



## Snake diversity in floodplains of central South America: Is flood pulse the principal driver?



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### ABSTRACT

Seasonal flood pulses drive important seasonal ecosystem changes, trigger ecological processes that control spatial and temporal distribution of organisms and their life-history strategies, and are considered a key ecological process shaping diversity in floodplains. We used generalized dissimilarity modelling (GDM) to analyse the relative importance of flooding as a driver of snake community composition in the Paraguay River Basin (PRB), which encompasses discontinuous seasonal flooded areas, including the Pantanal floodplain, one of the largest Neotropical wetland systems. We modelled the beta diversity of pairs of PRB snake communities (based on species occurrence and phylogenetic relationships) as a function of biogeographical and environmental dissimilarities between areas, considering predictors that represent distinct limitations of species' ability to use an area. Annual flooding directly drives snake diversity, mainly when ancient evolutionary relationships between species were considered to calculate the phylogenetic diversity of the communities. Floods recurrently produce major changes in the environment and probably limit the persistency of species extremely specialized in habitat use. Despite the confirmation of the effect of flooding, the most important predictor of beta diversity between snake communities in the PRB was forest cover where communities were placed. Forest cover seems to constrain the occurrence of some species in both gradient extremities through the absence of suitable conditions for either specialized habitat use or thermoregulatory behaviours. Geographical distance was also an important predictor of beta diversity, highlighting the importance of neutral process in the assembly of local communities in systems such as seasonally flooded areas, where annual disturbances of varying intensities continually disassemble and reassemble biological communities. For the first time, we quantified the relative importance of flooding affecting patterns of biological communities in the Pantanal floodplain, compared to multiple factors also acting on species turnover in the area.

### 1. Introduction

Species composition in a given area is a result of interactions of the evolutionary history of organisms and their environments with local factors that currently mediate species occurrence and coexistence, in addition to past and present stochastic events (Wiens and Donoghue, 2004; Cavender-Bares et al., 2009). By understanding how the turnover in community composition across a region (beta diversity) is related to the region's environmental variation, it is possible to infer the main processes driving regional species composition (Soininen, 2010; Fitzpatrick et al., 2013; Warren et al., 2014). Much of the communities

idiosyncrasies that are reflected on regional beta diversity can arise from the differences in prevalence and strength of a set of processes acting on local species assemblages (Vellend, 2010).

Flood pulses are considered a key ecological force shaping diversity in floodplains (Lewis et al., 2000; Junk and Wantzen, 2004). They drive important seasonal ecosystem changes and trigger ecological processes that control the spatial and temporal distribution of organisms as well as their life-history strategies (Lewis et al., 2000; Nicole et al., 2004; Gerisch et al., 2012; Lucas et al., 2016). Species adaptations to river flow regimes range from changes in individual behaviour to changes in species morphology or life cycle (Lytle and Poff, 2004; Parolin et al.,

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2004; Ferreira et al., 2007). In general, selective pressures imposed by recurrent flood pulse on several generations of the organisms shape floodplain biotic communities (Lewis et al., 2000; Lytle and Poff, 2004). Additionally, a seasonal floodplain can also be repeatedly colonized by terrestrial or interfluvial species of the surrounding uplands, increasing the set of processes and interactions involved in the assembly of its communities (Junk et al., 2011).

The largest continuous tropical floodplain is the Pantanal (Junk and Wantzen, 2004), located at the centre of South America, in the depression of the Paraguay River Basin (PRB). This basin encompasses other seasonal flooded areas and eight terrestrial ecoregions (Olson et al., 2001), being one of the most ecologically and geologically heterogeneous areas of South America. Because the intensity of the annual flood pulse varies spatially, a gradient in flood level results in a range of major habitats forming an environmental mosaic (Adámoli and Pott, 1999). The complex vegetation cover and highly seasonal productivity support an abundant fauna, composed of species representative of different ecoregions surrounding the floodplain (Junk et al., 2011). Nevertheless, biological communities in the Pantanal show lower richness than neighbouring regions (Junk et al., 2011; Alho and Silva, 2012). That has been attributed to the Pantanal's recent formation – 2.5 Ma, during the last Andean orogeny phase (Assine et al., 2015) – and the ecological hardships imposed on organisms by the flood pulse (Junk et al., 2011; Alho and Silva, 2012).

