Partitioning tadpole beta diversity in highland ponds with different hydroperiods

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Abstract: Pond hydroperiod and other aspects of environmental heterogeneity play important roles in metacommunity organization in freshwater systems. We examined tadpole species richness and dissimilarities among assemblages at different hydroperiods (3, 7, and 13 mo) in highland ponds in the Araucaria moist forest ecoregion of southern Brazil. We also investigated whether β diversity components changed in accordance with spatial and environmental factors. We sampled tadpoles at 18 ponds between September 2012 and April 2013. Tadpole species richness was lower in permanent than in temporary ponds, but pond hydroperiod was not associated with tadpole abundance and species dissimilarities. β diversity was almost completely caused by species replacement associated with pond area, presence of predatory fish, and type of margin. Despite its small contribution, the nestedness component was associated with water depth and geographic patterns. Our study suggests that tadpole communities in the highlands of Araucaria moist forests are niche structured.

Key words: species replacement, nestedness, environmental heterogeneity, Amphibia, grasslands, Araucaria moist forest

Understanding the factors that shape communities at different spatial and temporal scales has been a challenge in freshwater community ecology (Heino et al. 2015). Current views emphasize that environmental heterogeneity is an important variable associated with the local and regional control of community structure (Landeiro et al. 2012, Erős et al. 2014, Datry et al. 2016), despite the fact that dispersal limitations for most organisms are poorly understood. Such bias can complicate inferences when drawing conclusions about processes structuring freshwater communities.

Despite its long history, the relationship between ecological gradients and β diversity has recently benefited from partitioning frameworks (Legendre 2014). These new components of β diversity (namely, nestedness and species replacement) are opening up a range of new opportunities to explain processes that structure communities (Leprieur et al. 2011, da Silva et al. 2014). A nestedness pattern occurs when the biota of sites with lower species richness are subsets of the biota at richer sites (Ulrich and Gotelli 2007). Such pattern is usually attributed to different habitat quality, and selective colonization or extinction (Leprieur et al. 2011, Moreira and Maltchik 2015). Communities dominated by species replacement or balanced variation in abundance may be the result of environmental filtering, limited dispersal, and skipped breeding (Werner et al. 2007b, Melo et al. 2009).

Pond-breeding organisms, such as amphibians and aquatic invertebrates, offer an effective model for a metacommunity approach because they depend on habitats that are clumped in space (McAbendroth et al. 2005, Griffiths et al. 2010). Aquatic larval stages are influenced by environmental variation within ponds, such as water chemistry, pond area, and presence of fish (Richter-Boix et al. 2007, Werner et al. 2007a, Both et al. 2009). At same time, these breeding sites are often situated within a landscape consisting of habitats under varying degrees of modification (Youngquist and Boone 2014, Moreira et al. 2016a). Thus, dispersing individuals need to move through a semi-natural, and often hostile, environment. Environmental heterogeneity, such as terrestrial landscapes surrounding ponds, is an important driver of amphibian dispersal (Cosentino et al. 2011, Cline and Hunter 2014).

A recurrent pattern in freshwater environments is the positive relationship between species richness and hydroperiod (Werner et al. 2007a, Both et al. 2011, Fernandes et al. 2014). Pond hydroperiod affects amphibian occurrence and reproduction (Werner et al. 2007b, Amburgey et al. 2012). Ideally, hydroperiod must coincide with egg-laying, hatching, larval development, and metamorphosis (Bunnell and Ciraolo 2010). Short hydroperiod can exclude species with slow rates of development (Babbitt et al. 2003), but lon-

