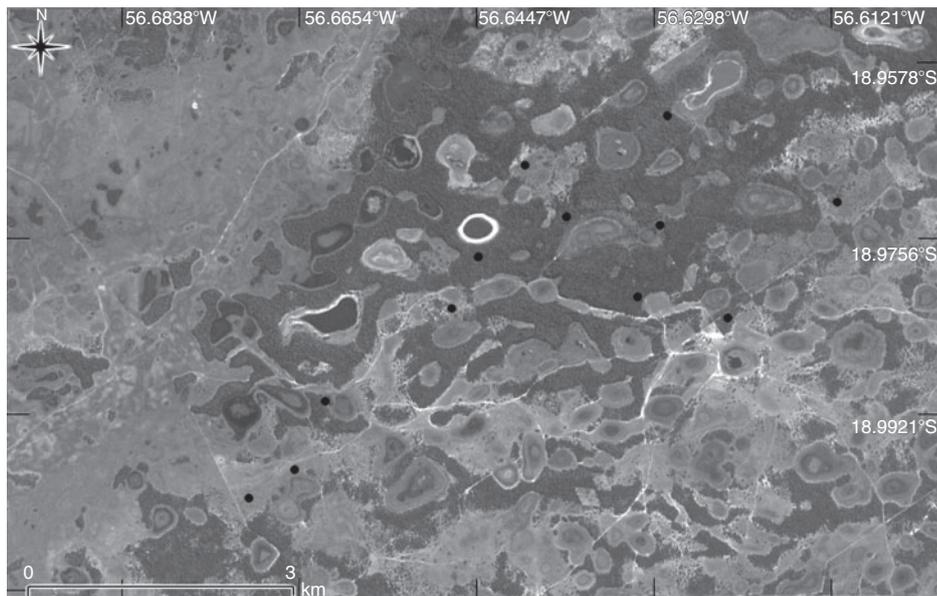
Fig. 1. Map of sampled areas (full circles) at Nhumirim Ranch experimental station, Pantanal, Brazil. Light grey tones correspond to grasslands and dark grey represents dense arboreal savanna patches.

Environmental and spatial variables

Despite the homogeneous topography of the low-level terrains in the Nhumirim Ranch (93–113 m above sea level), micro-topography is an important factor for local flooding patterns in the Pantanal areas (Girard 2011). Flood duration decreases with an increasing altitude, but there are spatio-temporal variations. In areas distant from the rivers, such as the Nhumirim Ranch, local rainfall can cause the flood, even before the overflow from the nearest river (Penha *et al.* 1999). Thus, we measured the altitude of each sampling site with a GPS, and used them as a proxy of flood duration. We also defined circular areas (250-m radius) centred on each sampling site, and measured land-cover data (percentage cover) grouped into eight land classes (freshwater lakes, channels, salty lakes, sand beaches, grasslands, dense arboreal savannas, scrub–woodlands, mono-specific stands) using ArcGis, ver. 10 (ArcGIS software, see www.esri.com/products/index.htm). We based GIS analysis on Google Earth imagery, using a land-cover classification developed by Embrapa (Rodela *et al.* 2008). Landscape diversity, based on Shannon's diversity index, was then calculated using the eight detected land classes. To represent unmeasured environmental factors that are spatially structured, we constructed spatial predictors through spatial eigenfunction analysis using Moran's eigenvector maps (MEM). Geographic coordinates of sampling sites were transformed using principal coordinates of neighbour matrices (Borcard and Legendre 2002), generating a set of six MEM. From this, three MEM modelling positive spatial autocorrelation were identified by Moran's *I* statistic for the threshold distance of 0–1.7 km.

