



ECOSYSTEMS

Seasonal changes in taxonomic and functional diversity of lizard communities in southern Brazilian Pantanal

KAROLINE R. DA SILVA, LIARA G. GOMES, VANDA L. FERREIRA, CHRISTINE STRÜSSMANN & LEONARDO F.B. MOREIRA

Abstract. Seasonal changes play a key ecological role, structuring biotic processes and communities. Yet we generally lack an understanding of how seasonal flood regimes affect communities in floodplains. Herein, we investigated the effects of seasonal changes in taxonomic and functional diversity of lizard communities in southern Pantanal ecoregion. Lizards were sampled in seven sites encompassing seasonally flooded grasslands and dense arboreal savannas, across rainy and dry seasons (2005-2006). Functional diversity metrics were based on three morphological traits and included intraspecific variability. We collected a total of 810 lizards from 13 species. Species richness did not differ across seasons or months. Lizard abundance varied among sampling months, but did not differ between rainy and dry season. Low values of abundance were recorded at drawdown period. Community composition did not vary between seasons. Functional diversity metrics exhibited random distributions, and both functional richness and evenness were not influenced by seasons. Although communities seem to be resilient to seasonal variations, our findings highlighted that transition from rainy to dry season may represent an important constraint on lizard abundance. Including traits related to food acquisition and predator avoidance could provide new insights into the effects of seasonal floods on floodplains' lizard communities.

Key words: abundance, floodplain, intraspecific variability, species traits.

INTRODUCTION

It is well appreciated that seasonal variations (i.e. shifts in temperature and precipitation patterns) can affect biotic communities through effects on productivity, habitat heterogeneity, and resources availability (Robinson et al. 2013, Ryan et al. 2016). In floodplains, biotic diversity is strongly affected by flood regimes, both directly and indirectly. The variation between aquatic and terrestrial phases may favor the development of plasticity (physiological and behavioral) or even limit species distribution (Ocock et al. 2014, Moreira et al. 2017). However, the consequences of flood pulses for reptile

communities from Neotropical areas are still a matter of debate. Flooded area influences phylogenetic beta diversity of snake communities in floodplains of Paraguay River basin (Piatti et al. 2019). In contrast, flooding has a strong effect on lizard species richness in floodplains of the Araguaia-Tocantins basin, but no impact on the phylogenetic community structure (Mesquita et al. 2015). In this sense, we need integrative approaches to understand how the flood pulse affects different dimensions of communities (i.e. taxonomic, functional, and phylogenetic).

Recently, functional trait approach has been used to reveal reptile responses to human disturbances (Trimble & van Aarde 2014,

Berriozabal-Islas et al. 2017). An organism's traits have direct and indirect consequences on its fitness, making functional traits a proxy for understanding the habitat requirements and responses to disturbances (Mouillot et al. 2013). However, many challenges remain to establish accurate generalizations concerning drivers of the observed patterns. For example, many animal trait data are not readily available or the investigated traits can be hard to quantify. Functional traits may also vary both among and within populations (e.g. Raffard et al. 2019; and references therein), so the spatial scale under which they are considered needs to be addressed. In addition, there is an ongoing debate on trait selection and types of functional diversity measures (Tsianou & Kallimanis 2016). For reptile communities, very little exists concerning the effects of natural disturbances—such as floods—on species traits (Piatti et al. 2019).

Ultimately, lizards inhabiting areas subject to floods must have abilities to occasionally live in trees, semi-aquatic habits or high vagility to dispersal (e.g. Iguanidae, Mabuyidae, and Tropiduridae). Otherwise persistence in seasonally flooded areas will rely on recruitment occurring from adjacent upland areas (McDonald et al. 2012, Treilibs et al. 2019). So, because floodplains are quite variable regarding environmental conditions across time and space, we expect lizard communities inhabiting them to consist of generalist species, rather than specialist species (e.g. Mesquita et al. 2015). Morphological characteristics are useful to discriminate niche gradients between lizards (Pianka et al. 2017), however categorical variables (such as diet, foraging activity, reproductive mode) have also been used in studies about lizard functional diversity (e.g. Trimble & van Aarde 2014, Berriozabal-Islas et al. 2017). Although discrete categories

are more easily compiled and may help us to infer general niches for broad comparisons, they make difficult to assess how intraspecific variability impacts functional diversity. In this sense, incorporating individual measurements instead of mean values would improve studies' accuracy (Violle et al. 2012). When traits are carefully selected, correlations between them may reveal important aspects of community functioning (Villéger et al. 2008).

In the center of South America, the Pantanal ecoregion encompasses a large variety of floodplain habitats (e.g. brackish and freshwater ponds, extensive seasonally flooded grasslands, channels, open and arboreal savannas). Although most of these habitats share similarities with Cerrado ecoregion, they are subject to a predictable flood pulse associated to seasonal, summer rainfall pattern (Junk et al. 2011). Currently, 47 lizard species are known for the region (Ferreira et al. 2017, Dorado-Rodrigues et al. 2018). Although their natural history is incompletely known, many species appear to show patchy distributions in the mosaic of grasslands-savannas in the central Brazil (Nogueira et al. 2009). Such microhabitat associations potentially prevent some species from colonizing areas subject to flood pulses, and result in reduced species richness in the floodplain when compared with localities situated in the neighboring plateaus (Strüssmann et al. 2011).

Here, we focus on lizard communities in the Pantanal to evaluate seasonal patterns. We considered three aspects of taxonomic diversity (richness, abundance, and species composition) and two aspects of functional diversity (richness and evenness). Lizards exhibit high selectivity for thermoregulatory microhabitats and intense competition for suitable microclimates can exert strong impact on individual's performance and habitat use (Rusch & Angilletta 2017, Benício

et al. 2021). So, species composition and traits associated to these species would be expected to change from the warm-wet to the cool-dry season, even with no seasonal change in the taxonomic richness. In addition, flood pulse may impose restrictions on microhabitats for thermoregulation or shelter. So, functional diversity would be lower in the rainy season than in the dry season, following disturbance associated to flood pulse.