Snakes are distributed across the globe in a wide variety of environments (Sites et al., 2011). In general, they show great adaptability to available resources and high speciation rates (Sites et al., 2011; Pyron, 2014). Global patterns of reptile distributions indicate that current environmental conditions (temperature, rainfall and environmental seasonality) constrain the spatial distribution of species (Saint Girons, 1982; Guisan and Hofer, 2003; Santos et al., 2006; Feldman et al., 2015). In South America, many studies suggested historical factors were more important to the structure of current communities than present environment (Cadle and Greene, 1993; França et al., 2008; Nogueira et al., 2011; Moura et al., 2017). However, recent studies found that the low levels of plasticity in habitat use of some snake species restrict their range and, consequently, structure local communities (Fraga et al., 2011; Cavalheri et al., 2015). Additionally, biotic interaction such as food competition are known to be strong among the sympatric snakes in other tropical areas (Andreone and Luiselli, 2000; Madson and Shine, 2000; Luiselli, 2006a), acting on species co-occurrence pattern and, consequently, possibly affecting snakes communities structure. These interactions are believed to be more pronounced in seasonal environments, such as areas with dry and wet season well defined or areas subject to seasonal flood, where in addition to environment constrains, the organism were subject to changing in prey availability (Friend and Cellier, 1990; Luiselli et al., 2005; Luiselli, 2006b).

Most studies on the effects of floods on biological communities have focused on plants and invertebrates (e.g. Lytle and Poff, 2004; Nicole et al., 2004; Parolin et al., 2004; Ferreira et al., 2007; Gerisch et al., 2012). These studies show that adverse effects from flooding are responsible for changes in distribution and species composition for several taxa and that different flow regime parameters (such as flooding frequency, duration and predictability) can affect how organisms adapt or fail to adapt to flooding. For the Pantanal, current knowledge includes records of some invertebrate species adaptations to cycles of flood and drought (Kretzschmar and Heckman, 1995; Nolte et al., 1996; Adis et al., 2001; Tissiani et al., 2015; Yamazaki et al., 2017). Also, there are studies that indicate differences in species composition between floodplain and upland communities (see Junk et al., 2011 for a review), while other studies showed how some floodplain communities or organisms are affected by local environmental factors or spatial processes (Wantzen et al., 2002; Rebellato and Nunes da Cunha, 2005; Delatorre et al., 2015; Dorado-Rodrigues et al., 2015; Valério et al., 2016; Moreira et al., 2017). However, the relative importance of the

flood pulse in shaping the composition of Pantanal communities, compared to other environmental and climatic features that also drive large-scale variations in biodiversity, has never been formally tested.

Here we analyse the relative importance of flooding as a driver of snake beta diversity in wetlands at Paraguay River Basin, which include the Pantanal floodplain and other discontinuous seasonally flooded areas. We expect that, given the high heterogeneity of this region, an array of climatic, physical and historical factors will influence beta diversity variation among communities. We probed the relative importance of these potential environmental predictors, however, because the large area that is periodically affected by flooding and the magnitude of change that this event causes in ecosystems, we believe flooding is a key factor that mediate the occurrence of different snakes in this basin, by shaping the replacement or loss of species in local communities.

## 2. Material and methods

To test the effect of the flood pulse on community composition we modelled the beta diversity of pairs of PRB snake communities (response variable) as a function of biogeographical and environmental differences between the areas where they are placed (predictors). We then investigated how each predictor can explain the total beta diversity (taxonomic and phylogenetic  $\beta$  diversity).

### 2.1. Study area

The Paraguay River basin (PRB) is located between 14° and 27° S and 53° and 67° W (Fig. 1). The entire catchment covers 1,135,000 km<sup>2</sup>, and includes the Pantanal, eight other ecoregions (Olson et al., 2001) and four biogeographical subregions (Morrone, 2014). The limits of the Paraguay basin and the Pantanal adopted here follow Petry and Sotomayor (2009) and Hamilton et al. (1996), respectively.

The Pantanal is an area of about 140,000 km<sup>2</sup> situated in the upper Paraguay River depression, and subject to an annual monomodal flood pulse (Assine et al., 2015). During the rainy season (November–March) the vast plain stores water flowing from nearby uplands and drains it to the lower sections of the Paraguay River during the dry season (April–October). On average, about one-third of the Pantanal area is inundated each year, with monthly estimates of total flooded area ranging from 10% to 70% of the entire Pantanal depression (Hamilton et al., 1996). Because of the very slight slope of the terrain (2–3 cm per km from North to South and 5–25 cm from East to West) floodwaters move slowly, and require about four months to surmount the entire Pantanal (Hamilton et al., 1996).

In addition to the Pantanal, the PRB encompasses other seasonally flooded areas, related to large alluvial fans from right margin tributaries to the Paraguay river, such as the Pilcomayo, Parapetí and Bermejo rivers. They are located in the Wet Chaco ecoregion, in Paraguayan, Bolivian and Argentinian territories. In the annual rainy season the flood pulse fills ephemeral channels and swamps that form the alluvial belts (Iriondo et al., 2000).

