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Temporal changes in fish species composition of headwater streams of the upper Paraguay and Paraná basins, Brazil

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ABSTRACT. This study was carried out in headwater streams in the Paraguay and Paraná river basins, with bi-monthly samples from January to November 2004, aiming to quantify the influence of environmental factors on the temporal rate of turnover in species composition of the fish communities. The environmental variables explained 73.5% of the variation in beta diversity and 52.5% of the variation in mean dissimilarity. Altitude was the only environmental descriptor that significantly explained the variation in beta diversity and mean dissimilarity in both basins.

Key words: community ecology, neotropical streams, environmental variables.

RESUMO. Alteração temporal na composição de espécies de peixes em riachos de cabeceira das bacias do alto Paraguai e Paraná, Brasil. O presente estudo foi realizado em riachos de cabeceira nas bacias dos rios Paraguai e Paraná, por amostragens bimestrais de janeiro a novembro de 2004, com o objetivo de se quantificar a influência dos fatores ambientais sobre a taxa de alteração temporal na composição de espécies nas comunidades de peixes. As variáveis ambientais utilizadas explicaram 73,5% da variação na taxa de alteração na composição de espécies, utilizando a diversidade beta e 52,5% da variação na taxa de alteração pelo coeficiente de Jaccard. A altitude dos locais amostrados foi o único preditor significativo da taxa de alteração temporal na composição de espécies para ambas as bacias.

Palavras-chave: ecologia de comunidades, riachos neotropicais, variáveis ambientais.

Introduction

Populations and communities are temporally variable, and understanding the causes and consequences of this variation is the goal of community ecology (COOK et al., 2004). Thus, the analysis of variation in richness and species composition over an area or time period has been an important component for studies in communities.

The meta-community concept proposes that local communities are linked by species migration (WILSON, 1992), and local and regional characteristics interact to define their characteristics (RICKLEFS, 1987). Therefore, the analysis of the influence of regional processes on the structure of ecological communities has emphasized the importance of spatial and temporal turnover in diversity and species composition and their contribution to regional diversity. Generally, biological communities have high turnover rates, which are usually associated with the migration as a result of changes in resource availability, environment, and reproductive migration (ARNOTT et al., 1999; BROWN et al., 2001; LA SORTE; BOECKLEN, 2005).

Turnover can reflect and reveal adaptations to climate change, the degree of partitioning of communities (MENA; VÁZQUEZ-DOMÍNGUEZ, 2005) and stochastic colonization/extinction dynamics or disturbance-related events (REILLY et al., 2006). Some authors have suggested that other environmental descriptors (BREHM et al., 2003; MCCOY, 1990; WERNER et al., 2007), anthropogenic factors, and local richness influence species diversity on the regional scale (KOLLEF; GASTON, 2002; LA SORTE; BOECKLEN, 2005).

Stream fish communities can be viewed as unstable, as a result of the greater unpredictability in flow variation and consequent fluctuations in chemical and physical water characteristics (MOYLE; VONDRACEK, 1985; OBERDOFF et al., 2001). However, Taylor and Warren Jr. (2001) suggested that stream instability makes species composition more predictable, whereas in

portions with less environmental variability the turnover in species composition is higher, because of the ease of colonization of these habitats, which increases the migration rate. Langeani et al. (2005), analyzing fish species composition in riffle and pool habitats in streams of the upper Paraná basin, reported that pool portions have a higher variability in species composition, suggesting that the local hydrological characteristics may influence the variability in fish species composition.

Despite the increase of ecological studies in neotropical freshwaters, the differences in beta diversity among the sites analyzed have merely been mentioned, and little attention has been given to the rate of temporal turnover in species composition. Therefore, the present study aimed to quantify the turnover in fish communities in headwater streams of the upper Paraguay and Paraná river basins, and to answer the following questions: 1) Is there a difference in the rate of temporal turnover in fish species composition of headwater streams in the upper Paraguay and Paraná basins? 2) Is the rate of temporal turnover in species composition influenced by environmental characteristics of the streams sampled?

Material and methods

The study region is located in a 200-km-long part of the interface between the Paraguay and Paraná basins, between the latitudes S20º54' and 22º18' and longitudes W54º56 to 56º05' (Figure 1). The streams sampled are relatively pristine, with well-preserved riparian vegetation and a low density of human population.

Samples were collected bi-monthly in 10 streams of each basin (Figure 1), from January to November 2004. In each basin, the selected streams are located in four sub-basins. The streams of the Apa and Miranda sub-basins in the Paraguay basin include sites with uneven relief, with countless waterfalls higher than 30 m, which act as barriers to fish migration within the basin (SÚAREZ et al., 2007a).