ger hydroperiod can increase the abundance of fish, thereby enhancing competition and predation on amphibian larvae (Finlay and Vredenburg 2007, Hartel et al. 2007). Some species display strategies, such as egg deposition in foam nests, explosive reproductive activity, and fast larval development to reproduce in short-hydroperiod ponds (Zina 2006, Laufer et al. 2015), whereas others have strategies, such as immobility behavior, large body size, and tadpole unpalatability, that enables them to co-occur with predators in permanent ponds (Teplitsky et al. 2003, Nomura et al. 2011). Despite the importance of hydroperiod in shaping amphibian communities, investigators seldom disentangle the effects of hydroperiod per se from other aspects of environmental heterogeneity (but see Werner et al. 2007a, De Almeida et al. 2015, Valério et al. 2016). Thus, some aspects of environmental heterogeneity often correlated with hydroperiod (i.e., habitat size, structure of vegetation, and microhabitat availability) may have strong and independent effects on freshwater organisms (Eterovick and Barata 2006, Vasconcelos et al. 2009, Moraes et al. 2014).

Many investigators have examined the role of hydroperiod in shaping larval amphibian communities, but few have examined the role of the hydroperiod in shaping the relative importance of the components of β diversity. The main goal of our study was to analyze the influence of hydroperiod on tadpole communities in highland ponds. We compared richness, abundance, and β diversity among ponds in 3 classes of hydroperiod. We also evaluated the influence of the environmental heterogeneity and spatial factors on species distribution. Our hypotheses were: 1) ponds with intermediate hydroperiod will show greater tadpole richness and abundance, 2) β diversity among ponds will be determined mainly by the species replacement associated with hydroperiod, 3) pond hydroperiod will be a better predictor of species composition than other aspects of pond environmental heterogeneity.

METHODS
Study area

We conducted our study in the Araucaria moist forest ecoregion in an area formed by a mosaic of grasslands and Araucaria forest in the municipality of Bom Jesus, state of Rio Grande do Sul, southern Brazil (Fig. 1). The region is a highland (altitude ~1200 m), and its climate is classified as temperate superhumid, with annual rainfall from 1500 to 1700 mm evenly distributed throughout the year and an-
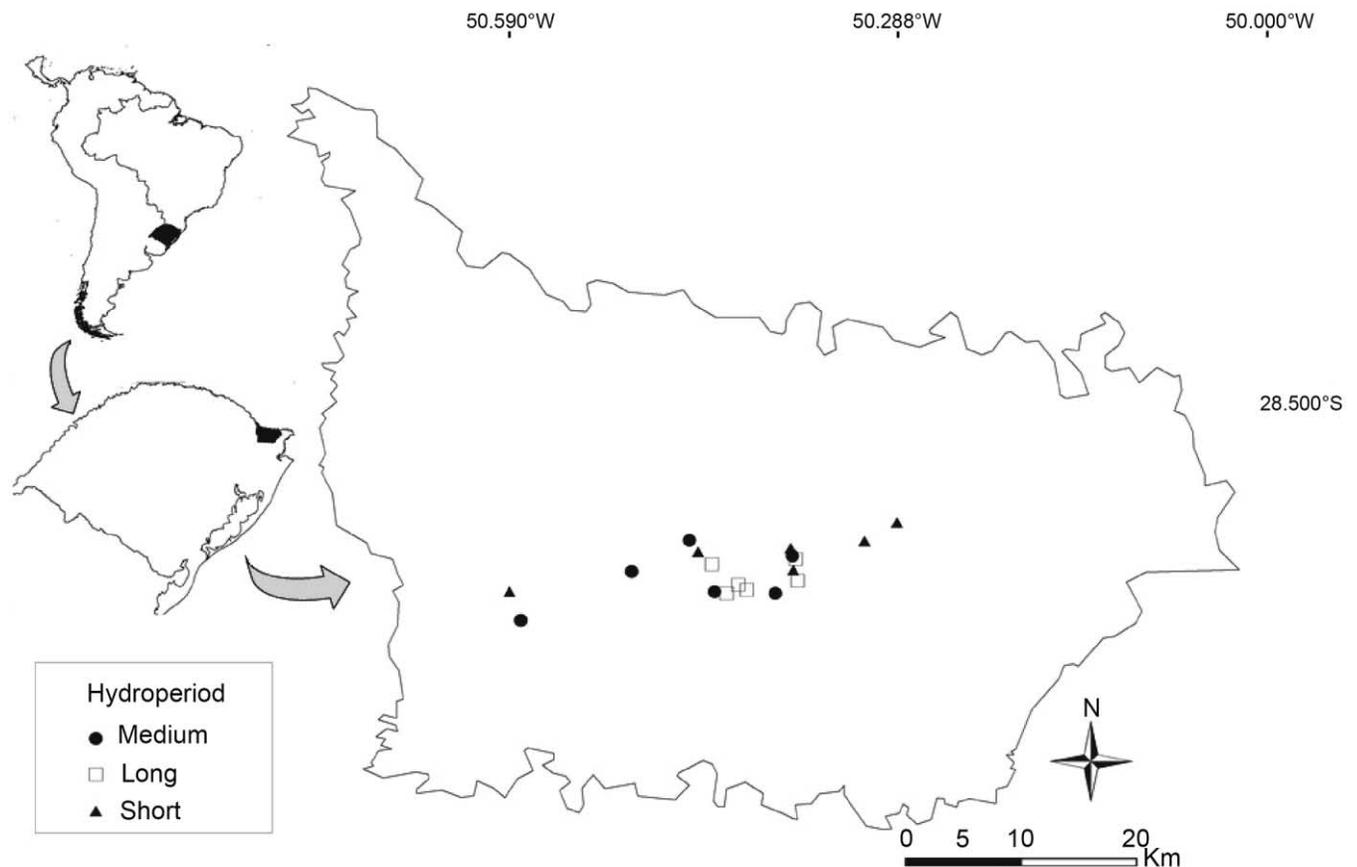
Figure 1. Location of the study area, in Bom Jesus municipality, Araucaria moist forest, Brazil. Dots indicate the 18 ponds sampled.