MATERIALS AND METHODS

Study area and sampling procedures

The study area was located in the Negro-Taquari interfluvium, in part of the Taquari alluvial megafan, a region known as Nhecolândia (for more details see Oliveira et al. 2018). Field samplings were done at the Nhumirim Ranch (18.9833°S, 56.6500°W; 103 m a.s.l.; ca. 4300 ha), an experimental station belonging to the Empresa Brasileira de Pesquisa Agropecuária, with 20% of its area converted to Natural Heritage Private Reserve. The topography is basically flat with low level terrain, and the soil comprises fluvial and lacustrine sands with high aluminum saturation (Junk et al. 2006). The predominant landscape includes a mosaic of dry and seasonally flooded grasslands of both native and cultivated pastures, open and dense arboreal savannas on higher terrains locally called “cordilheiras” (Pott et al. 2011). The tropical climate implies a mean annual temperature of 25.5°C with maximum temperatures above 35°C (October to January), although the minimum can go down to 15°C (June and July). Annual rainfall varies from 675 to 1185 mm and is highly seasonal, concentrated between December and March (~70%; Soriano & Alves 2005). In the rainy season, floods are common in the region as a result of rainfall runoff with a limited influence of overflow water from rivers. Although interannual variations may

occur, the flood often begins at mid-December (Delatorre et al. 2015). The steady flood period occurs from January to March, and water drawdown may last until June.

At the Nhumirim Ranch, we sampled sites within grassland areas (N = 4) and dense arboreal savannas (N = 3), with a minimum distance of 1.2 km each other (Supplementary Material - Figure S1). Lizards were captured in each site using sets of pitfall traps. During rainy season, the area can be almost completely covered by surface water, except for patches with a higher elevation (i.e. 1 m above the flood level). Thus, traps were constrained by logistic issues and installed in sites above the mean flood level. At each site, we installed two sets of pitfall traps with drift fences (spaced a minimum of 600 m apart). Each pitfall trap set consisted of four plastic buckets (100 L; diameter: 59 cm; height: 71 cm) sunk in the ground and arranged in a “Y” shape, with a central bucket connected to each of three peripheral buckets by a 10 m plastic drift fence (Figure S1). Samplings were conducted 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). All traps remained open for nine consecutive days during each sampling event. Each captured individual was transported to field laboratory, marked individually by toe clipping and released in their original capture location in the morning of the next day. Toe clipping followed approved protocols and was provided for in the field permit. Marked individuals recaptured in the same sampling event were not considered in the analysis. We recorded: body mass, snout-vent length (SVL), and tail length (TaL). Additional information on sex, evidence of regenerated or broken tail, presence/absence of eggs, and natural marks was also recorded. Voucher specimens were anesthetized and killed with an overdose of thiopental, fixed in

10% formalin, and conserved in 70% alcohol. They are housed in the zoological collections of the Universidade Federal de Mato Grosso do Sul (ZUFMS, Campo Grande, Brazil).

Diversity measures and statistical analysis

We assessed sampling saturation overall and per season using rarefaction and extrapolation curves based on Hill numbers (Chao et al. 2014). We also estimated species richness per season with two non-parametric richness estimators: one abundance-based (Chao 1) and one incidence-based (Chao 2). Sampling curves were generated using the *iNext* R package (Hsieh et al. 2016).

Although taxonomic/functional diversity is frequently used in ecology, there are open questions as to the best ways of how to measure it (e.g. Tucker et al. 2016). Several authors argued that diversity cannot be summarized by a single metric, because mechanisms driving community patterns did not affect in the same way aspects of richness, divergence, and regularity. So, we choose metrics that account for presence-absence and abundance separately. Lizard richness and abundance were the total number of species and individuals by species captured in each site, respectively. We tested whether species richness and abundance varied between seasons using linear mixed-effect models (LMM). Season (two levels) was included as fixed effect and site was included as a random effect. Statistical significance was obtained using anova function. As there might be a lag between rainy season and flooding in the southern Pantanal, we also tested if richness and abundance varied over the months using LMMs. Site was also included as a random effect in these models. Significant interactions were investigated with a Tukey's test with Bonferroni correction. Abundance data were square-root transformed to reduce the heteroscedasticity and to give less

weight to the few dominant taxa. LMMs were computed using the *nlme* R package (Pinheiro et al. 2020). We used a permutational variance analysis (PERMANOVA) to assess differences in lizard community composition between rainy and dry seasons, based on Bray-Curtis dissimilarity. Before PERMANOVA, quantitative lizard data was Hellinger-transformed (Legendre & Gallagher 2001). A compound graph (Dambros 2014) was used to characterize species distribution across seasons.

To quantify changes in functional diversity across seasons, we calculated two components: functional richness (FRic) and functional evenness (FEve) (Villéger et al. 2008). Functional richness is independent of species' abundance, while FEve value is proportional to species' relative abundance. All metrics were based on trait variation rates instead of species' mean trait values, and included intraspecific variability (Violle et al. 2012). Thus, we built three matrices as recommended by Taudiere & Violle (2016): i) a trait matrix where columns and rows were traits and individuals, respectively; ii) a matrix assigning a site name to each individual; iii) a matrix assigning a species name to each individual. Trait matrices included data reflecting habitat use and resource use requirements (body mass, SVL, and TaL). Body size is correlated with foraging mode, while tail length may be used as an indicator for primary microhabitat (i.e. fossorial, terrestrial, scansorial; Pianka et al. 2017). Because tail autotomy can vary markedly with age and across lizard taxa (Bateman & Fleming 2009), we included only individuals without regenerated or broken tails in the functional diversity analyses. Body mass was measured to reflect reproductive aspects, such as clutch size (Meiri et al. 2020). To facilitate comparison between the different metrics, the magnitude of the differences was calculated based on standardized effect size (SES). So, we can

estimate the extent of over- or underdispersion in functional metrics. Standardized effects were derived from a null model that randomizes trait values for all individuals in all communities—regional model (Taudiere & Violle 2016). We used a paired Student's t test to compare SES. FRic/FEve between dry and rainy season.