Statistical analysis

Beta diversity and its partition in species turnover and nestedness components were calculated using Sorensen-based indices, following Baselga (2013). We computed pairwise matrices for all possible comparisons of vegetation types. Next, we obtained the ratio between nestedness and total β diversity, henceforth referred to as β ratio. Values greater than 0.5 were considered indicative of β diversity being determined mainly by nestedness (Dobrovolski *et al.* 2012). We analysed separately pairs formed by the same vegetation type and pairs of mixed vegetation. Quantitative matrices were constructed considering the composition of the amphibian assemblage, for each sampling site, in the following two ways: (1) data were pooled within each dry or rainy season; or (2) data were pooled within all sampling periods. To assess the significance of differences, we estimated the distribution of β ratio, taking 100 random samples of four sites in each group of matrices. Next, we assessed whether β ratio was larger or smaller than 0.5, and *P*-values corresponded to the probability of obtaining the opposite result by chance. Beta-diversity indices were computed using the 'beta.div.comp' function in adespatial package (S. Dray, G. Blanchet, D. Borcard, G. Guenard, T. Jombart, G. Larocque, P. Legendre, N. Madi and H. H. Wagner, see http://cran.r-project.org/package=adespatial, accessed 4 September 2016) in R, ver. 3.2.0 (R Foundation for Statistical Computing, Vienna, Austria, see www.R-project.org).

Altitude, landscape diversity and spatial variables were considered to explain the variation contained in the dissimilarity matrices. A distance-based redundancy analysis (dbRDA) was used to investigate the relation between the components of β diversity and explanatory variables. The model was submitted to a backward selection procedure. Because dissimilarity matrices were non-Euclidean, we took the square root of the dissimilarities, as recommended by Legendre (2014). In view of some criticisms of the nestedness component of Baselga's framework (Almeida-Neto *et al.* 2012), we also quantified nestedness on the basis of WNODF (weighted nestedness based on overlap and decreasing fill) for matrices with β ratio > 0.5. This is a straightforward extension of NODF for quantitative data that
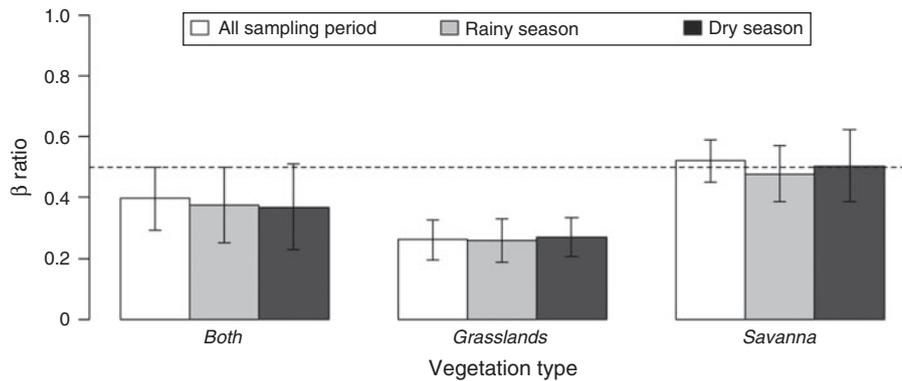
Fig. 2. Proportion of total β diversity explained by nestedness (β ratio) for non-arboreal amphibians of the Nhumirim Ranch, Pantanal, Brazil. The dashed line indicates reference value for the most important component of β diversity: nestedness (>0.5) or turnover (<0.5).

allows assessment of nestedness owing to species composition only or owing to species incidences only (Almeida-Neto and Ulrich 2011). Index of Baselga's framework does not depend on the order of sites, hindering the evaluation of environmental gradients on the nested component. Using WNODF allowed us to overcome this and quantify differences in species composition owing to nestedness more accurately (Almeida-Neto *et al.* 2012). Because the species could be subject to different environmental pressures, we set quantitative matrices in the following two ways: (1) sorted by increasing altitude, which is a proxy for flood duration; and (2) according to decreasing landscape diversity. To evaluate the significance of nestedness, we used a null model that preserves fill and column and row frequencies in which individuals are shuffled separately for each column, with 5000 simulations to validate model significance. All analyses were performed in vegan package (J. Oksanen, F. G. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlinn, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, E. Szoecs and H. Wagner, see http://cran.r-project.org/package= vegan) in R (R Foundation for Statistical Computing).

Results

In total, 9672 individuals belonging to 22 amphibian species were captured in the study area (see Table S1, available as Supplementary material for this paper). Five species of primarily arboreal frogs (*Dendropsophus nanus*, *Pithecopus azureus*, *Scinax acuminatus*, *S. nasicus* and *Trachycephalus typhonius*, $n = 43$) were excluded from further analyses. We chose to exclude arboreal frogs, because our sampling method was not adequate for detecting arboreal species. Two species were found only in the grassland areas (*Leptodactylus labyrinthicus* and *Pseudopaludicola motorzinho*), and one species was found only in the savanna areas (*Adenomera dyptix*). Total abundance was similar between grasslands and savannas, and species of leptodactylids and microhylids were the most abundant. Samplings registered 16 amphibian species in the rainy season and 15 species in the dry season, and approximately two-thirds of individuals ($n = 6791$) were registered in the rainy season.