nual mean temperature of 14.5°C. Temperatures <0°C can occur from April to November because of high altitude.

Sampling design

We selected 18 ponds that were 0.7 to 30 km apart based on 3 criteria: distance between ponds, absence of dams, and pond size. The study ponds were separated by ≥700 m to minimize spatial correlation and were <1.5 ha in area (0.49 ± 0.35). We avoided ponds that had been dammed or dug up because many ponds in the region are modified for pisciculture or cattle ranching. We assigned ponds to 1 of 3 hydroperiod classes based on monthly surveys from September 2012 to October 2013: 1) 6 permanent ponds ('long' ponds) that held water for the entire 13 mo of study; (2) 6 temporary ponds ('medium' ponds) that held water for 7 to 12 mo of the study, and (3) 6 temporary ponds ('short' ponds, hereafter) that held water for <3 mo.

Data collection

We collected tadpoles with a dipnet (30 cm wide, 250-µm mesh) in 3 sampling periods (September and November 2012, April 2013). Sampling allowed us to track variation in breeding phenology, such as species that overwinter as tadpoles, early spring and late summer breeders. The sampling effort was 8 sweeps (~1 m^2) per sampling period distributed in 2 groups: 4 sweeps next to the margins (~50 cm from the margin and 30-cm water depth) and 4 sweeps in the central region of the pond (1-m water depth). Sweeps were pooled into 1 sample/pond (3.5-L plastic bucket). We anesthetized all tadpoles with benzocaine solution and fixed them in situ with 10% formaldehyde.