### 2.2. Snake beta diversity

The species turnover between different snake communities of the Paraguay River basin (PRB) was based on a database with around 6300 records of snake occurrence in the region (map in Appendix A). Records were gathered either by revision of databased voucher specimens in 12 Brazilian zoological collections (about 60% of the records; collections list in Appendix A) or by the compilation of reliable literature records (around 25%). The database was completed with unpublished occurrence records (another 15%) obtained from management plans of protected areas, unpublished technical reports of environmental impact studies, and with unpublished data from partner researchers, when they could be confirmed through examination of voucher material. To

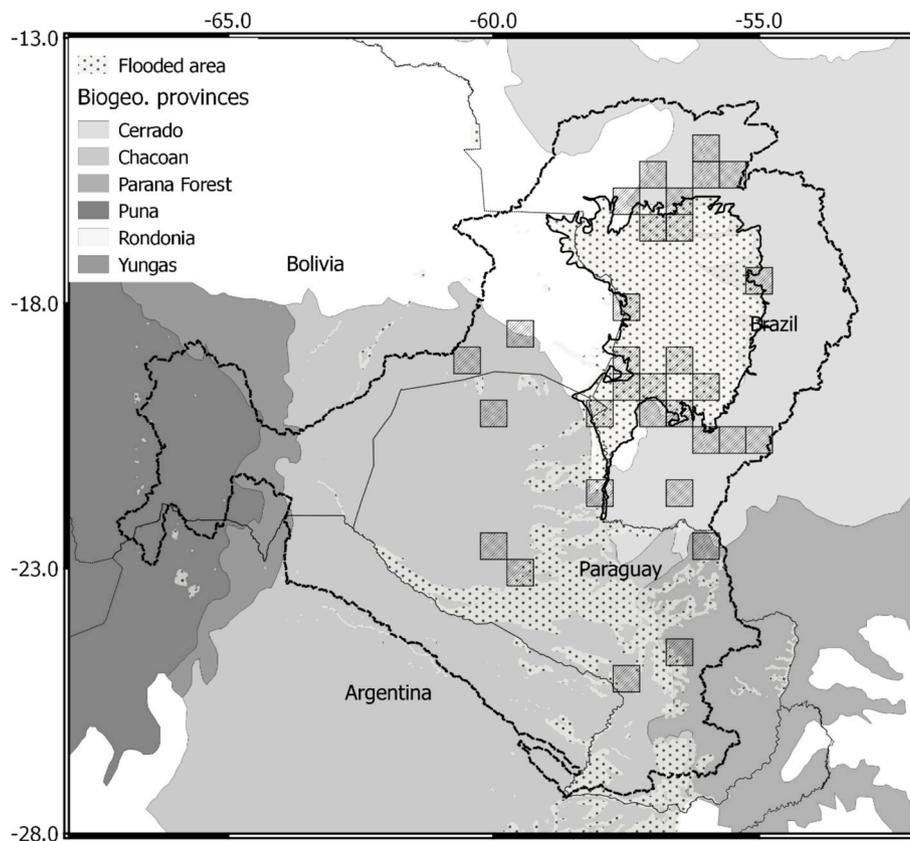


Fig. 1. Map showing the limits of Paraguay River Basin (outer black line) and its flooded areas, the biogeographic provinces that it encompasses and the Pantanal floodplain (internal black line). The 31 boxes were the  $0.5 \times 0.5^\circ$  cells used to delimit snake communities.

delimit our sample units (local communities), we superimposed this species occurrence dataset on a  $0.5 \times 0.5^\circ$  grid that covered the entire basin. We then considered the species recorded within each grid cell to comprise a local snake community. From 510 grid cells that covered the PRB area, 254 had at least one snake record. We carefully compared the communities of each grid cell with systematic studies from the same ecoregions (e.g., Strüssmann and Sazima, 1993; Leynaud and Bucher, 1999; Souza et al., 2010; Bellini et al., 2015) and similar latitudes, and only included a cell in our analysis if the species richness was similar to that found in those studies (with richness difference not higher than 10 and with all regionally common species registered inside the grid cell). The 31 cells considered well-sampled included around 64% of all records and a broad environmental variation (Fig. 1). Although our criterion for well-sampled cells is subjective at some level, we opted to keep just those cells to avoid bias from false absence that could blur consistent relationships between community composition and environment. Species of the families Anomalepididae and Aniliidae were not considered in our analyses. Species from Anomalepididae that occur in the PRB are taxonomically poorly resolved (Hedges et al., 2014) and, like Aniliidae, have a much smaller probability of detection compared to other species, especially when no systematic survey method is used. In addition, these taxa are the most ancient of the entire basin. Their phylogenetic relationships with other snake species are much older than those among members from other snake families, and thus their presence records, though patchy, would tend to dominate the phylogenetic beta diversity signal for the cells where they are recorded.