The partitioning of β diversity showed that both turnover and nestedness contributed similarly (β ratio = 0.40 ± 0.11) for

Table 1. Measure of nestedness for dense arboreal savanna areas of Nhumirim Ranch

Matrices were ordered by increasing altitude and decreasing vegetation diversity. WNODF, total matrix nestedness; WNODF(q), nestedness of null model where individuals are shuffled separately for each column, but fill and column and row frequencies are preserved; P(q), significance of WNODF differences based on the null model

Matrix	Order	WNODF	WNODF(q)	P(q)
All samplings	Altitude	42.182	39.267	0.007
	Vegetation	42.561	39.667	0.009
Dry season	Altitude	53.832	50.058	0.08
	Vegetation	52.471	48.933	0.09

differences in non-arboreal amphibian assemblages (Fig. 2). However, when we separately assessed the composition differences by vegetation type, the proportion of turnover component was higher for grassland areas (Fig. 2). Values of β ratio were significantly ($P < 0.01$) lower than 0.5 for both seasons across grassland matrices. In contrast, nestedness contributed, for more than 50%, to β diversity in two matrices of savanna (all sampling periods and dry season). However, β ratio was not significantly higher than 0.5 in the empirical comparison of the distributions of the dissimilarity indices across samples ($P = 0.60$ for all sampling periods and $P = 0.56$ for the dry season). Besides β ratio, we also assessed the separated components of β diversity (see Fig. S1, available as Supplementary material for this paper). Total β diversity was similar between vegetation types, and absolute values of turnover and nestedness showed only subtle differences.

In the rainy season, the spatial variables and altitude explained 26% of the variation in the turnover component ($F = 1.98$, $P = 0.046$). The nestedness component was not related to any explanatory variable. In the dry season, both components were not related to environmental or spatial variables. In savanna habitats, WNODF showed that amphibian assemblages were nested for all sampling periods (Table 1). The matrix ordered by landscape diversity showed a slightly higher degree of nestedness than did the matrix ordered by altitude.

Discussion

Our results indicated that non-arboreal amphibian species dissimilarities at Nhumirim Ranch were a result of both balanced variation in abundance between sites and abundance gradients towards lower landscape diversity. However, the pattern was dependent on the vegetation type. In grassland areas, β diversity was almost completely caused by turnover, whereas in dense arboreal savanna, both turnover and nestedness contributed similarly. Despite the importance of the turnover component, these savanna areas showed nested patterns associated with altitude and landscape diversity. In the rainy season, species turnover showed association with altitude and factors that induce spatial patterns. Although it has been suggested that amphibian β diversity is synergistically driven by environmental filtering and limited dispersal (Watling *et al.* 2009; Almeida-Neto *et al.* 2012), an alternative generalisation suggests that competitive interactions are important forces structuring amphibian communities (Barnett and Richardson 2002; Melo *et al.* 2014). Historically, species co-occurrence has been investigated through analysis of presence or absence matrices (Gotelli and McCabe 2002). However, recent evidence suggests that patterns of species distribution might be more clearly expressed in abundance matrices (Ulrich and Gotelli 2010; Legendre 2014). In this sense, our work has provided valuable insights into the mechanisms underlying amphibian species assembly in the Pantanal ecoregion.

Contrary to the hypothesis proposed here, balanced variation in abundance was an important component in many areas of the Nhumirim Ranch. Many amphibians inhabiting the Pantanal are widely distributed and generalist species (Prado *et al.* 2005). Therefore, we would expect low levels of habitat specialisation for Pantanal-dwelling amphibians, and, so, nestedness related to habitat heterogeneity and hydroperiod constraints would be the dominant pattern, as in other floodplain areas (Ficetola and De Bernardi 2004; Tockner *et al.* 2006). Recent studies have highlighted the stochastic effect of habitat homogenisation imposed by floods on amphibian communities (Delatorre *et al.* 2015; Martins *et al.* 2015). In these studies, authors found low turnover rates and no spatial signal associated to species distribution and phylogenetic structure of the communities. However, it is possible that the conflicting between such results and those presented here reflects a deeper, guild-dependent, response to environmental filters (Landeiro *et al.* 2014; Moreira and Maltchik 2015). In fact, terrestrial movements of non-arboreal amphibians are mainly restricted to horizontal displacements, whereas adhesive discs enable arboreal tree frogs to climb different types of substrates. Although we lacked specific information on displacement preferences, a plausible hypothesis is that turnover in amphibian assemblages is driven both by species functional traits related to terrestrial movements and by stochastic processes associated with floods.