Within hydroperiod categories, we used 5 additional variables to further characterize environmental heterogeneity: 1) pond area, 2) water depth, 3) type of margin, 4) presence of predatory fish, and 5) abundance of aquatic invertebrate predators. We measured pond area in situ with a global positioning system and water depth with a measuring pole (cm) in the same spot where tadpoles were sampled. We classified margins into 2 groups: flat border and angular border. We considered ponds with angular borders those whose margins were ≥15 cm higher than the surface water. We recorded the presence of predatory fish and abundance of macroinvertebrates during tadpole sampling. We considered 3 groups of potentially predacious invertebrates: dragonfly larvae, giant water bugs, and adult predaceous diving beetles (Kopp and Eterovick 2006, Gambale et al. 2014). To represent unmeasured environmental factors that are spatially structured, we constructed spatial predictors through spatial eigenfunction analysis based on Moran's Eigenvector Maps (MEM; Dray et al. 2006). Geographic coordinates of sampling sites were transformed using principal coordinates of neighbor matrices (Borcard and

Legendre 2002), generating a set of 9 MEMs that ranged from broadest to finest scales (from the perspective of our study 0–5.9 km). We were interested in positive spatial correlations (i.e., more similar values among ponds that are closer together), so we used Moran's I statistic to identify only eigenvectors modeling positive spatial correlation (Dray et al. 2006). We retained 2 broad MEM modeling scales (MEM1 ≈ 5.5 km, MEM2 ≈ 2.5 km) that corresponded to the spatial factors used in the subsequent analysis.

Data analysis

We pooled data from different times in the analysis. Tadpole richness and abundance were the total number of species and individuals sampled in the study, respectively. In practice, the sample size for the analysis was 6 for each hydroperiod class. We performed 1-way analyses of variance (ANOVAs) to test whether tadpole richness and abundance varied among hydroperiod categories. Abundance data were $\sqrt{(x)}$-transformed to meet ANOVA assumptions. We used Tukey's Honestly Significant Difference multiple-comparison tests for differences among species when the main-effect ANOVA was significant.

We calculated β diversity based on Sørensen pairwise dissimilarity (β_{sor}) and partitioned it in 2 components based on methods described by Baselga (2013): 1) species replacement (β_{sim} = Simpson pairwise dissimilarity) indicates change in the composition caused by balanced variation in abundance between the pairs analyzed, and 2) nestedness (β_{nes} = nestedness-resultant dissimilarity) that indicates abundance gradients between the pairs analyzed. First, we computed pairwise matrices for all possible comparisons of hydroperiod classes. Next, we obtained the ratio between nestedness and total β diversity (β_{ratio}). Values <0.5 indicated that species replacement was the most important component, otherwise species dissimilarities would be driven primarily by nestedness (Dobrovolski et al. 2012). To assess the significance of differences, we estimated the distribution of β_{ratio} by taking 100 random samples of 9 ponds. Next, we assessed whether β_{ratio} was larger or smaller than 0.5. p-values corresponded to the probability of obtaining the opposite result by chance. β diversity indices were computed with the *beta.div.comp* function in *adespatial* package (Dray et al. 2016) in R (version 3.2.0; R Project for Statistical Computing, Vienna, Austria).

Hydroperiod, other measures of environmental heterogeneity, and spatial factors were considered to explain the variation contained in the dissimilarity matrices. Potential correlation of variables was explored to avoid collinearity in models (Table S1). A distance-based redundancy analysis (dbRDA) was used to investigate the relationships between β diversity components and the explanatory variables (Legendre 2014). The models were submitted to a backward-selection procedure, based on the adjusted R^2 statistic. All candidate models for turnover and nestedness components

are available in the supplementary material (Tables S2, S3). Dissimilarity matrices were non-Euclidean, so we used √(dissimilarity) as recommended by Legendre (2014).