### 2.3. Environmental and historical predictors

We used three climatic variables, here considered as surrogates for the physiological limitations of snake ranges: isothermality, minimum temperature of the coldest month and precipitation of the driest quarter

of the year. These were obtained from the WorldClim database ([www.worldclim.org](http://www.worldclim.org) – Hijmans et al., 2005) and were a priori chosen, among those available, for their importance in snakes ecology (Di Cola et al., 2008; Mullin and Seigel, 2009; Zanella and Cechin, 2009). In addition, these variables showed lower intercorrelations ( $r^2 < 0.35$ ) in the PRB than other variables available in the WorldClim database. For each grid cell we calculated the average value of each of the three chosen variables from layers with 10 min (around 18 km) resolution.

The percentage of forest cover in a grid cell was calculated based on the sum of the coverage of two land cover classes (Evergreen and Deciduous Broadleaf Forests) obtained from EarthEnv database ([www.earthenv.org/landcover](http://www.earthenv.org/landcover), Tuanmu and Jetz, 2014). These two classes include virtually all types of vegetation that can form a forest cover that provides arboreal substrates for snakes in the PRB area (Petry et al., 2012; see Tuanmu and Jetz, 2014 for details from each class). Because we are considering variables that could have acted on species occurrence during their evolutionary history, we corrected the values of Deciduous Broadleaf presence for cells between  $-21.8$  and  $-23.8$  S and  $-59.2$  and  $-60.7$  W. In those cases, the current values of coverage result from massive anthropic deforestation in recent decades (Huang et al., 2009), so we used the average value found in the eight neighbouring cells that surround the focal cells.

The variables describing intensity of flood were created by calculating the percentage of the grid cell that is periodically flooded, based on a map of seasonally flooded areas (Lehner and Döll, 2004) obtained from [www.worldwildlife.org/pages/global-lakes-and-wetlands-database](http://www.worldwildlife.org/pages/global-lakes-and-wetlands-database). Our two flood variables indicate the percentage of area flooded within a grid cell and the total flooded area in the neighbourhood of a cell (within a  $0.5^\circ$  buffer, excluding the focal cell).

We used a biogeographical distance variable as a surrogate for historical information about the communities. From the biogeographical regionalization of Morrone (2014) we calculated a

biogeographical distance index that considers the occurrence of the communities in four biogeographical subregions and six provinces that occur in the PRB (South Brazilian Dominion, with Rondonia and Yungas provinces; Chacoan Dominion, with Cerrado and Chacoan provinces; Paraná Dominion, with Paraná Forest province; and South American Transition Zone, with the Puna province - [Morrone, 2014](#)). Pairs of grid cells from the same biogeographical province were given a biogeographical distance of zero; pairs from the same subregion but different provinces, 1; and pairs from different subregions, 2. When a grid cell comprised two biogeographical provinces, we assumed it belongs to the larger province in that cell.

#### 2.4. Diversity modelling

We investigated the relative importance of each predictor as a driver of beta-diversity using Generalized Dissimilarity Modelling (GDM), a multivariate extension of matrix correlation analysis ([Ferrier et al., 2007](#)). GDM models dissimilarity in community composition between pairs of locations as a nonlinear function of environmental differences between the locations and their geographical distance ([Ferrier et al., 2007](#)). Unlike other diversity modelling approaches, GDM can accommodate the curvilinear relationship between environmental or geographic separation between sites and compositional dissimilarity, by considering the variation in the rate of compositional turnover at different points along environmental gradients ([Ferrier et al., 2007](#)).

Our species presence-absence matrix was used to derive the Jaccard dissimilarity measure of inter-site dissimilarity as the biological response variable for the GDM. We started the modelling using the seven environmental predictors described above (isothermality, minimum temperature of the coldest month, precipitation of the driest quarter of the year, flood percentage in a grid cell, flood percentage in grid cell surroundings, coverage of trees in a grid cell and biogeographical distance) and the geographical distance, and we further reduced this set using 2 steps of backward-elimination variable selection.

In the first step of elimination, variables with all coefficients equal to zero were dropped, as they were not helping to explain the biological pattern ([Ferrier et al., 2007](#)). In the second step, we successively removed predictors contributing less than 0.1% to the explained deviance ([Ferrier et al., 2007](#); [Williams et al., 2012](#); [Rosauer et al., 2014](#)). In our case, this value represents a reasonable trade-off in parsimony between over and under-fitting the model. The significance of the final model was calculated by permutations of the site-pair table 999 times by randomizing the order of the rows ([Thomassen et al., 2010](#); [Fitzpatrick et al., 2011](#)). New GDMs were fitted to these permuted site-pair tables to estimate an overall p-value for model significance. We used the “gdm” package ([Manion et al., 2016](#)) for R software ([R Core Team, 2016](#)) to implement the modelling and significance value. Because the attribute biogeographical distance is not a continuous variable, we set the knots of the corresponding I-splines to 1, 2 and 3, which are the values that can be reached by this attribute. For all other variables, we used knots set at zero (minimum), 50 (median), and 100 (maximum) percentiles ([Ferrier et al., 2007](#)).