The samples were taken during daylight with a 1.2 x 0.8 m rectangular sieve, with 2-mm mesh size and standardized effort (20 throws) at each site, with approximately 50-m-long hauls. This method was selected because of the difficulty in using electroshocking in streams with water of low electrical conductivity, difficult to access, and with variable turbidity that made it difficult to see the fish.

Specimens were fixed in 10% formalin and preserved in 70% ethanol for counting and identification. Voucher specimens are deposited in the Museu de Zoologia da Universidade de São Paulo (MZUSP) and in the Museu Nacional do Rio de Janeiro (MNRJ).

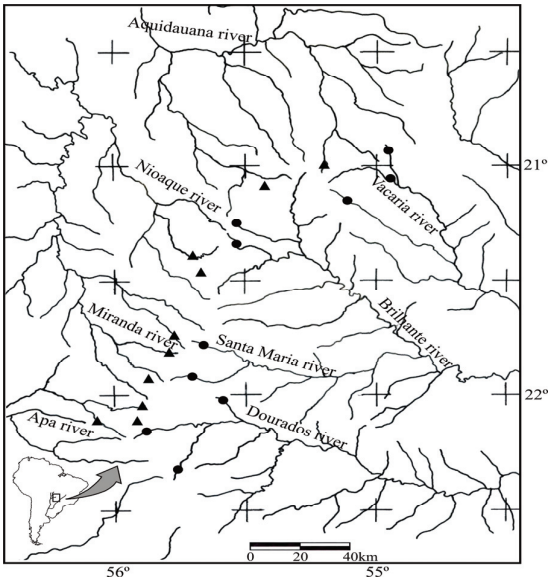

Figure 1. Map of interface area between the Paraguay and Paraná basins, Mato Grosso do Sul, showing the streams sampled in Paraguay (triangles) and Paraná (circles).

For each sample we obtained a set of environmental data: pH, electrical conductivity (mS cm^{-1}), water temperature (°C), and dissolved oxygen (% saturation), using a YSI Model 556 field multi-probe. Turbidity was obtained with a portable turbidity meter. Stream depth (m) was obtained at 10 locations on each transect (50 m long), with a graduated wooden stick. Water velocity (m s^{-1}) was measured three to five times in different parts of the transect, using a float method. For each site/transect, the mean values of stream depth and water velocity were used. Stream width (m) was measured with a measuring tape, and altitude (m) using the altimeter of a Garmin Etrex GPS.

The turnover rate in species composition (TR) for each stream was calculated by two methods. The first method uses the Jaccard coefficient, where $TR_{jaccard}$ = 1-Jaccard, quantifying the temporal changes in species composition with a value that varies from 0 to 1. Low values indicate that species composition varies little during a sampling period. The second method utilizes the equation for β diversity proposed by MacArthur et al. (1966), in that beta diversity in each stream is

equal to total richness minus mean richness ($\beta = \gamma - \alpha$), this being TR_{beta} = total richness - mean richness. Thus, sites that have higher total richness (over the entire sampling period) but a low mean number of species per sample have higher rates of turnover in species composition (high β diversity).

The influence of environmental characteristics as well as the difference between basins (Paraguay and Paraná) on the turnover rate (TR) of species composition was quantified by co-variance analysis. The TR was utilized as the response variable, the hydrographic basin as a factor, and the environmental variables as co-variables.

Results

A total of 4,605 fish, members of 60 species, were caught. The most abundant species in the Paraguay basin streams was *Astyanax* cf. *marionae* Eigenmann, 1911 (1,896 individuals), which comprised 68.4% of the 2,773 individuals collected in this basin. For the Paraná basin streams, *Bryconamericus stramineus* Eigenmann, 1908 was the most abundant species with 242 individuals, representing 13.2% of the total (1,832) individuals collected.

We found no significant influence of hydrographic basin on the turnover rate in species composition for $TR_{jaccard}$, or for TR_{beta}. Of the environmental variables analyzed, only altitude significantly explained the turnover rate in species composition ($TR_{jaccard}$ and TR_{beta}). Thus, both basins showed equivalent rates of temporal changes in species composition (Table 1 and Figure 2) and elevation is the only turnover rate descriptor, where streams located at higher altitudes have communities less susceptible to temporal variations in species composition (Figure 3). Graphically, it was also possible to observe that the sampled streams in the basin of the Paraguay river showed a clearer linear pattern than the streams of the Paraná river basin.