RESULTS

We collected 612 individuals belonging to 13 species and 3 families: Hylidae, Leptodactylidae, and Odontophrynidae (Table 1). Across all study ponds, the most abundant species was *Scinax squalirostris*, corresponding to 22% of all the collected individuals. *Leptodactylus latrans* was the most abundant species in short-hydroperiod ponds (31%), *S. squalirostris* was the most abundant species in medium ponds (40%), and *Boana pulchella* was the most abundant species in long ponds (37%). Of the 13 species detected, all but 3 (*Dendropsophus microps*, *Physalaemus lisei*, and *Julianus uruguayus*) occurred in ponds containing predatory fish. Fish were collected in 6 long ponds, 3 medium ponds, and 1 short pond. Predatory fish species observed were *Hoplias malabaricus*, *Cnesterodon brevirostratus*, *Cnesterodon* sp., and *Phalloceros caudimaculatus*. Aquatic invertebrate predators were water bugs (Belostomatidae) and larvae of dragonflies (Aeshnidae, Coenagrionidae, Lestidae, and Libellulidae). Table 2 summarizes environmental heterogeneity variables.

Tadpole richness varied among hydroperiod classes ($F_{2,15} = 4.822$, $p = 0.0241$). Richness in long ponds differed

Table 1. Tadpole species registered in highland ponds of southern Brazil, by hydroperiod classes. Total abundance corresponds to the total number of individuals collected in each hydroperiod over the sampling period (2012–2013).

Family/Species	Hydroperiod		
	Short	Medium	Long
Hylidae			
Dendropsophus microps	4		
Dendropsophus minutus	36	12	5
Boana leptolineata	12	25	9
Boana pulchella	11	25	14
Julianus uruguayus	15		
Pseudis cardosoi	16	9	
Scinax granulatus		4	3
Scinax squalirostris	35	80	7
Leptodactylidae			
Leptodactylus latrans	73	11	
Physalaemus lisei	12	32	
Physalaemus henselii		2	
Physalaemus gracilis	71		
Odontophrynidae			
Odontophrynus americanus	44	45	
Total abundance	329	245	38

significantly from in medium ponds ($p = 0.02$), but not between short and medium ponds (Fig. 2A). Tadpole abundance did not differ with respect to hydroperiod ($F_{2,15} = 2.687$, $p = 0.101$; Fig. 2B).

Partitioning of β diversity components revealed that the species replacement was the major reason for differences in tadpole assemblages ($β_{ratio} = 0.30 ± 0.05$). Values of $β_{ratio}$ were significantly <0.5, the empirical comparison of the distributions of the dissimilarity indices across samples ($p < 0.01$). The species replacement and nestedness components were related to different spatial and environmental variables. The backward-selection procedure revealed that the species replacement component variation was related to measures of environmental heterogeneity other than hydroperiod ($R^2_{adj} = 0.33$, $F = 3.49$, $p = 0.004$), and pond area, presence of predatory fish, and type of margin were the main drivers. The first 2 axes together explained 37.2% of the total variance in the dissimilarities caused by species replacement. The 1st axis alone explained 21.9%.

In the dbRDA plot (Fig. 3A), type of margin (flat or angular) played an important role along the 1st axis, and differences in the area and presence of fish were responsible for a higher dissimilarity between ponds along the 2nd axis. Spatial factors and water depth explained 23% of the variation in the nestedness component ($F = 3.33$, $p = 0.045$; Fig. 3B). The 2 axes together explained 34% of the dissimilarities caused by nestedness. Almost all explanation for the nestedness component was associated with the 1st axis (30%). Thus, shallow ponds seem to be a subset of deeper ponds (Fig. 3B). Spatial variables representing unmeasured, spatially structured environmental factors (MEM2) explained the nestedness variation along the 2nd axis.

DISCUSSION

Our results showed that hydroperiod was important for tadpole species richness, but the effect of pond hydroperiod on species dissimilarities was indirect. In highland ponds, β diversity was almost completely caused by species replacement, and when other aspects of environmental heterogeneity were disentangled from hydroperiod, the independent effect of hydroperiod was small. Overall, these findings are in line with the idea that hydroperiod length and water levels are important environmental filters for amphibian communities (Werner et al. 2007b, Both et al. 2011, Cayuela et al. 2012). Both local and landscape factors could account for the various results found here (i.e., spawning site selection, biotic interactions, land use).

