Are Assemblages of Aquatic-Breeding Anurans (Amphibia) Niches Structured or Neutral?

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ABSTRACT

Local niche-based processes and dispersal are important determinants of assemblage composition and species diversity. However, there is no consensus about the relative importance of niche and spatial processes to explain the distribution of anuran species in tropical systems. In our study, we analyzed the niche and neutral effects on anuran assemblages and found that biotic interactions were a predictor of assemblage structure. The Eltonian concept of niche was the best predictor for the structure of aquatic-breeding anuran assemblages, as species tended to co-occur more often than would be expected by chance. We suggest that the lack of environmental effect could be explained by differences in the pattern of movement between arboreal and non-arboreal anurans. Once there is a reduction in the number of arboreal anurans in open areas, the importance of habitat heterogeneity to explain assemblage composition should decrease. The lack of correlation between the spatial component in our model and species composition is evidence that spatial processes, such as migration, did not play a major role in structuring local assemblages. Anurans are generally assumed as having poor dispersal ability, yet this assumption is not true for all anuran species. We suggest that future studies should include key behavioral traits, such as site fidelity and homing behavior, as these traits can represent the dispersal abilities of anurans and dispersal ability seems to be important when we try to predict patterns of anuran distribution.

Key words: Cerrado; community structure; co-occurrence; Eltonian niche; Grinnellian niche; null models; redundancy analysis.

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Menin et al. 2011) better explained the structure of anuran assemblages. Thus, anuran assemblage would be a function of habitat change throughout a landscape (Loyola et al. 2008). For example, in a study conducted in the Amazonian rain forest, the structure of an aquatic-breeding anuran assembly was explained by the interstream distance, whereas the structure of terrestrial-breeding species was explained by topography and soil properties (Menin et al. 2011). We were interested in how these niche and spatial processes affected the structure of anuran assemblages in the Cerrado biome. We addressed if these assemblages were: (1) niche-structured and reflecting interspecific interactions among anuran species instead of habitat heterogeneity; (2) controlled by habitat complexity (environmental effect); or (3) structured by spatially structured processes.

METHODS

STUDY AREA.—The Extractivist Reserve of Lago do Cedro (ERLC) (14°37’ S 50°59’ W) is the largest remaining protected area of Brazilian savanna, located in the northeastern region of Goiás state, Brazil. It is approximately 173.37 km², with a mean elevation of 250 m, mean temperature around 38.0°C, and annual rainfall of 1751 mm (SIMEGO 2012). The regional climate is tropical, with a well-defined dry season, classified as ‘Aw’ Köppen-Geiger (Lautrubesse & Stevaux 2002). Our study was conducted at the floodplain of the middle Araguaia basin, which is a priority area for biodiversity conservation of threatened aquatic and terrestrial species in the Cerrado biome (Klink & Machado 2005). The ERLC is composed of a mosaic of vegetation types (e.g., cerradas, seasonal forests, and savannas).

SAMPLING DESIGN.—The ERLC was previously surveyed about its anuran biodiversity by Melo et al. 2013. In this study, we considered only the samples obtained by the survey at breeding sites method (Scott & Woodward 1994). The sampling was carried out at night, during the rainy season, in December 2010, February 2011, and March 2011 (Melo et al. 2013). As we were interested in estimating the contribution of the spatial effect to anuran diversity, we surveyed 32 ponds at least 500 m aside from each other, representing the regional landscape mosaic (Fig. S1). Overall, the species richness found in the Brazilian Cerrado ranged from 23 to 43 species, but the areas that were sampled more times did not necessarily have a higher diversity (e.g., Ni- quelândia-GO: 25 ponds, 36 species, Nomura et al. 2012, north-western region of Goiás state: 45 ponds, 36 species, Morais et al. 2011, and Serra da Bodoquena-MS: 29 ponds, 36 species, Utemabaro et al. 2007). Thus, although the anuran biodiversity of the Brazilian Cerrado is high, the alpha diversity is relatively low and the beta diversity is higher, especially in the core area of the Cerrado extension (Diniz-Filho et al. 2008, 2009). Because the spatial effect was important to our questions, and we had limited resources, our choice was to conduct a survey throughout a large spatial area at the cost of more accurate temporal information. However, all sampling methods were standardized. Thus, although all surveyed sites were visited only one time, we are confident that our survey represents a real estimate of the anuran diversity in the ERLC. With this sampling design, we obtained a total of 1135 individuals of 31 aquatic-breeding anuran species from four families: Bufonidae (Rhinella, two species); Hylidae (Dendropsophus, four species; Hypsiboas, six species; Lysapua, one species; Phyllomedusa, one species; Pseudis, one species; Scinax, three species; Trachypholis, one species); Leptodactylidae (Euphryne, one species; Leptodactylus, five species; Physalaemus, two species; Pseudopaludicola, two species); and Microhylidae (Elabioncistela, one species; Chiromantis, one species). The complete species list used in this study is presented in Table S1.