Table 1. Results of co-variance analysis of environmental descriptors on turnover rate in fish species composition in streams of the Paraguay and Paraná basins.

Turnover rate	Environmental descriptors	F	P
$TR_{jaccard}$ ($r^2 = 0.525$)	Basins	3.52	0.08
	Altitude	6.07	0.03
	Width	0.76	0.40
	Depth	0.10	0.76
	Velocity	0.01	0.92
TR_{beta} ($r^2 = 0.735$)	Basins	3.26	0.09
	Altitude	14.01	< 0.01
	Width	0.25	0.63
	Depth	0.71	0.41
	Velocity	0.32	0.58

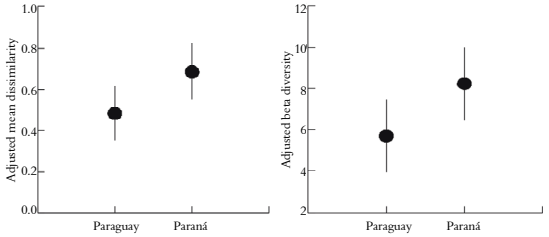

Figure 2. Mean values and confidence interval of turnover rate in species composition, obtained using Jaccard coefficient and beta diversity, from January to November 2004 for streams sampled in the Paraguay and Paraná basins.

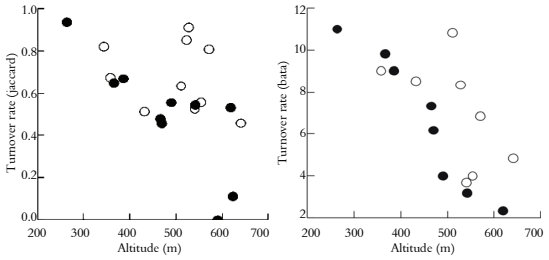

Figure 3. Scatterplot of turnover rate in species composition in response to altitude variation for streams sampled in the Paraguay (black circles) and Paraná (open circles) basins, from January to November/2004.

Discussion

Despite the differences in species composition between the basins, with only 30% common species (VALÉRIO et al., 2007), we did not observe a difference in turnover rate in species composition between the Paraguay and Paraná basins, and the same environmental descriptor determined the variation in turnover rate for both basins. Therefore, our results suggest that, regardless of biogeographical differences between analyzed basins, the temporal pattern of variation in species composition is determined by the same factor (altitude), corroborating other characteristics of these communities (e.g., species/abundance pattern) observed by Valério et al. (2007).

Other studies found that in lotic environments, hydrological characteristics such as flow variation, width, depth, and water velocity can be determinants of fish communities, determining the intensity in the turnover rate of fish populations and communities (BARRETTO; UIEDA, 1998; MARTIN-SMITH, 1998; OBERDORFF et al., 2001; POFF; ALLAN, 1995; SÚAREZ, 2008). However, in this study, among the variables examined, only altitude had a significant influence on turnover rate in species composition in both basins, suggesting that altitude best summarizes the

hydrological characteristics of the streams and their influence on fish communities. Environmental factors such as temperature, flow, and predation rate are frequently associated with altitude. Therefore, altitude is a good landscape indicator, able to represent multiple environmental factors that are important in understanding the fish species distribution (COOK et al., 2004; RAHEL; HUBERT, 1991). In addition, many species have wide distribution limits for elevation (MATTHEWS, 1998). The altitude acts as an environmental filter for species migration, and a few species occurring in the upper portion of the basin show a clear differentiation from the lower portions of the basin (BARRETTO; UIEDA, 1998; BISTONI; HUED, 2002; GERHARD et al., 2004; SÚAREZ; PETRERE-JÚNIOR, 2003; 2006; 2007; SÚAREZ et al., 2007b; VALÉRIO et al., 2007).

Súarez (2008), analyzing fish communities in streams of the lower portion of the Ivinhema basin, found that stream width and depth significantly influenced beta diversity; however, altitude was not included in the explanatory variables in this study. Despite these conclusions, we believe that small altitudinal variation (326-384 m) in the streams sampled by Súarez (2008), compared to our data (264-641 m), may have influenced the importance of other environmental descriptors, because elevation constraints, discussed here, did not affect the turnover rate in species composition in the study by Súarez (2008).