RESULTS

Summarizing data over all sampled sites, we found a total of 810 lizards from 13 species (Table I). Functional diversity indices were calculated based on three morphological measurements from 717 individual captured at the seven sites—note that some specimens had regenerated

or broken tails and could not be included in the analyses. The most abundant species was *Ameivula* aff. *ocellifera* (*Ameivula* sp. 2 of Arias et al. 2018), corresponding to 52% of all collected individuals (Table I). Throughout the study period recaptures were recorded for only two species: *A. aff. ocellifera* (N = 39) and *Vanzosaura rubricauda* (N = 3). However, for the former, many recaptures (61%) occurred in the same sampling event. Fifteen individuals of *A. aff. ocellifera* were recaptured at the same sites at intervals of three to eight months, and three individuals were recaptured at different sites, from 2 to 4 km apart. All recaptures of *V. rubricauda* occurred at the same site at intervals of two to three months. Table SI summarizes additional

Table I. Composition and abundance of lizard communities by season in the Nhimirim Ranch in Pantanal, Brazil, from February 2005 and March 2006.

Family and Species	Season	
	Dry	Rainy
Dactyloidae		
<i>Norops meridionalis</i> (Boettger, 1885)	1	
Gymnophthalmidae		
<i>Bachia bresslaui</i> (Amaral,1935)	1	1
<i>Micrablepharus maximiliani</i> (Reinhardt & Luetken, 1862)	10	9
<i>Vanzosaura rubricauda</i> (Boulenger, 1902)	190	90
Polychrotidae		
<i>Polychrus acutirostris</i> Spix, 1825	1	
Scincidae		
<i>Manciola guaporicola</i> (Dunn, 1935)	4	15
<i>Notomabuya frenata</i> (Cope, 1862)	2	1
<i>Copeoglossum nigropunctatum</i> (Spix, 1825)		1
Sphaerodactylidae		
<i>Coleodactylus brachystoma</i> (Amaral, 1935)	6	1
Teiidae		
<i>Ameiva ameiva</i> (Linnaeus, 1758)	13	16
<i>Ameiva</i> sp.	5	9
<i>Ameivula</i> aff. <i>ocellifera</i> (Spix, 1825)	182	241
Tropiduridae		
<i>Tropidurus lagunablanca</i> Carvalho,2016	7	4

data about sex, age class, and reproductive period of the individuals captured along the study. Observed species richness was similar to estimated richness for both estimators (Table II). Rarefaction curves (individual-based and sample-based) were similar between dry and rainy seasons (Figure 1).

Species richness did not differ across seasons ($F_{1,48} = 0.011$; $p = 0.915$) or months ($F_{7,42} = 1.951$; $p = 0.094$). Lizard abundance varied among sampling months ($F_{7,42} = 7.484$; $p < 0.001$), but did not differ between rainy and dry season ($F_{1,48} = 0.747$; $p = 0.746$). Post hoc tests indicated lower values of abundance in June of 2005 (one month after drawdown period) and at the end of the rainy season of 2006 ($p < 0.01$; Figure 2).

Comparison of communities did not show significant differences in species composition associated with season (PERMANOVA, $F_{1,7} = 3.044$; $p = 0.081$). Four out of 13 species were recorded in all sampling events (Figure 3). Based on SES, functional diversity metrics exhibited random distributions (Figure 4). Although the variation of FRic was lower in the rainy season, both functional richness and evenness did not differ between seasons (FRic: $t = 1.233$, $df = 6$, $p = 0.131$; FEve: $t = 1.298$, $df = 6$, $p = 0.129$). A post hoc power analysis indicated that more than 11 sites would be needed to have adequate power to test differences given the observed effect sizes.

DISCUSSION

In this study, we found no relationship between richness (taxonomic or functional) and seasonal flooding; however, lizard abundance declined at drawdown period. At the community level, the absence of trait clustering indicates that flood did not directly influence habitat use and resource use requirements, herein described by snout-vent length, tail length, and body mass. However, assembly mechanisms within communities operate on various spatial scales, and lizard communities have shown divergent trends between local and regional scales (Rabosky et al. 2007, Ramm et al. 2018). So, the idea of no association between lizard communities and flood pulse may be not necessarily true. If analyses rely on different spatial scales, inappropriate species pool can potentially bias the likelihood of detecting a pattern of clustering or overdispersion (Cadotte et al. 2017). In the Pantanal, there is recent evidence suggesting that flooding effects occur in a direct and localized way in snake assemblages (Piatti et al. 2019). Thus, the assessment of other traits related to behavior and reproduction, integrating intraspecific variability at different scales, would be particularly useful to understand lizard responses in unpredictable environments.

The recorded species richness in the Nhumirim Ranch agree with other estimates of lizard species richness found in surrounding uplands of the Cerrado-Pantanal border (15–20 spp.; Uetanabaro et al. 2007, Nogueira et al.

Table II. Lizard species richness, lizard abundance, and abundance (Chao 1)/incidence based (Chao 2) richness estimators across different seasons.