Theory predicts that species composition should change along a hydroperiod gradient, according to differences in life-history traits of amphibian species (Babbitt et al. 2003, Both et al. 2011). However, recent studies have highlighted a greater influence of other aspects of environmental heterogeneity in spatial mesoscales and within a metacommunity of freshwater organisms (Heino 2013, De Almeida et al.

Table 2. Study pond locations and variables used to describe environmental heterogeneity.

Pond		Water depth (cm)	Pond area (ha)	Hydroperiod	Type of margin	Invertebrate abundance	Fish
Lat (°S)	Long (°W)						
28.6360	50.4962	45	1.4	Medium	Flat	19	Absent
28.6536	50.4214	100	0.3	Long	Flat	36	Present
28.9508	50.4058	104	0.7	Long	Flat	18	Present
28.6469	50.4121	109	0.4	Long	Angular	26	Present
28.6304	50.4327	100	0.22	Long	Angular	41	Present
28.6166	50.4450	66	0.17	Short	Flat	06	Absent
29.6106	50.4501	71	0.16	Medium	Flat	33	Present
28.6520	50.4306	110	1.52	Medium	Angular	37	Absent
28.6531	50.3830	48	0.68	Medium	Angular	8	Absent
28.6159	50.3699	25	0.2	Short	Flat	38	Present
28.6229	50.3963	45	0.5	Medium	Flat	82	Present
28.5967	50.2882	21	0.15	Short	Angular	63	Absent
28.6114	50.3136	18	0.03	Short	Flat	11	Absent
28.6840	50.3663	102	0.8	Long	Flat	46	Present
28.6520	50.5906	54	0.2	Short	Flat	122	Absent
28.6750	50.5818	25	0.37	Medium	Flat	20	Present
28.6337	50.3687	62	0.12	Short	Flat	0	Absent
28.6264	50.3671	100	0.44	Long	Flat	459	Present

2015). We found niche-structured assemblages organized mainly by local factors (pond area, presence of predatory fish, and type of margin). The effects of pond area on amphibian assemblages may be either: 1) a direct effect of area (decreasing extinction probabilities of local populations), interacting with pond connectivity; or 2) other attributes associated with area, such as vegetation diversity. In the Araucaria moist forest, amphibians that use vertical calling sites can be favored by larger pond areas because of an increase in vegetation around the ponds (Gonçalves et al. 2015). The benefits and drawbacks of pond margins are likely to be specific for species or guilds. For example, flat margins and wet ground can provide nesting and foraging habitats for adults and tadpoles, respectively (Burger et al. 2002, Eterovick and Barata 2006, De Andrade et al. 2014). Steep margins might create a barrier for terrestrial frogs or emerging juveniles, hindering movements to upland habitats and enhancing juvenile mortality (Rothermel 2004, Moreira and Maltchik 2015).

The finding that variation in species distribution depended on the presence of fish suggests that biotic interactions underlie the observed patterns. The role of predatory fish in shaping amphibian assemblages is in clear concordance with the literature (Wellborn et al. 1996, Werner et al. 2007b). Amphibian species that breed in habitats with fish tend to have a mix of defense strategies to enhance chance of survival (Hero et al. 2001, Teplitsky et al. 2003, Nomura et al. 2011). In relation to the tadpole species found here, such strategies include cryptic behavior (e.g., *Boana leptolineata*),

