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Research Letters

The likely effects of river impoundment on beta-diversity of a floodplain zooplankton metacommunity

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ABSTRACT

Using a long-term dataset, we tested whether beta diversity of the zooplankton community in the Upper Paraná River floodplain increases during periods of high environmental heterogeneity and productivity and decreases with increases in water level (when there is higher connectivity between sites). We detected temporal trends of increasing beta diversity. A temporal decrease in species occupancy was more frequent than a temporal increase. Our results do not support a generalized association between beta diversity and environmental heterogeneity or productivity. Water level variation was an important explanatory variable only for rotifers and in the opposite direction expected. Taken as whole, our results suggest that we are far from a comprehensive understanding of the processes underlying variation in beta diversity. We speculate that the large number of dams built upstream from the study area may account for the positive trend in beta diversity.

Introduction

The search for biodiversity patterns across different spatial and temporal scales and for the mechanisms behind these patterns is a central goal in ecology. In this context, an ever-growing number of studies have focused on β-diversity patterns (Anderson et al., 2011). However, few studies have modeled temporal changes in β-diversity (see review in McGill et al., 2015). This scarcity is related to financial and logistical constraints involved in conducting long-term studies at multiple sites with standardized methods (Magurran et al., 2010).

Studies of β-diversity over time may be based on at least two approaches. The first considers changes in species

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composition between different periods (similarity decay in time; Korhonen et al., 2010). The second considers the magnitude of changes in species composition between sites over time. Therefore, for this latter approach, data must be obtained from *n* sites and *t* times (Langenheder et al., 2012; Bonecker et al., 2013; Dornelas et al., 2014).

Changes in species composition are driven by local extinctions, disturbances, species colonization/invasion and environmental variability. The relative importance of these processes may change over time. Thus, the proximate cause of temporal variation in β-diversity can be related to the levels of synchronicity of the processes cited above. For example, the invasion of the same species in pairs of local communities with different species compositions would decrease the β-diversity between sites from time *t* (before invasion) to time *t* + 1 (after invasion). Similarly, local extinctions of different rare species would also decrease β-diversity between pairs of local communities. In contrast, the colonization of different species at each site would increase β-diversity. These processes are also dependent on the level of connectivity between local communities and on the dispersal ability of the species. For example, a decrease in β-diversity would occur in periods of high connectivity between sites due to the increase in dispersal rates (Gonzalez, 2009).

An increase in β-diversity with primary productivity has been detected. For instance, Chase (2010) found a positive relationship between β-diversity and productivity and attributed it to an increased role of stochastic assembly processes (e.g., dispersal limitation, ecological drift), when compared to deterministic processes (e.g., species sorting and priority effect), in more productive environments. Other empirical evidence suggests that environmental heterogeneity is positively correlated with β-diversity (Veech and Crist, 2007). Sites presenting higher rather than lower environmental heterogeneity increase the probability that different species from the regional pool find suitable conditions according to their environmental requirements.

Floods markedly affect the levels of connectivity between the habitats of floodplain systems. An increase in hydrological connectivity occurs during flood periods, reducing environmental heterogeneity and β-diversity. In contrast, during low water seasons (when floodplain habitats are more isolated), local driving forces cause an increase in environmental and biological heterogeneity (Thomaz et al., 2007). For instance, while a small lagoon may be drying out, another may contain a high density of predatory fish and a third may have a high rate of deoxygenation. Thus, it is expected a more idiosyncratic dynamic of the environmental characteristics and structure of local communities, increasing the environmental and biological heterogeneity of the system. However, an increased number of hydroelectric dams upstream the floodplain systems may be disrupting these patterns.

In this study, we examined long-term data (2000–2011) on zooplankton communities from 12 sites in the Upper Paraná River floodplain (Brazil) to evaluate the following predictions: zooplankton β-diversity (spatial variation in species composition) should be positively correlated with environmental heterogeneity and primary production and negatively correlated with water level.

Materials and methods

Our sampling sites were distributed over the Upper Paraná River floodplain, which represents the last area without dams in the Brazilian portion of the Paraná River Basin (Fig. 1). Samples were collected during 12 years (from 2000 to 2011) from 12 permanent sites. Standardized fieldwork was performed every three months except in 2001, when samples were collected only twice. Zooplankton samples were collected in the limnetic zone of each site by filtering 600 L of water through a plankton net of 68 μm mesh size. The samples were preserved in formaldehyde (4%, buffered with calcium carbonate), microscopically counted and identified in the laboratory following Bottrell et al. (1976).

Water level in the Paraná River (Porto Rico Municipality) was measured daily with a meter stick. We also measured the following environmental variables according to APHA (2005): water temperature, dissolved oxygen, pH, conductivity, water transparency, turbidity, total suspended solids, total alkalinity, chlorophyll-*a*, total nitrogen and total phosphorus.

Statistical analysis

We estimated β-diversity by calculating the Simpson multiple-site dissimilarity index (β_{SIM}) at each time *t* (Baselga, 2013). β_{SIM} was calculated for the whole zooplankton community and separately for rotifers and microcrustaceans, given the differences in the life histories between these broad taxonomic groups (e.g., parthenogenesis in the case of rotifers). In turn, these differences may account for different patterns of β-diversity.

To model the temporal variation in β-diversity (i.e., β_{SIM} for the whole zooplankton community, rotifers and microcrustaceans), we used a Generalized Least Squares (GLS) model incorporating an autoregressive structure (Zuur et al., 2009). The response variable was β-diversity (β_{SIM} as estimated for total zooplankton, rotifers and microcrustaceans), and it was modeled as a function of mean water level (considering the mean values estimated with data from 10, 20, 30, 40 and 50 days before sampling), mean chlorophyll-*a* concentration, mean total phosphorus (total P) concentration (both as proxies for primary production) and environmental heterogeneity. Thomaz et al. (2007) show that there are time lags between hydrological variation and is effects on biological communities. This was the reason for estimating mean water level according to different temporal windows. Our first measure of environmental heterogeneity (*dc*) consisted of the average dissimilarity between individual sampling sites and their group centroid (as defined by the sampling dates; Anderson et al., 2006). Second, for each variable, we calculated the coefficient of variation over the sites. The resultant coefficients of variation were then averaged for each month (*cv*).

The set of candidate models (20 in total) included time, one measure of water level (considering different time lags: 10, 20, 30, 40 or 50 days before the sampling), one proxy for primary production (chlorophyll-*a* or total P concentrations) and one measure of environmental heterogeneity (*dc* or *cv*). We used Akaike's Information Criterion (AIC), AIC differences (delta AIC) over all candidate models in the set and Akaike's