Chernoff and Willink (2000), analyzing the differences in species composition among sub-basins in the Pantanal, found larger spatial variation (sub-basins) in species composition in headwater portions, suggesting that less migration occurs among them; whereas in the lower portion (floodplain), the fish communities were more homogeneous, apparently as a result of higher migration rates among these habitats. Although the study of Chernoff and Willink (2000) addressed spatial variation, while our study focused on temporal variation in the same sites, the concepts discussed are the same; that is, the lower basin portion showed a higher migration rate, as a result of less-constraining environmental characteristics, leading, qualitatively, to greater similarity in species composition among basins. However, the migration rate in each portion of a stream in its lower portion may be higher compared to its headwater portions, because the pool of potential colonizers is larger, as corroborated by our results.

Many studies on fish species diversity and distribution in the upper Paraná have suggested that differences in altitude significantly influence fish communities. Barretto and Uieda (1998), analyzing longitudinal variation in fish species composition in a tributary of the Tietê river, observed a clear differentiation between two portions of higher (900 m) and two with a lower altitude (600 m), indicating that the water velocity and flow between the two altitude portions determine differences in species diversity. Gerhard et al. (2004), studying fish communities in Atlantic Rain Forest streams, found that elevation variation was the main determinant of fish communities. Valério et al. (2007) found a similar result for headwater streams in the upper Paraguay and Paraná basins. Súarez et al. (2007b), analyzing the occurrence probability in streams of the Ivinhema river basin in the upper Paraná basin, observed that, of four species analyzed, three were negatively influenced by altitude. Cook et al. (2004), discussing the pattern of nestedness in stream-fish assemblages, found no significant relationship between the annual variation in species composition and elevation. However, similarly to the observations in the present study, these authors stressed that the assemblages of the montane regions examined appeared to be more stable. Therefore, it seems that the difficulty of colonizing these sites results in communities that contain only a few species with high dispersal ability and resistance to hydrological changes (SÚAREZ et al., 2007b). This makes these communities little affected by temporal migration dynamics, since few species of all possible colonizers are able to live in these locations, reducing the rate of variation in species composition, according to the proposal of Taylor and Warren Jr. (2001). Similarly, Reilly et al. (2006) studied the turnover of some plant species and found that the environmental gradient defines the composition of the community and that these communities are more similar as the altitude increases, which is consistent with our results.

Magurran and Henderson (2003) suggested that the higher richness of rare species in tropical communities may be a result of two species groups: one composed by resident species and another by transient species, which are a random sample of the regional species pool, always making small migrations in a search for favorable habitat. In our study, the lower basin portion may show a higher richness of random transients, as a result of its greater hydrological stability and, consequently, less-constraining environmental characteristics, increasing the rate of change and total species richness, by the increase of "rare" species (random transients). A similar result was also obtained by Uieda and Barretto (1999), who found a defined

longitudinal pattern of ichthyofauna, with a higher rate of addition of rare species, considered transitory, in the lower portion of the river, which afforded a gentler relief and smaller seasonal fluctuations in the environment.

Valério et al. (2007), analyzing the fish communities in the same streams used in this study, found for the Paraguay basin a significant influence of stream distance on fish species composition; however, no such relationship was found for the streams of the Paraná basin. This result may be explained by the presence of waterfalls in the Paraguay basin, which isolate the fish communities. For these reasons, the migration rate between the streams sampled may be higher in streams of the upper Paraná river. However, this hypothesis was not statistically confirmed by our results, although the difference in the graphical turnover rate in species composition and the values of probability of error of just over 5% suggest that the increase in sample size (number of streams) may make a difference.

Among the few studies of species migration are those by Davis et al. (1999) on a beetle assemblage in South Africa; Taylor and Warren Jr. (2001) on stream fish assemblages; Mena and Vázquez-Domínguez (2005) on rodent species in diverse altitudinal gradients; and Werner et al. (2007) on amphibians in ponds of North America, all emphasizing the effect of altitude on the aquatic and terrestrial assemblages. Therefore, regardless of biological group and biogeographical and ecological differences, altitude seems to be a good descriptor of environmental gradient, influencing not only the composition and species diversity, as observed by Valério et al. (2007) and Súarez et al. (2007b), but also the turnover rate in the species composition of the fish communities in the Paraguay and Paraná basins.

This influence of altitude on temporal changes in species composition can be also applied to the conservation of freshwater fish communities, thereby complementing the findings of many other authors who have suggested that headwaters are important (CHERNOFF; WILLINK, 2000). As demonstrated in this study, these habitats also have lower migration rates, making these communities extremely vulnerable to changes of anthropogenic origin.

Conclusion

This study suggests that temporal variation in fish species composition in streams of upper Paraguay and Paraná basins present a predictable pattern constrained by altitude, despite of biogeographical differences between regions.

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