larger body sizes (e.g., *Pseudis cardosoi*), and toxic/unpalatable tadpoles (e.g., *Leptodactylus latrans*) (Fabrezi et al. 2009, Junges et al. 2010, Lourenço-de-Moraes et al. 2014). Effects of fish on species composition could be synergetic through direct predation on tadpoles and selection of breeding sites by adults (Teplitsky et al. 2003, Werner et al. 2007b). Thus, the low species richness in the long ponds also could be influenced by predation pressure. The presence of fish can be used, at least in part, as an oviposition cue by some species (Resetarits 2005). However, the presence of tadpoles depends on the location selected for egg-laying by adults. When selecting oviposition sites, adult amphibians also may have to deal with constraints related to habitat splitting and pond connectivity (Becker et al. 2007, Dixo and Metzger 2010). Contrary to our hypothesis, medium ponds did not show greater tadpole richness and abundance than long or short ponds. In highlands of southern Brazil, ponds and streams may flood small areas after brief rainfall as a result of fairly steep relief. This surface–flood dynamic may weaken the constraints imposed on tadpoles by short hydroperiods.

Despite the importance of the species replacement component, we were able to find spatial patterns associated with nestedness. Spatial processes are often related to dispersal limitations of organisms (Watling et al. 2009, Landeiro et al. 2014). We focused on local environmental conditions, but we cannot rule out landscape effects associated with past and current landuse practices. In grasslands of southern Brazil, crops (rice/soybean) and exotic tree plantations (*Eu-*
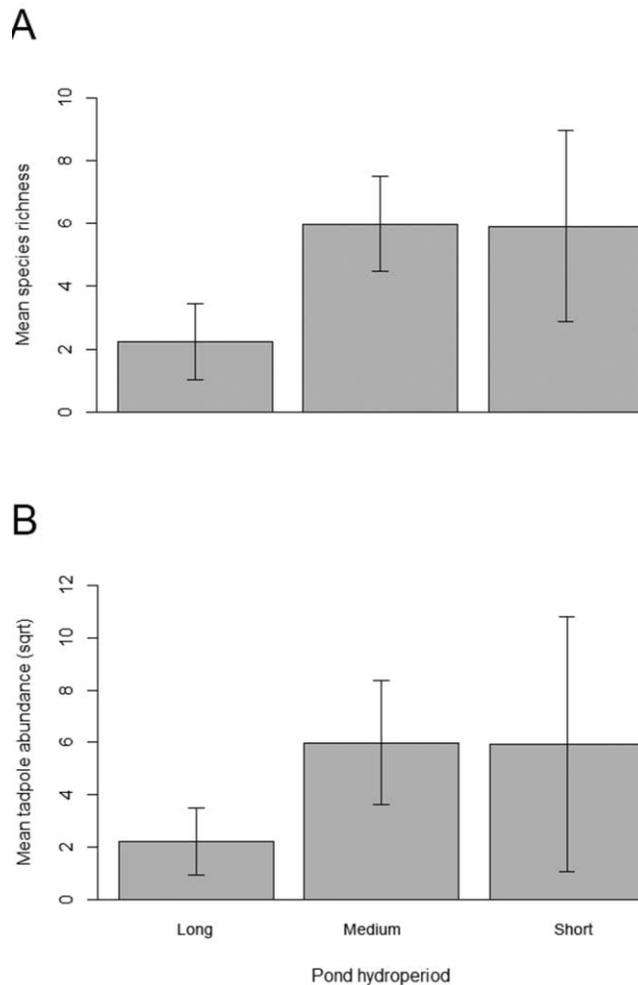
Figure 2. Mean values (±SD) of tadpole species richness (A) and abundance (B) in 18 highland ponds with different hydroperiods in the Araucaria moist forest ecoregion. Long = permanent ponds, medium = temporary ponds with hydroperiod ≥3 mo, short = temporary ponds with hydroperiod <3 mo.

calyptus spp. and *Pinus* spp.) have greatly expanded since the 2nd half of the 20th century. Such alteration of natural areas has had a negative effect on amphibians, both larvae and adults (Machado et al. 2012, Moreira et al. 2016a, Saccol et al. 2017). Thus, our results might be attributable, in part, to the selective colonization/extinction associated with species responses to land use. Our approach cannot definitively establish a causative mechanism, but the importance of water depth as a correlate with nestedness strengthens the idea of processes related to land use. In agricultural landscapes, not all forms of land use have similar water management and can differ depending on hydrological phases or crop rotation.