We then repeated the modelling process using the phylogenetic dissimilarity between sites as a response variable. The spatial structure of biodiversity can be better described by patterns of phylogenetic turnover compared to species turnover, for example in cases in which communities share no species but do share taxa with some degrees of relatedness ([Rosauer et al., 2014](#)). Phylogenetic dissimilarity, also called phylo beta diversity ([Graham and Fine, 2008](#)), was calculated for each grid cell pair using the PhyloSor index ([Bryant et al., 2008](#)), which computes the fraction of branch-length shared between two communities. We used Mesquite 2.75 to assemble by hand a composite phylogeny of the snakes of Paraguay River basin, based primarily on [Tonini et al. \(2016\)](#) and [Pyron et al. \(2013\)](#) and information from various additional phylogenies (see details [Appendix B](#)). The placement of each species that was not included in the published phylogenies was inferred according to the relationships of sister species or included as a

polytomy in nodes containing its closely related species. The branch lengths not available in [Tonini et al. \(2016\)](#) were estimated by evenly interpolating the nodes between originally placed nodes, using the BLADJ module of Phylocom 4.1 ([Webb et al., 2008](#)).

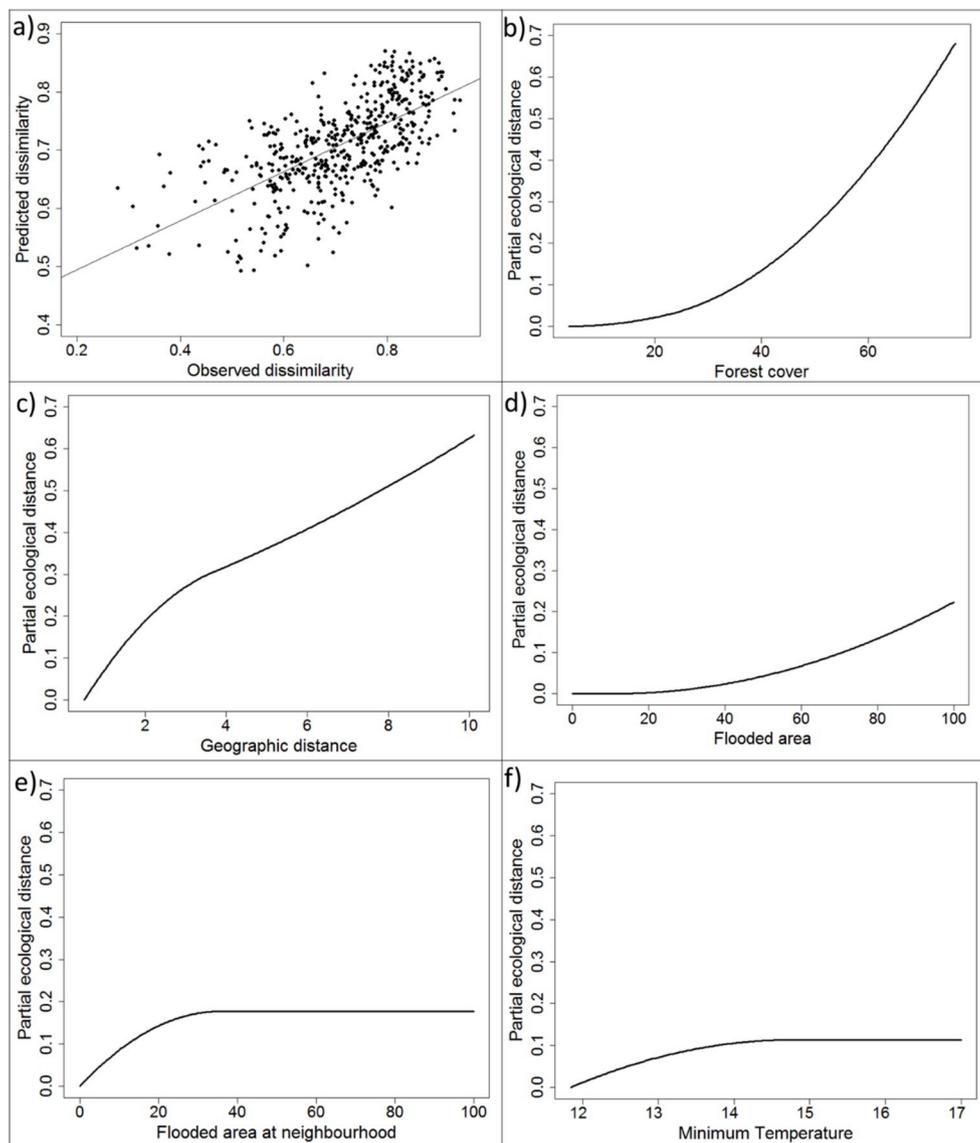
Considering that a phylogeny represents lineages ancestral to current species, which may have lived in different locations and environments to their current descendants, the use of older phylogenetic relationships between species may blur rather than reinforce the relationship between phylogenetic dissimilarity and current environmental community dissimilarity ([Rosauer et al., 2014](#)). We thus fitted models considering different age cutoffs of the phylogeny. This generated phylo beta diversity values calculated from phylogenies with different age limits, and helped to find the phylogenetic tree depth with the strongest relationship to the current day environment. Following [Rosauer et al. \(2014\)](#), we generated nine versions of our species phylogeny, in each version creating a root polytomy at a specified cutoff age. Any branches, or parts of branches, older than this age were removed and the portions of the tree closer to the tips than this cutoff were retained and used to calculate the PhyloSor metric. The cutoff age started including 90% of the tree depth and eliminated a further 10% of total depth in each version of the phylogeny.