	Species recorded	Total abundance	Chao 1 (95% CI)	Chao 2 (95% CI)
All period	13	810	17(13–45)	17(13–42)
Dry season	12	422	16(12–44)	13(12–22)
Rainy season	11	388	17(11–40)	17(11–49)

2009, Valdujo et al. 2009) or in seasonal flooded areas in the Cerrado-Amazon transition (14 spp.; Mesquita et al. 2015). Rarefaction curves suggested that species richness was similar for both seasons (~ 17 spp.), however confidence intervals for the rainy season were particularly large. Although we lack knowledge about lizard dispersal capacities across taxa, conditions in the flooded matrix probably constrain dispersal to varying extents for different species. So, strictly terrestrial species may face a reduction of habitats at rainy season. A subtle issue here is that imperfect detection could have influenced our results. For example, the low abundance or absence of fossorial species would be likely a limitation of the sampling methodology. Functional metrics seem to be robust to imperfect detection, although detectability has the potential to bias trait-environment relationship

(Roth et al. 2018). Absences of primarily arboreal families—such as Iguanidae, Gekkonidae, and Phyllodactylidae— and semi-aquatic lizards, such as *Dracaena paraguayensis*, may also stem from our sampling method. However, only few species (between one and three) belonging to these families have been recorded in the Pantanal ecoregion so far (Ferreira et al. 2017). So, such absences (even considering they are truly sampling artifacts) would have only a modest bias in our level of trait variance (i.e. functional richness).

It is interesting to note that the community structure recorded in the Nhumirim Ranch seems quite similar to available studies for other open habitats of South America. Overall, there is much overlapping among the genera recorded in open formations (e.g. *Ameiva*, *Micrablepharus*, *Notomabuya*, *Tropidurus*; Nogueira et al. 2009,

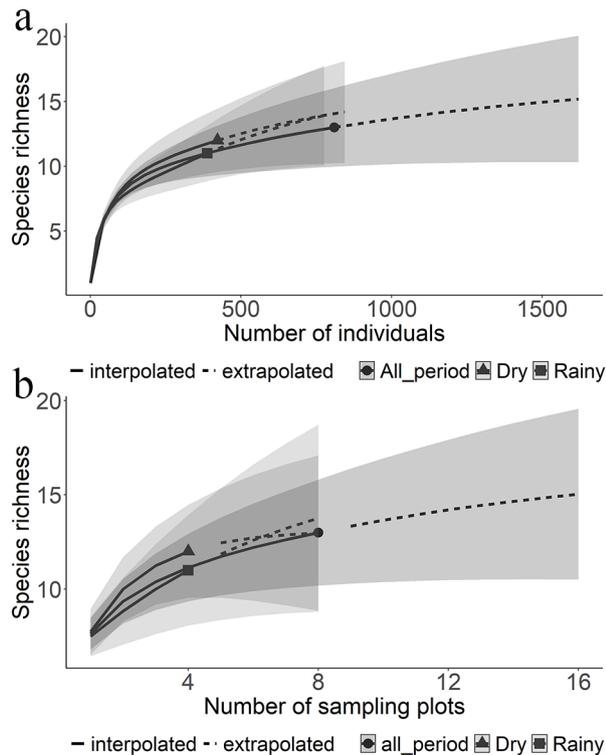


Figure 1. Individual-based (a) and sampled-size based (b) rarefaction (solid line segment) and extrapolation (dotted line segment) sampling curves for lizard data set. Shaded areas represent 95% confidence intervals

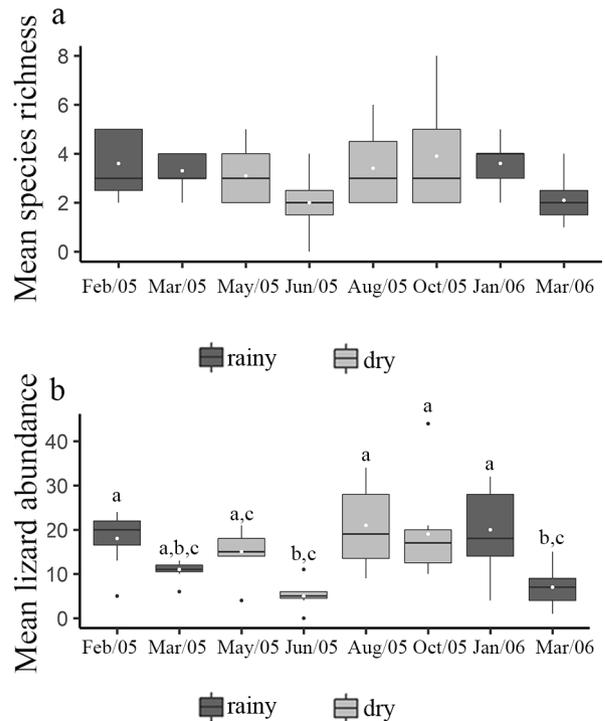


Figure 2. Variation of: (a) species richness; (b) lizard abundance in the Nhumirim Ranch, Pantanal, Brazil, from 2005 to 2006. * represent mean values. Different letters mean statistically significant differences.

Mesquita et al. 2015), with some species turnover according to soil heterogeneity, topography, and land use. Many of the lizard species in open habitats could be considered as generalists with widespread distribution. However, there are issues of taxonomic uncertainty and extensive cryptic diversity (i.e. multiple lineages within a species; Fenker et al. 2020). Here, the occurrence of two species in process of formal description (*Ameiva* sp. and *Ameivula* aff. *ocellifera*; V.L. Ferreira, personal communication) highlights that disentangling unrecognized taxa is important to relate diversity and disturbances, allowing more informed conclusions.

According to our findings, it seems that transition from rainy to dry season represents an important constraint on lizards in the Pantanal ecoregion. There was a significant decrease in lizard abundance during months that correspond to the end of drawdown period, being the captures mainly of *Vanzosaura rubricauda* (~70%). In the drawdown period, the plains are still moist, but residual flood water

is concentrated in small puddles and channels. Moreover, large aggregations of both resident and migratory birds close to wet environments are common when the water level drops, making fish and other aquatic organisms easy preys (Donatelli et al. 2017). Many bird species nest at the beginning of the dry season, and once aquatic prey availability in temporary puddles is depleted, they are likely feed on terrestrial vertebrates in surrounding areas. Although we lacked specific information on predation rates upon lizards, a plausible hypothesis is that abundance patterns are linked to seasonal predation associated with flood ebb. It is well appreciated that predation pressure is an important driver of lizards' behavior and body size (Downes & Hoefer 2004, Schalk & Cove 2018). In addition, we have evidence in northern Pantanal that predation upon lizards is a common event during bird breeding season, even among primarily insectivorous birds (Smaniotto et al. 2017). Therefore, lizards' lower incidence could be related predation pressure.