HABITAT CHARACTERIZATION AND SPATIAL VARIABLES.—We characterized ponds by vegetation heterogeneity and the physical and chemical parameters of the water, resulting in the following descriptors: (1) site dimensions (greatest length, width, and depth); (2) water quality (pH, conductivity, turbidity, dissolved oxygen, and temperature); (3) pond structure (percentage of vegetation cover [herbaceous, shrub, and arboreal] in margins and inside the pond, the margin inclination [ravine, sloped, and plane], and the substrate type of pond bottom [clay, sand, litter, mud, and stones]); and (4) the geographic coordinates (latitude and longitude), obtained in decimal degrees by the Global Positioning System (GPS) (Table S1).

SPATIAL AND LOCAL EFFECTS ON ANURAN ASSEMBLAGE COMPOSITION.—To represent the abiotic components of the niche, we applied a principal coordinate analysis on the matrix formed by the site dimensions, water quality, and pond structure variables used to measure their environmental heterogeneity. The principal coordinate analysis reduced the collinearity in the dataset (Legendre & Legendre 1998) and extracted the eigenvalues and eigenvectors that explained 90 percent of the matrix variation. These eigenvectors were used as a measure pond environmental heterogeneity. The same procedure was applied to the species composition matrix.

We used the geographic coordinates of the ponds to represent the spatial relationship (as a proxy for the neutral theory) among the sampled communities (Table S1). These coordinates were transformed by Principal Coordinates of Neighbor Matrices (PCNM) (Borcard & Legendre 2002); for each PCNM generated, we calculated the Moran’s I index and selected those PCNM that displayed positive spatial correlation (i.e., with Moran’s I larger than the expected value). The PCNM calculations were made with the PCNM package and the statistical test of Moran’s I index by a two-tailed parametric test in the AEM package in the R software v. 2.15.1 (Legendre et al. 2012).

The PCNM vectors and the environmental heterogeneity eigenvectors were used as predictors of species composition in the partial redundancy analysis (RDA) (see Borcard et al. 1992, Peres-Neto et al. 2006). We used variance partitioning to investigate the relative importance of spatial and environmental variables (Oksanen et al. 2011). For statistical significance, we tested the contribution of the pure environmental and pure spatial components to the total variance of anuran composition.
using an ANOVA-like permutation procedure, after 9999 permutations of the RDA at the 5 percent significance level (Anderson 2001). All statistical analyses were performed using the vegan package in R v. 2.15.1 (Oksanen et al. 2011).

CO-OCCURRENCE PATTERNS.—We tested whether species interactions were controlling the assemblage structure by comparing the observed co-occurrence pattern of anuran species among reproductive sites with a null model representing the expected frequency of co-occurrence among anuran species (Gotelli 2000). We measured the co-occurrence pattern by the checkerboard score index (Stone & Roberts 1990). The checkerboard score measures the degree to which species can co-occur, quantifying the mean number of checkerboard unities within all possible pairs of species (Gotelli & Entsminger 2003). We generated the null model by 5000 randomizations of the observed matrix of species co-occurrence, calculating a checkerboard score, after each iteration, with the software Ecosim, v. 7.2 (Gotelli & Entsminger 2001). We tested if the observed index was beyond the 95% confidence limits of the randomized matrices, which denotes the existence of biological mechanisms determining species co-occurrence.