### 3. Results

A total of 122 snake species occurred in the 31 grid cells with a reasonable amount of information spread across the PRB ([Appendix C Table C1](#)). The GDM model for taxonomic diversity accounted for 42.6% ( $p < 0.001$ ) of the deviance in observed turnover of PRB snake species ([Fig. 2](#)). The variables isothermality, precipitation of the driest quarter of the year, and biogeographical distance showed no relationship with the diversity gradient and were eliminated during the process of model selection.

The variables that contributed most to the explained deviance of the model were forest cover (around 13%) followed by geographical distance (around 8%). Coverage of flooded area in the grid cell (3.93%), flooding in surrounding areas (1.97%) and minimum temperature of the coldest month (0.59%) were important as well, as they helped to increase the explained model deviance ([Table 1](#)). However, in those cases, the contribution to the dissimilarity between communities were always less than half of those shown by forest cover and geographical distance. The total amount of beta diversity associated with each variable can be visualized by the maximum height, and the rate of change in composition with changing environment is shown by the slope of the regression curves in [Fig. 2](#).

When phylogenetic distance between pairs of communities was considered as the response variable, the model explained 26.5% of total deviance ( $p = 0.002$ ). The predictor that contributed most to the explained deviance of the model was forest cover, followed by flooded area in the grid cell and geographic distance ([Table 1](#)). Precipitation and flooding in surrounding areas were also considered significant predictors in the phylogenetic distance model, whereas isothermality, minimum temperature, and biogeographical distance were excluded from the model after the backward elimination process. The models fitted to phylogenetic distances calculated with different phylogeny cutoff ages showed successive decreases of the explained deviance, as larger amounts of ancient relationships were considered: the model considering just the 10% most recent relationships between species explained 39% of the total deviance of the model, whereas the model considering 90% of phylogenetic relationships explained 27% of the total deviance (bars in [Fig. 3](#)). Cover of flooded area in a grid cell was the most variable predictor considering the contribution to the explained deviance of the models fitted using different levels of phylogenetic relationships. When values of phylogenetic diversity were calculated considering all phylogenetic relationships between species, the importance of flood was twice the value found when only the earlier relationships were considered ([Fig. 3](#)).



**Fig. 2.** Generalized dissimilarity model for snake composition in the Paraguay River Basin using five predictor variables. a) Observed dissimilarity between pairs of communities plotted against the predicted dissimilarity based on the model b-f) Fitted functions for each of the predictors.

**Table 1**

Percentage contribution to explained deviance of each predictor in the models using taxonomic and phylogenetic diversity as response variable.

Predictor	Taxonomic diversity	Phylogenetic diversity
Forest cover	12.95	9.04
Geographical distance	8.36	4.16
Flooded area coverage	3.93	6.51
Flood coverage on surrounding areas	1.97	0.2
Minimum temperature	0.59	-
Precipitation	-	0.22

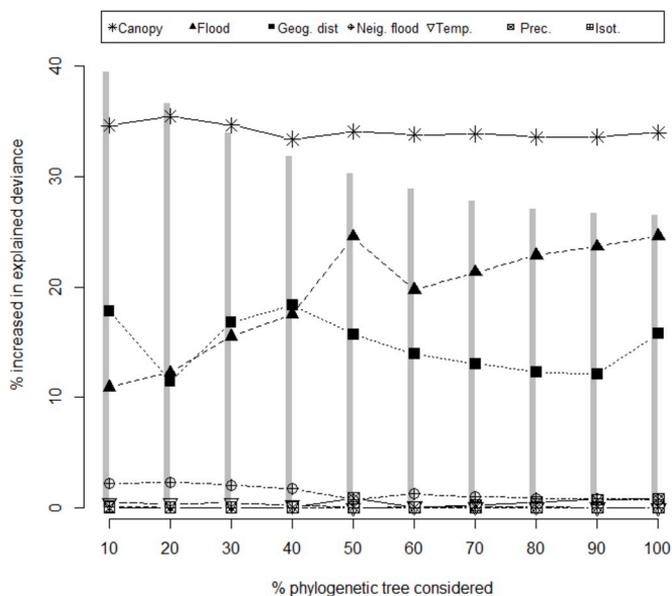
#### 4. Discussion

Contrary to our expectations, seasonal flooding was not the most important predictor of snake beta diversity in the Paraguay River basin (PRB). Nevertheless, flooding was one of the drivers of community composition, showing increased importance when phylogenetic beta diversity was considered.