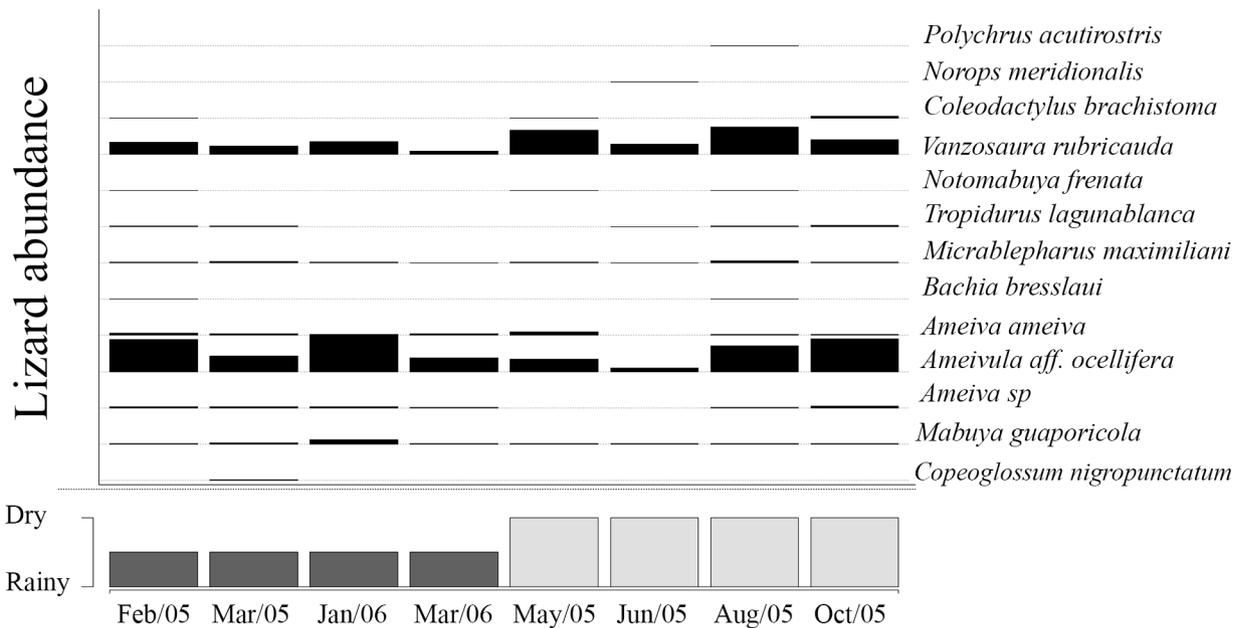


Figure 3. Distribution of lizard species in relation to season in the Nhumirim Ranch, Pantanal, Brazil. Bar thickness is proportional to lizard abundance (full bar ~ 90 individuals). Sampling in the rainy season (dark-gray bars); Sampling in the dry season (light-gray bars).

This idea did not exclude other effects that may act simultaneously to flood ebb, such as decrease in the food availability. Stable isotope analyses have shown that terrestrial lizards may receive trophic subsidy from both terrestrial and aquatic sources (Martins et al. 2021), but there are effects of lizard size and species identity (Magnusson et al. 2001). So, decreases in the food availability, at a particular stage of the flood cycle, may constrain lizard abundance to varying extents for different species and even for cohorts of the same species (Moreira et al. 2022).

Random patterns of functional richness indicate that, alternatively: i) flood disturbance was not strong enough to constrain species with

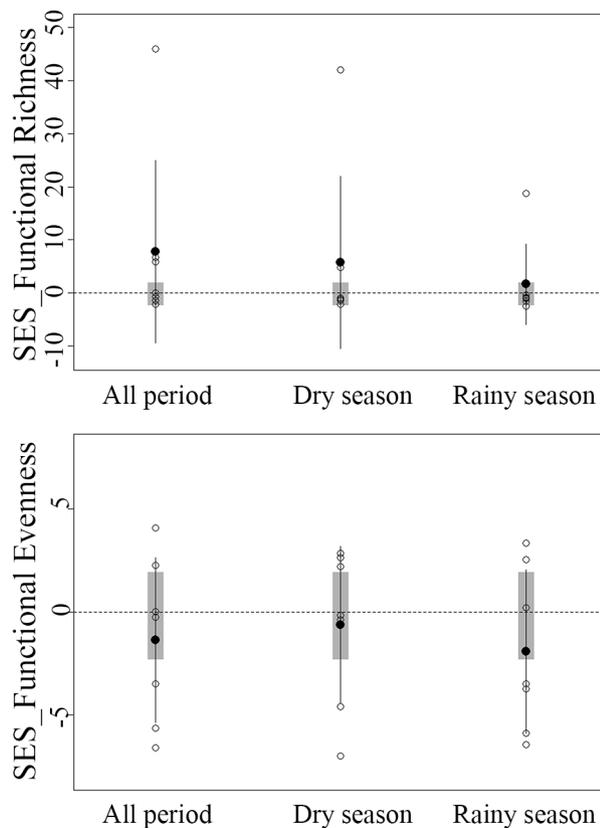


Figure 4. Variation of standardized effect size (SES) for functional diversity metrics among lizard communities of Nhumirim Ranch, Pantanal Brazil. Black dots and segments: mean and standard deviation of community values, gray box: distribution under a null model.