RESULTS

We found no significant correlation that was explained by variation partitioning, which presented a higher unexplained variation (Fig. 1). Thus, both the PCNM ($F = 1.107$, $P = 0.41$) and environmental ($F = 1.036$, $P = 0.45$) components were weak predictors of the anuran assemblage composition. Therefore, we were unable to detect any environmental or spatial effects to explain the composition of the anuran assemblage (Fig. 1). Conversely, the observed checkerboard score index was significantly lower than expected by chance (Fig. 2). Thus, we found that the anuran assemblage was structured by interspecific relationships among anuran species, with some species pairs co-occurring more often than expected by chance. As we did not detect any spatial or environmental effects in the previous analysis, we interpreted this result as indicative of the relative importance of Etlonian niche on the structure of anuran assemblages in the ERLC.

DISCUSSION

In this study, we were concerned with the underlying process that regulates the diversity patterns of aquatic-breeding anuran species. Specifically, we investigated if these processes could be better explained by niche or neutral theories. Currently, there is no consensus regarding how tropical anuran assemblages are structured, with some authors presenting evidence of a strong signal of the niche effect (Parris 2004, Bastazini et al. 2007, Nomura et al. 2012), while other authors found more evidence of a neutral or spatial effect (Ernst & Rödel 2006, 2008, Menin et al. 2011). Our study demonstrated a non-random co-occurrence pattern among the studied assemblages.

Other authors also observed niche-structured assemblages organized by non-random co-occurrence patterns (Baber et al. 2004, Nomura et al. 2012). These assemblages were controlled by differences in life-history traits of anuran species, such as body shape, size, and microhabitat use (Crump 1974, Kneitel & Chase 2004, Nomura et al. 2012). Niche processes that cause species coexistence are mostly related to intraspecific competition, resource partitioning, and predator-prey relationships (Gotelli 1997, Prado et al. 2005). Here, competition does not explain the observed co-occurrence pattern, given that we found a higher than expected chance of some species co-occurring. Both predation and environmental heterogeneity can generate patterns in which species pairs have a higher than expected chance of co-occurrence. Predation could decrease or eliminate the effects of competition (Lawler & Morin 1993) and constrain a set of species in patches where predators do not occur. In theory, the environmental effect could generate the same pattern as that generated by predation, because species with the same biological requirements can be constrained by the spatial distribution of habitat components (Bastazini et al. 2007). As we did not find any evidence of the environmental or spatial effects organizing the assemblages of anurans in the ERLC, however, we can only support the idea that predation is the main structuring force explaining the co-occurrence pattern we observed. In reports that evoked the environmental effect to explain patterns of anuran species distribution, environmental traits were the only predictors used to explain the anuran diversity (e.g., Bastazini et al. 2007), and an association between pond structure and reproductive mode diversity was indicated as the main process that generated this pattern (Haddad & Prado 2005). Although there are obvious requirements for anuran occurrence (e.g., moisture), several authors hypothesized that predation was the main driver for the evolution of specialized reproductive modes in anurans (e.g., Downie 1990, Magnusson & Hero 1991, Prado et al. 2002, Haddad & Prado 2005). This supports the idea that the association between pond structure and reproductive mode diversity could be an indirect measurement of predation as an evolutionary driver of anuran species distribution.

We were unable to detect any significant pure environmental effect in our model on the species composition. Theory
predicts that more structurally complex habitats should facilitate niche diversification, allowing a large number of species to coexist (Parris 2004). We suggest that the lack of any environmental effect could be related to a difference in the functional responses of arboreal and non-arboreal anurans to habitat heterogeneity. Thus, the lack of an environmental effect may be related to the relatively high proportion of non-arboreal anurans in the ERLC. Arboreal and non-arboreal anurans differ in their pattern of movement: arboreal anurans can have vertical and horizontal displacements, while non-arboreal anurans are restricted mainly to horizontal ones. These differences in pattern of movement should lead to restrictions in microhabitat availability—non-arboreal anurans are restricted to a two-dimensional habitat and hence experience less environmental heterogeneity than arboreal anurans that experience a three-dimensional one. Access to the arboreal dimension would improve the opportunities for niche differentiation and increase the importance of abiotic structural predictors of anuran distribution. For example, when we compare the diversity of reproductive modes between open and forested areas, forested areas generally have higher diversity (Haddad & Prado 2005). This increases the importance of a heterogeneous environment for aquatic-breeding arboreal anuran species (Parris 2004).