Spatial patterns are frequently related to dispersal limitations of organisms (Watling *et al.* 2009; Landeiro *et al.* 2014). The importance of spatial component for species turnover in the rainy season fits well with the purported flood-pulse effects on the Pantanal biota (Junk *et al.* 2006). Although the flood pulse increases the similarity among sites for many aquatic organisms (e.g. Thomaz *et al.* 2007; Bozelli *et al.* 2015), species that are not entirely aquatic may face a reduction of upland habitats at this

time. In the Pantanal, most amphibian species are explosive breeders with rapid larval development (1–3 months; Prado *et al.* 2005). Because the reproductive events occur mainly in temporary ponds during beginning of the rainy season, the newly metamorphosed amphibian should emerge as flood begins. At the height of the rainy season, grassland areas are partially or entirely flooded (mean depth of <30 cm), except for patches with higher elevation, which also tend to have different vegetation types. These flooded areas are prone to huge daily fluctuations in water temperature (>25°C) and are occupied by water bugs, predatory fish and water birds. We, here, posit that environmental conditions in the flooded matrix may hinder amphibian dispersal during the rainy season, because juvenile movement is primarily designed to escape the high rates of predation that occur at pond edges (Pittman *et al.* 2014). The importance of altitude as a correlate of the turnover component strengthens the idea of dispersal limitation related to the flood duration. Differences in micro-relief and the presence of low sandy ridges lead to discontinuity in flooded areas of Nhecolândia region (Girard 2011), and could serve as places where non-arboreal juveniles could pause and rest.

The finding that variation in species distribution was not dependent on spatial and environmental constraints during dry season suggests that stochastic processes are underlying the observed patterns. Because rates of evaporative water loss affect patterns of amphibian activity and species distribution (Watling *et al.* 2009; Ocock *et al.* 2014), landscape diversity should favour species with different traits that minimise risks of desiccation, such as burrowing behaviour and cocoon formation. However, mosaics of grasslands and savannas, such as those found in the Pantanal, often exhibit a scarcity of potential surface shelters and amphibian species rely mainly on termite nests and burrows constructed by other animals as daytime retreats (Tozetti and Toledo 2005; Simioni *et al.* 2014). As moist retreat sites are fundamental to escape temperature extremes (Vences *et al.* 2000; Seebacher and Alford 2002), it is not surprising that species would disperse without clear direction, according to availability and quality of shelters. For example, burrowing frogs are known to prefer soft soils and sands and avoid densely vegetated areas, because roots may hinder their burrowing activities (Booth 2006; Nomura *et al.* 2009; Mitrovich *et al.* 2011). In addition, some Pantanal amphibians, such as *Leptodactylus chaquensis* and *Ceratophrys cranwelli*, have been described as eager predators of other amphibians (Wells 2007; Costa-Pereira *et al.* 2015). Species of non-burrowing frogs would be more dependent of burrows constructed by other animals, and would avoid burrows with high densities of potential predators. However, information concerning distribution and habitat use outside of the breeding season is meagre for most Neotropical amphibian species.