extreme trait values or, ii) the chosen traits were not good enough to perceive flood effects. Since the Quaternary, fauna and flora have faced an unstable environment in the Pantanal (Junk et al. 2006). Flood amplitude is known to vary a lot at inter-annual scales (Junk et al. 2011) and lizards should be able to cope with periods of extreme flood or extreme drought, similarly to other organisms living in the floodplain. Our results were based on a restricted study period (~ 1y), and this snapshot view must be recognized as a constraint to find trends of seasonal flooding. In field studies, long-term assessments are rare, because high temporal replication is a challenging task. Recent evidence shows that lizard densities are more associated to multiple factors acting on different short-term snapshots than by accumulated long-term changes in savannas subject to seasonal disturbance (Souza et al. 2021). We cannot rule out, also, the possibility that other traits may restrict the occurrence of some lizard species in flooded areas. Our traits' choice was based on a specific biological hypothesis (habitat filtering; Trimble & van Aarde 2014, Berriozabal-Islas et al. 2017), besides being subject to field constraints (time and manpower available). In addition, the lack of significance for the functional diversity metrics may be a function of the low sample sizes. All these limitations could have influenced our results and should be considered in future studies on the topic. Still, it would be valuable to investigate data of the same season from different years to confirm issues of pattern predictability.

In conclusion, we showed that lizard communities seem to be resilient to seasonal variations in the Pantanal. However, variations in abundance suggest that flood regimes may regulate ecological factors, such as biotic interactions. Lizards are often important links for energy transfer within Neotropical ecosystems.

So, including traits related to food acquisition and predator avoidance could provide new insights into the effects of different seasons on lizard communities.

Acknowledgments

We thank researchers and students from the Universidade Federal de Mato Grosso do Sul (UFMS) and Empresa Brasileira de Pesquisa Agropecuária—unidade Pantanal (Embrapa-Pantanal)—for help with field sampling. We are grateful to Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis and Sistema de Autorização e Informação em Biodiversidade for the collecting permit (Sisbio #49877). We thank Embrapa-Pantanal, UFMS, and Centro de Pesquisa do Pantanal (CPP) and Ministério do Meio Ambiente (MMA) for logistic and/or financial support. KRS and LGG are grateful to Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES), Fundação de Amparo à Pesquisa do Estado de Mato Grosso (FAPEMAT), and Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) for MSc fellowships. VLF and CS thank CNPq for researcher fellowship (PQ2 #309305/2018-7 and #3123038/2018-1, respectively) and partial support (CNPq # 480414/2009-2).

REFERENCES

- ARIAS FJ, RECODER R, ÁLVAREZ BB, ETHCEPARE E, QUILPIDOR M, LOBO F & RODRIGUES MT. 2018. Diversity of teiid lizards from Gran Chaco and Western Cerrado (Squamata: Teiidae). *Zool Scr* 47: 144-158.
- BATEMAN PW & FLEMING PA. 2009. To cut a long tail short: A review of lizard caudal autotomy studies carried out over the last 20 years. *J Zool* 277: 1-14.
- BENÍCIO RA, PASSOS DC, MENCÍA A & ORTEGA Z. 2021. Microhabitat selection of the poorly known lizard *Tropidurus lagunablanca* (Squamata: Tropicuridae) in the Pantanal, Brazil. *Pap Avulsos Zool* 61: e20216118.
- BERRIOZABAL-ISLAS C, BADILLO-SALDAÑA LM, RAMÍREZ-BAUTISTA A & MORENO CE. 2017. Effects of habitat disturbance on lizard functional diversity in a tropical dry forest of the pacific coast of Mexico. *Trop Conserv Sci* 10: 1-11.
- CADOTTE MW, DAVIES TJ & PERES-NETO PR. 2017. Why phylogenies do not always predict ecological differences? *Ecol Monogr* 87: 535-551.
- CHAO A, GOTELLI NJ, HSIEH TC, SANDER EL, MA KH, COLWELL RK & ELLINSON AM. 2014. Rarefaction and extrapolation with Hill numbers: A framework for sampling and estimation in species diversity studies. *Ecol Monogr* 84: 45-67.
- DAMBROS C. 2014. poncho.R. <https://raw.githubusercontent.com/csdambros/R-functions/master/poncho.R>. Accessed 4 Apr 2020.
- DELATORRE M, CUNHA N, RAIZER J & FERREIRA VL. 2015. Evidence of stochasticity driving anuran metacommunity structure in the Pantanal wetlands. *Freshw Biol* 60: 2197-2207.
- DONATELLI RJ, EATON DP, SEMENTILI-CARDOSO G, VIANNA RM, GEROTTI RW, RODRIGUES FG & MARTINS RM. 2017. Temporal and spatial variation of richness and abundance of the community of birds in the Pantanal wetlands of Nhecolândia (Mato Grosso do Sul, Brazil). *Rev Biol Trop* 65: 1358-1380.
- DORADO-RODRIGUES TF, PANSONATO A & STRÜSSMANN C. 2018. Anfíbios e répteis em municípios da Bacia do Rio Cuiabá. In: FIGUEIREDO DM, DORES EFGC & LIMA ZM (Eds), *Bacia do Rio Cuiabá: uma abordagem socioambiental*, Cuiabá: EdUFMT, p. 461-496.
- DOWNES S & HOEFER AM. 2004. Antipredatory behaviour in lizards: Interactions between group size and predation risk. *Anim Behav* 67: 485-492.
- FENKER J ET AL. 2020. Evolutionary history of Neotropical savannas geographically concentrates species, phylogenetic and functional diversity of lizards. *J Biogeogr* 1-13.
- FERREIRA VL ET AL. 2017. Répteis do Mato Grosso do Sul, Brasil. *Iheringia - Ser Zool* 107: 1-13.
- HSIEH TC, MA KH & CHAO A. 2016. iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). *Methods Ecol Evol* 7: 1451-1456.
- JUNK WJ, CUNHA CN, WANTZEN KM, PETERMANN P, STRÜSSMANN C, MARQUES MI & ADIS J. 2006. Biodiversity and its conservation in the Pantanal of Mato Grosso, Brazil. *Aquat Sci* 68: 278-309.
- JUNK WJ, DA SILVA CJ, NUNES DA CUNHA C & WANTZEN KM. 2011. The Pantanal: Ecology, biodiversity and sustainable management of a large neotropical wetlands. Moscow: Pensoft Publishers, 870 p.
- LEGENDRE P & GALLAGHER ED. 2001. Ecologically meaningful transformations for ordination of species data. *Oecologia* 129: 271-280.
- MAGNUSSON WE, LIMA AP, FARIA AS, VICTORIA RL & MARTINELLI LA. 2001. Size and carbon acquisition in lizards from Amazonian savanna: Evidence from isotope analysis. *Ecology* 82: 1772-1780.