Two subtle issues should be recognized here: 1) the temporal extension of the study, and 2) imperfect detectability of the species. We have data for ~1 y, and this snapshot view prevents us from confirming whether species dissimilarities

follow a predictable pattern in diversity. Second, the probability of tadpole detection is often low and may fluctuate in response to the environmental heterogeneity among sites (Moreira et al. 2016b, Iwai 2017). Pond hydroperiod and other aspects of environmental heterogeneity are not static factors and can vary in long-term scales (>5 y; Werner et al. 2007b). Such variance could contribute to the observed pattern in the studied ponds, but high temporal replication is a very challenging task in field studies. In addition, a suite of recent studies have highlighted that a stable view of metacommunity organization probably is inaccurate, especially in intermittent systems (i.e., intermittent rivers, floodplains, and temporary ponds; Heino et al. 2015, Datry et al. 2016). Even in a short-term perspective, our results express the complexity of natural communities, and show that the heterogeneity gradient was not generated directly by pond hydroperiod.
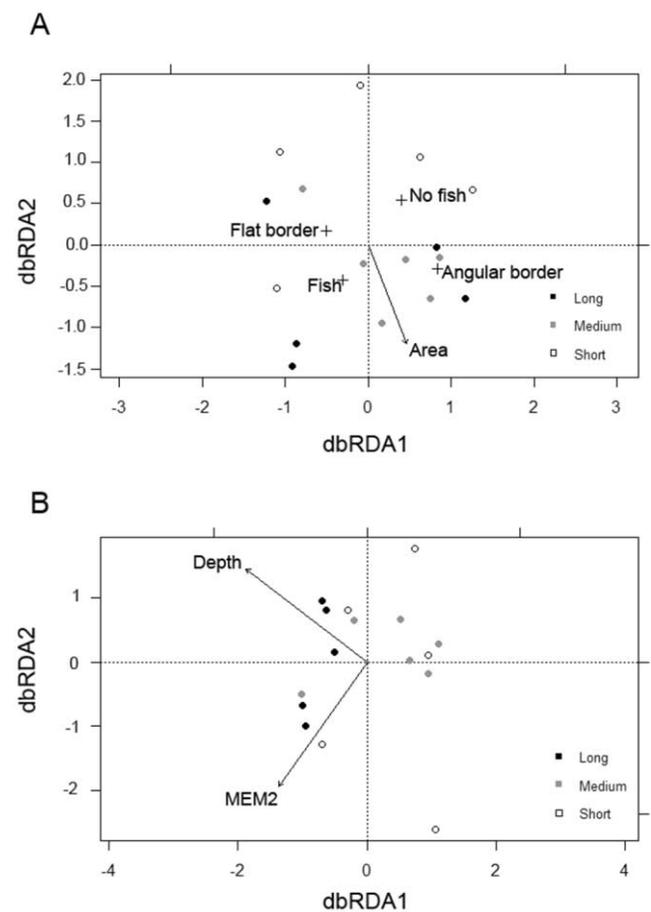

Figure 3. Distance-based redundancy analysis (dbRDA) describing the relationship between β-diversity turnover (A) and nestedness (B) components and explanatory variables in 18 highland ponds with different hydroperiods. MEM2 = Moran eigenvector map, long = permanent ponds, medium = temporary ponds with hydroperiod ≥3 mo, short = temporary ponds with hydroperiod <3 mo.

In conclusion, we partitioned how different aspects of environmental heterogeneity explained species dissimilarities in highland ponds of the Araucaria moist forest of southern Brazil. Biotic interactions and traits related to terrestrial movements might cause these dissimilarities. β diversity is linked to environmental conditions that are dynamic in space and time. Understanding such unpredictability in the processes regulating species distribution will help to elucidate the synergetic effects of land use and climate changes.

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