A metacommunity approach has been often used to explain patterns of distribution in freshwater organisms, such as amphibians (Richter-Boix *et al.* 2007; Werner *et al.* 2007). Conflicting spatial patterns between dry and rainy seasons were consistent with recent ideas that metacommunity mechanisms may act ephemerally and simultaneously on communities (Driscoll and Lindenmayer 2009; Spasojevic *et al.* 2014). Our findings indicated that mass effects (i.e. dispersal from source to sink habitats) predominate in non-arboreal amphibian communities

of open areas, such as the Pantanal (Leibold *et al.* 2004). Mass-effect predictions permit a moderate spatial structure and the strength of environment would be weaker than in the species-sorting perspective (Spasojevic *et al.* 2014). Although it seems unlikely that amphibians would engage in dry-season dispersal, there is evidence that amphibian movements could be more likely during transition from rainy to dry season, in hyperseasonal environments (Watling *et al.* 2009). In the drawdown period, predatory fish are restricted to isolated ponds, and grassland patches are still moist. Our results are consistent with the idea of massive dispersal in the end of drawdown period; amphibian captures in dry season at Nhumirim Ranch occurred mainly in June (~70%, $n = 2033$), 1 month after drawdown. Moist conditions at the beginning of dry season would contribute to enhanced landscape permeability, especially for juveniles. However, we cannot rule out stochastic effects that may act simultaneously to other processes.

An important point here is that the nestedness component was higher in the savanna than in the grassland areas, following Baselga's framework. We also were able to identify nestedness patterns, using WNODF, only for savanna amphibian fauna. The nested habitat hypothesis (Hylander *et al.* 2005) offers one possible explanation for the observed pattern in savanna matrices. Risk of desiccation associated with water loss is known to cause both territorial and gregarious behaviour in amphibians, particularly when retreat sites are in short supply (Gautier and Miaud 2003; Gautier *et al.* 2006). Dense shrub cover may offer shelter to amphibians and other resources not readily available in grasslands (Cosentino *et al.* 2011; Dorado-Rodrigues *et al.* 2015); however, shrub coverage depends on the plant competition intensity and fine-scale site characteristics (soil attributes, topography, land use; Predick and Turner 2007). We did not directly access microclimate conditions, but it is not unexpected that amphibians would track different savanna patches, according to species-specific tolerances to desiccation (Marsh *et al.* 2004; Cline and Hunter 2014; Watling and Braga 2015). In this case, species (i.e. leptodactylids with foam nests) or life-stages (i.e. adults) more tolerant to desiccation should be widely distributed through coverage gradient, and species or life-stages more limited by hydric stress (i.e. semi-aquatic hylids, juveniles and pos-metamorphic) should occur in a subset of sites with dense shrub cover and less harsh conditions. Although we know little about the dynamics of stress avoidance and habitat shelters in amphibians from open areas, competition for retreat sites can have strong effects on amphibian abundance (Grover 1998).

Our study was undertaken in an area not directly influenced by the riverine flood pulse, and it is important to consider here that our results were based on a restricted study period. Because flood amplitude is known to vary at inter-annual scales, large variation in the yearly composition of amphibian communities may be expected in seasonal floodplains (McGinness *et al.* 2014). Although it would be valuable to repeat the analyses on data of the same climatic season from different years and to confirm issues of pattern predictability, high temporal replication is a very challenging task in field studies, when compared with more controlled experiments. However, the loss of information because of the temporal scale is compensated by the increase in the realism, as the complexity of natural communities may jeopardise attempts to infer processes based on laboratory or mesocosm experiments. Indeed, recent studies have highlighted that a stable view of metacommunity organisation is likely to be inaccurate, mainly in highly dynamic systems (i.e. estuaries, floodplains, intermittent rivers; Fernandes *et al.* 2014; Heino *et al.* 2015; Datry *et al.* 2016). Although we did not observe seasonal differences in the dominant patterns, factors associated with components of β diversity changed over very short time scales, mainly for turnover.

In conclusion, we found patterns of β diversity to be associated with different constraints in the Pantanal ecoregion. Contrary to our expectations, we did not find that these dissimilarities derived mainly from nestedness, but savanna habitats were more structured by nestedness than were grasslands. Biotic interactions and traits related to terrestrial movements might be assumed to cause the balanced variance in abundance. Although the seasonal differences associated with vegetation type have been slight, the turnover was related to distinct factors in the rainy and dry seasons. Much recent research on metacommunity structure has pointed to the role of season or guild-specific effects (e.g. Hill *et al.* 2011; Cisneros *et al.* 2015). Our approach, focusing on non-arboreal amphibians, allowed a more consistent insight into mechanisms of community assembly and the role of flood and drought dynamics. Furthermore, a better understanding of seasonal constraints will help elucidate possible effects of changes in intensity and duration of the flood regime, as might occur under conditions of climate change.

Acknowledgements

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