- MARTINS LS, COSTA-SCHMIDT LE, GARCIA AM, BASTOS RF, REBELATO MM & TOZETTI AM. 2021. The contribution of aquatic plants to the trophic ecology of a sand dune lizard in southern Brazil. *S Am J Herpetol* 21: 12-24.
- MCDONALD PJ, PAVEY CR & FYFE G. 2012. The lizard fauna of litter mats in the stony desert of the southern Northern Territory. *Aust J Zool* 60: 166-172.
- MESQUITA DO, COLLI GR, PANTOJA DL, SHEPARD DB, VIEIRA GHC & VITT LJ. 2015. Juxtaposition and disturbance: Disentangling the determinants of lizard community structure. *Biotropica* 47: 595-605.
- MEIRI S ET AL. 2020. The global diversity and distribution of lizard clutch sizes. *Glob Ecol Biogeogr* 29: 1515-1530.
- MOREIRA LFB, DORADO-RODRIGUES TF, FERREIRA VL & STRÜSSMANN C. 2017. An inter-dependence of flood and drought: Disentangling amphibian beta diversity in seasonal floodplains. *Mar Freshw Res* 68: 2115-2122.
- MOREIRA LFB, SMANIOTTO NP, FERREIRA VL & STRÜSSMANN C. 2022. The flood or the woods: natural history of the red-tailed vanzosaur. *Herpetol Conserv Biol* 17: 85-94.
- MOUILLOT D, GRAHAM NAJ, VILLÉGER S, MASON NWH & BELLWOOD DR. 2013. A functional approach reveals community responses to disturbances. *Trends Ecol Evol* 28: 167-177.
- NOGUEIRA C, COLLI GR & MARTINS M. 2009. Local richness and distribution of the lizard fauna in natural habitat mosaics of the Brazilian Cerrado. *Austral Ecol* 34: 83-96.
- OCCOCK JF, KINGSFORD RT, PENMAN TD & ROWLEY JLL. 2014. Frogs during the flood: Differential behaviours of two amphibian species in a dryland floodplain wetland. *Austral Ecol* 39: 929-940.
- OLIVEIRA APG, MACHADO R, RIBEIRO AA, MIOTO CL, JÚNIOR JM, SAAD AR, SÍGOLO JB & FILHO ACP. 2018. The expression of neotectonics in the Pantanal da Nhecolândia, state of Mato Grosso do Sul-Brazil. *An Acad Bras Cienc* 90: 1293-1308.
- PIANKA ER, VITT LJ, PELEGRIN N, FITZGERALD DB & WINEMILLER KO. 2017. Toward a periodic table of niches, or exploring the lizard niche hypervolume. *Am Nat* 190: 601-616.
- PIATTI L, ROSAUER DF, NOGUEIRA CC, STRÜSSMANN C, FERREIRA VL & MARTINS M. 2019. Snake diversity in floodplains of central South America: Is flood pulse the principal driver? *Acta Oecol* 97: 34-41.
- PINHEIRO J ET AL. 2020. nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-147. <https://CRAN.R-project.org/package=nlme>.
- POTT A, OLIVEIRA A, DAMASCENO-JUNIOR G & SILVA J. 2011. Plant diversity of the Pantanal wetland. *Brazilian J Biol* 71: 265-273.
- RABOSKY DL, REID J, COWAN MA & FOULKES J. 2007. Overdispersion of body size in Australian desert lizard communities at local scales only: No evidence for the Narcissus effect. *Oecologia* 154: 561-570.
- RAFFARD A, CUCHEROUSET J, PRUNIER JG, LOOT G, SANTOUL F & BLANCHET S. 2019. Variability of functional traits and their syndromes in a freshwater fish species (*Phoxinus phoxinus*): The role of adaptive and nonadaptive processes. *Ecol Evol* 9: 2833-2846.
- RAMM T, CANTALAPIEDRA JL, WAGNER P, PENNER J, RÖDEL MO & MÜLLER J. 2018. Divergent trends in functional and phylogenetic structure in reptile communities across Africa. *Nat Commun* 9: 4697.
- ROBINSON TMP, LA PIERRE KJ, VADEBONCOEUR MA, BYRNE KM, THOMEY ML & COLBY SE. 2013. Seasonal, not annual precipitation drives community productivity across ecosystems. *Oikos* 122: 727-738.
- ROTH T, ALAN E, PEARMAN PB, AMRHEIN V. 2018. Functional ecology and imperfect detection of species. *Methods Ecol Evol* 9: 917-928.
- RUSCH TW & ANGILLETTA MJ. 2017. Competition during thermoregulation altered the body temperatures and hormone levels of lizards. *Funct Ecol* 31: 1519-1528.
- RYAN MJ, LATELLA IM, GIERMAKOWSKI JT, SNELL H, POE S, PANGLE RE, GEHRES N, POCKMAN WT & MCDOWELL NG. 2016. Too dry for lizards: short-term rainfall influence on lizard microhabitat use in an experimental rainfall manipulation within a piñon-juniper. *Funct Ecol* 30: 964-973.
- SCHALK CM & COVE MV. 2018. Squamates as prey: Predator diversity patterns and predator-prey size relationships. *Food Webs* 17: e00103.
- SMANIOTTO NP, MOREIRA LFB & DORADO-RODRIGUES TF. 2017. Registro de predação de espécies de répteis por *Guiraguira* (Aves: Cuculidae). *Neotrop Biol Conserv* 12: 71-74.
- SORIANO B & ALVES M. 2005. Boletim agrometeorológico ano 2002 para a sub-região da Nhecolândia, Pantanal, Mato Grosso do Sul, Brasil. Corumbá: Embrapa, 28 p.
- SOUZA E, LIMA AP, MAGNUSSON WE, KAWASHITA-RIBEIRO R, FADINI R, GHIZONI R, GANANÇA P & FRAGA R. 2021. Short-and long-term effects of fire and vegetation cover on four lizard species in amazonian savannas. *Can J Zool* 99: 173-182.