The most important predictor to explain beta diversity between

snake communities in the PRB was forest cover. It acts mainly on species richness, with communities from different parts of the gradient of forest cover being different sized subsets of all species present in the region. This result indicates that habitat use can be a strong constraint on snake species ranges in our study region. When comparing Neotropical snake communities from forests with those from grasslands and savannas, Cavalheri et al. (2015) found that less vertically structured habitats represent a strong filter in these latter communities, because arboreal and semi-arboreal species are less prone to occupy them due to the lower abundance of adequate substrate. This process may be reflected in the variation of the beta diversity in the PRB.

Moreover, a stronger constraint on species occurrence seems to exist in areas with higher forest cover. About one fourth of the species are absent from areas with more than 50% forest cover. Open areas in the Pantanal often have more reptile species than forested areas (Terra, 2012; V.L. Ferreira, unpublished) as is commonly observed in the Cerrado (Nogueira et al., 2009; Valdujo et al., 2009). A balance between availability of vertically structured habitats for arboreal species and heterogeneity of thermoregulatory conditions might be acting to shape the range of snake species along the PRB tree cover gradient. In our GDM models, the minimum temperature of the coldest month was



**Fig. 3.** Variation of the proportion of contribution to explained deviance of the model for each predictor, related to the percentage of the phylogenetic tree considered to calculate phylogenetic dissimilarity between communities. Bar height indicates the explained deviance of the GDM fitted to each tree. Lines show the variation of the importance of each predictor: asterisks represent forest cover, squares represent geographical distance, diamonds represent flooded area cover, crosses represent flooded area cover in surrounding areas, triangles are minimum temperature and circles represent precipitation.

also a variable explaining beta diversity. Low temperature is known to be a limiting factor for the activity of most snakes (Gibbons and Semlitsch, 1987; Sawaya et al., 2008) probably because it can reduce their metabolic rates to extreme levels (Lillywhite, 1980; Blouin-Demers and Weatherhead, 2008). Whereas our study areas have tropical climate and then thermal constraints on snake are thought to be minimal (Shine and Madsen, 1996; Luiselli et al., 2002), minimum temperature may be important in this case because extreme minimum temperature events may cause high individuals mortality (Boucek et al., 2016), mainly in closed areas where direct sunlight for thermoregulation is absent. Additionally, the flooded areas in the PRB are mostly surrounded by ecoregions with dominance of open habitats (such as Cerrado and Chaco). Snake species adapted to open areas are probably more frequent in the regional pool than those specialized in forest habitats, which could help to limit the number of species able to occupy forest areas in the PRB. Differences in the “biogeographic species pool” also were claimed as probably explaining divergences in snake communities from north and south of Atlantic Forest (Moura et al., 2017).

While the model using species beta diversity as a response variable represents extant biotas whose distributions are mediated mostly by present environmental factors, the model using phylogenetic beta diversity includes data from past lineages (shared ancestry - Rosauer et al., 2014). The reduced model fit using phylogenetic compared to taxonomic diversity may have occurred because the former considers the environments occupied by clades of species which may have radiated into a diverse range of environments (if the ancestral niche is not strongly conserved), weakening the environmental signal in phylogenetic turnover. Even so, the models using phylogenetic beta diversity agreed with the model using taxonomic diversity - both indicate forest cover and flooded area as the main environmental predictors of turnover among communities. This result might indicate that the processes shaping communities through tree cover and flooding and gradients nowadays may be under the effect of conserved traits. Additionally, the increased contribution of flooding to explain model deviance as older phylogenetic relations were included in the calculation may be

evidence that the ability to occur in flooded areas can be related to ancient characters or lineages.