Even among sites surveyed within the Cerrado biome, we noted high variability in the importance of arboreal and non-arboreal anurans to the composition of anuran assemblages. For example, the high representation of Hylidae (mainly arboreal) and Leptodactylidae (mainly non-arboreal) species is a common pattern in anuran assemblages in tropical biomes (Duellman 1999, Ribeiro-Júnior & Bertoluci 2009). However, the relative importance of these two families for the assemblage species pool could range from 31 percent to 50 percent for Hylidae (Vaz-silva et al. 2007, Valdujo et al. 2009), or 10 percent to 31 percent of Leptodactylidae (Uetanabaro et al. 2007, Oda et al. 2009). Once the number of arboreal anurans is reduced in open areas in relation to non-arboreal species (Brasileiro et al. 2005, Conte & Rossa-Feres 2006, Melo et al. 2013), the importance of habitat heterogeneity for explaining assemblage composition should decrease (Santos et al. 2007, Silva et al. 2011). Such an interaction between environmental effect and the set of natural histories of the species in a given assemblage can generate a multitude of evolutionary scenarios. This could explain why it is so hard to identify general patterns for the structuration of anuran assemblages (Gotelli & McCabe 2002, Melo et al. 2013).

The proximity of neighboring assemblages, i.e., ponds that were geographically close, did not influence the assemblage structure. This is evidence that spatial processes such as migration do not play a major role in structuring local assemblages. The influence of spatial effects on anuran assemblages has been poorly investigated in the Neotropical region, but it is often highlighted as a main factor (Ernst & Rödel 2008, Menin et al. 2011). In general, dispersal ability is considered a key trait to explain spatial effects (Hubbell 2001) and anurans are generally assumed to have poor dispersal ability (Duellman & Trueb 1994). However, we believe that the mean dispersal ability of anuran species from the Cerrado biome should be greater than species from forested biomes, which would explain the lack of spatial effect. There is some evidence that species from open biomes have better dispersal ability than species from forested ones (Rhinella marina, Llewelyn

FIGURE 2. Histograms of the expected values of checkerboard score index generated after 5000 randomizations of the species composition matrix for the 32 ponds sampled in the Extractivist Reserve Lago do Cedro, Goiás state, Brazil. The asterisk denotes the position of the observed checkerboard score index.
et al. 2010, Rana lessonae and Rana esculenta, Tunner 1992, Dermatotus muelleri, F. Nomura, unpubl. data), but information about the home or movement ranges of anuran species is scarce. There is an association between behavior and dispersal ability in anurans, with species that have low dispersal ability being associated with territoriality and site fidelity behaviors and species with high dispersal ability being associated with homing and migratory behaviors (Sinsch 1990). Thus, we could measure the number of species in a given assemblage with territorial, site fidelity, homing, and migratory behaviors to estimate the dispersal ability of the assemblage. In this case, we predict that the number of species with site fidelity and territorial behaviors will be greater in forested biomes and the number of species with homing and migratory behaviors will be greater in open biomes. Although we did not test this prediction, this should demonstrate that the mean dispersal ability of anuran assemblages is filtered by the biome and, therefore, affects the importance of spatial effects as a structural force.

Our findings are particularly important for amphibian conservation, as anuran assemblages could be highly dependent on life-history traits (Becker et al. 2007) such as arboreal habits or migratory behavior. Despite our failure in detecting any environmental effect, several studies focused on the structure of anuran assemblage found different results to explain assemblage compositions (Ernst & Rödel 2006, Keller et al. 2009). The proportion of species with natural history traits such as site fidelity or territoriality in a regional species pool could explain the structural differences between assemblages in open versus forest habitats, as these traits affect frog dispersal and competitive abilities. Forested areas would favor assemblages in which species have lower dispersal ability and a higher degree of habitat specialization. For open areas, such as the Cerrado, the species are more generalist in habitat requirement and have greater dispersal abilities. However, it is important to note that our findings should be interpreted with caution because our sampling design could not efficiently detect explosive-breeding anurans in the ERLC assemblages. The proportion of each reproductive strategy in a given assemblage, i.e., explosive versus prolonged breeders, could also be an important behavioral trait for understanding how assemblages of anuran species are structured.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

FIGURE S1. Localization of the RESEX Lago do Cedro, Aruana, GO.

TABLE S1. Relative abundance of species, habitat characterization and spatial variables of the RESEX Lago do Cedro, Aruana, GO.

LITERATURE CITED