STRÜSSMANN C, PRADO CPA, FERREIRA VL & RIBEIRO RAK. 2011. Diversity, ecology, management and conservation of amphibians and reptiles of the Brazilian Pantanal: a review. In: JUNK WJ, DA SILVA CJ, NUNES DA CUNHA C & WANTZEN KM (Eds), *The Pantanal: Ecology, biodiversity and sustainable management of a large neotropical wetland*, Moscow: Pensoft Publishers, p. 497-522.

TAUDIERE A & VIOLLE C. 2016. cati: an R package using functional traits to detect and quantify multi-level community assembly processes. *Ecography* 39: 699-708.

TREILIBS CE, PAVEY CR, GARDNER MG, ANSARI MH & BULL CM. 2019. Spatial dynamics and burrow occupancy in a desert lizard floodplain specialist, *Liopholis slateri*. *J Arid Environ* 167: 8-17.

TRIMBLE MJ & VAN AARDE RJ. 2014. Amphibian and reptile communities and functional groups over a land-use gradient in a coastal tropical forest landscape of high richness and endemism. *Anim Conserv* 17: 441-453.

TSIANOU MA & KALLIMANIS AS. 2016. Different species traits produce diverse spatial functional diversity patterns of amphibians. *Biodivers Conserv* 25: 117-132.

TUCKER CM ET AL. 2016. A guide to phylogenetic metrics for conservation, community ecology and macroecology. *Biol Rev* 92: 405-417.

UETANABARO M, SOUZA FL, LANDGREF-FILHO P, BEDA AF & BRANDÃO RA. 2007. Amphibians and reptiles of the Serra da Bodoquena National Park, Mato Grosso do Sul, central Brazil. *Biota Neotrop* 7: 279-289.

VALDUJO PH, NOGUEIRA CC, BAUMGARTEN L, RODRIGUES FHG, BRANDÃO RA, ETEROVIC A, RAMOS-NETO MB & MARQUES OAV. 2009. Squamate reptiles from Parque Nacional das Emas and surroundings, Cerrado of Central Brazil. *Check List* 5: 405-417.

VILLÉGER S, MASON H & MOUILLOT D. 2008. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology* 89: 2290-2301.

VIOLLE C, ENQUIST BJ, MCGILL BJ, JIANG L, ALBERT CH, HULSHOF C, JUNG V & MESSIER J. 2012. The return of the variance: Intraspecific variability in community ecology. *Trends Ecol Evol* 27: 244-252.

SUPPLEMENTARY MATERIAL

Figure S1.
Table S1.

How to cite

SILVA KR, GOMES LG, FERREIRA VL, STRÜSSMANN C & MOREIRA LFB. 2022. Seasonal changes in taxonomic and functional diversity of lizard communities in southern Brazilian Pantanal. *An Acad Bras Cienc* 94: e20201793. DOI 10.1590/0001-376520220201793.

Manuscript received on November 17, 2020;
accepted for publication on January 17, 2022

KAROLINE R. DA SILVA¹

<https://orcid.org/0000-0001-7848-5763>

LIARA G. GOMES¹

<https://orcid.org/0000-0001-6784-7095>

VANDA L. FERREIRA²

<https://orcid.org/0000-0001-5032-6752>

CHRISTINE STRÜSSMANN³

<https://orcid.org/0000-0001-9880-9489>

LEONARDO F.B. MOREIRA⁴

<https://orcid.org/0000-0002-2753-9933>

¹Programa de Pós-Graduação em Ecologia e Conservação da Biodiversidade, Universidade Federal de Mato Grosso/UFMT, Instituto de Biociências, Av. Fernando Corrêa da Costa, 2367, 78060-900 Cuiabá, MT, Brazil

²Universidade Federal de Mato Grosso do Sul/UFMS, Instituto de Biociências, Av. Costa e Silva, s/n, 79070-900 Campo Grande, MS, Brazil

³Universidade Federal de Mato Grosso/UFMT, Faculdade de Medicina Veterinária, Av. Fernando Corrêa da Costa, 2367, 78060-900 Cuiabá, MT, Brazil

⁴Instituto Nacional de Pesquisa do Pantanal/INPP, Museu Paraense Emílio Goeldi, Av. Fernando Corrêa da Costa, 2367, 78060-900 Cuiabá, MS, Brazil

Correspondence to: **Leonardo F.B. Moreira**
E-mail: leonardobm@gmail.com

Author contributions

KRS: Conceptualization, Formal analysis, Data Curation, Methodology, Visualization, Writing—original draft. LGG: Formal analysis, Writing—review & editing. VLF: Funding acquisition, Project administration, Data Curation, Writing—review & editing. CS: Project administration, Data Curation, Writing—review & editing. LFBM: Conceptualization, Validation, Formal analysis, Supervision, Writing—original draft, Writing—review & editing.