In different regions, flood disturbance has been reported as an important driver not only of traditional species diversity measures, but also of the functional diversity of communities (Lytle and Poff, 2004; Parolin et al., 2004; Gerisch et al., 2012). Maybe the alternation of floods and droughts, coupled with the high variation in the inter-annual flood cycles in the central South American wetlands, may restrict the occurrence in the floodplain of species with more specialized resources use (such as fossorial species or food specialist) and favor species with broad or plastic environmental niches. The fact that the amount of flooded area in a grid cell contributed more in our models than flooding in surrounding grid cells could suggest that the effects of floods occur in a direct and localized way. Seasonal floods probably limit suitable abiotic and biotic conditions on a smaller spatial and temporal scale, instead of acting indirectly (for example, interfering in population establishment by the lack of migrants that could reach a flooded area). Different studies about snakes co-occurrence patterns and resource partitioning found the flood cycles regulated the seasonal prey dynamics and then, affected the interspecific relations between sympatric snakes (Friend and Cellier, 1990; Madson and Shine, 2000; Luiselli et al., 2005; Luiselli, 2006b). The pronounced seasonality caused by flooding may be requiring the snake species of Pantanal and other flooded surrounding areas to be plastic regarding resource uses in multiples axes, such as food and space, in a temporal scale relatively small. However, some studies show (Arzamendia and Giraud, 2009) or suggest (Santos et al., 2013) that rivers and their flow regimes can also act as dispersal corridors. Indeed, some snakes of the PRB are present throughout the inundation gradient and seem not to be negatively affected by seasonal flood regimes, which includes aquatic snake species of the genus *Helicops*, *Hydrops* and *Eunectes*. Future studies on habitat use of species from seasonally flooded habitats could elucidate which and how processes triggered by floods shape species distributions.

Particular occurrence patterns highlight the interaction of multiple factors on species turnover in the PRB, like that of the three species of the *Bothrops neuwiedi* complex in the region. These species are part of a monophyletic, highly geographically structured species group within the genus *Bothrops*, which is widespread in open ecosystems of South American (Machado et al., 2014). These three terrestrial species can be found in sympatry at some localities in the PRB. However, *B. diporus* is present throughout the entire forest cover gradient and is confined to areas with less flood (0–33% of flooded area), *B. pauloensis* occurs throughout the flood gradient but is present only in cells with tree cover below 30%, and *B. mattogrossensis* occurs across all the variation of tree and flooded area cover. These results indicate that *B. mattogrossensis* has a broader niche and can range through more areas of the PRB than the other two *Bothrops* species. In fact, Martins et al. (2001) showed that *B. mattogrossensis* has a relatively slender body and long tail when compared to other species in the *Bothrops neuwiedi* complex, perhaps because individuals of *B. mattogrossensis* could occasionally be forced to climb the vegetation during seasonal floods.

The high importance of geographical distance to explain beta diversity may be a result of two non-mutually exclusive factors. First, as already found in other snake communities (Cadle and Greene, 1993; Cavalheri et al., 2015), neutral processes such as dispersal limitation seem to also act on turnover of PRB snake species, and thus communities close to each other tend to be more similar than those farther apart. The importance of neutral process in the assembly of local communities is probably larger in systems such as seasonal flooded areas, where annual disturbances of varying intensities continuously disassemble and reassemble biological communities (Delatorre et al., 2015). Furthermore, there might be spatial autocorrelation among other predictors that vary together with the variables used in our analysis, but were not used in our models (e.g. average temperatures, rainfall). Therefore, compositional similarities among communities close to each other might have been mistakenly attributed only to

geographical proximity, even though they could also be the result of similar climatic conditions experienced by such geographically close communities.

Model fitting is a widely used approach to make inferences about mechanisms acting on species distribution, because it reveals occurrence patterns through associations between the geographic location of the species and a set of variables. Even using fewer predictors, our models explain a relatively large amount of model deviance compared to other GDM models (e.g. Leathwick et al., 2011; Andersen et al., 2009; Jones et al., 2016) and we believe they indicate the relative importance of different factors acting on snake diversity in the PRB. In summary, forest cover seems to be constraining the occurrence of some species (at both extremes of the forest cover gradient) by shortening of suitable conditions for either specialized habitat use or thermoregulatory behaviour. Although in a lesser extent, annual flooding also directly drives snake beta diversity. It produces recurrent large alterations in environments and probably limits the range of species with specialized habitat use. Phenomena at different temporal and spatial scales, like community level interactions and even spatial signals of evolutionary history, also must act on community composition at some level. The search for evidence of environmental filtering acting on the assembly of the communities from different flood levels can help to show how diversity patterns of these unique areas are created and maintained, and how the organisms have adapted to novel environmental conditions during their evolutionary history.

#### Author contribution statement

LP, DR, CN and MM conceived the idea. LP, VLF, CS and CN contributed to snake data collection. LP and DR performed statistical analyses. LP, VLF and CS, wrote the paper. All authors contributed significantly to the writing of the manuscript stimulating a fruitful discussion on several aspects of the work.

#### Disclosure

No potential conflicts of interest declared.

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#### Appendix A. Supplementary data

Supplementary data related to this article can be found at <https://doi.org/10.1016/j.actao.2019.04.003>.

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