Original Articles

Hard to predict: Synchrony in epiphytic biomass in a floodplain is independent of spatial proximity, environmental distance, and environmental synchrony

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ABSTRACT

Population synchrony occurs when local population abundances increase and decrease simultaneously over time. In terms of other characteristics that can be measured in ecosystems, such as biomass and nutrient content, intrinsic and extrinsic processes have also been used to explain synchronic variation patterns. Synchrony may clarify whether regional processes are more important than local processes. This study used epiphytic biomass data (chlorophyll-a) collected from eight locations in a floodplain over 11 years. The goal was to estimate epiphytic biomass synchrony. We anticipated that high synchrony levels would be consistent with the strong impact of floods, which affect different floodplain habitats simultaneously. This is equivalent to the Moran effect. In contrast, low synchrony levels would be consistent with the hypothesis that the high environmental heterogeneity of floodplains hampers synchrony. Our results indicated low synchrony, and its variation was not correlated with geographic or environmental distances nor with environmental synchrony. Also, regression models demonstrated low predictive power of local environmental variables in predicting biomass variation in the different sites. In addition, we performed a meta-analysis that confirms the generality of our findings. In conclusion, these results challenge the efficiency of epiphytic biomass as an ecological indicator, at least in floodplain systems.

1. Introduction

Frequently, even when distributed over large spatial extents, local populations vary synchronously, which means that their abundances increase and decrease concordantly through time (Liebhold et al., 2004). This concept was originally proposed by Moran (1952), and currently, it has been used to study the tendency of populations, communities, and ecosystem properties to vary similarly in different locations throughout time. Spatial synchrony can result from spatially correlated environmental stochasticity (Moran's effect), dispersal-related effects and trophic interactions, even though these effects are difficult to disentangle (Abbott, 2007; Walter et al., 2017). For ecosystem variables, such as biomass and nutrient concentrations, the concepts of temporal coherence and intrinsic/local and extrinsic/regional forces have also been used to describe and explain synchronic patterns (Kratz et al., 1998; Magnuson et al., 1990; Rusak et al., 1999). Temporal coherence occurs when temporal series of environmental or ecosystem variables (e.g., temperature, biomass, and nutrient concentrations) from different locations oscillate similarly (e.g., Baines et al., 2000). From this pattern, one can infer that extrinsic/regional processes (e.g., climate) are more important than intrinsic/local processes (e.g., point sources of nutrients) in controlling the dynamics of the variable of interest. Conversely, intrinsic/local processes are likely to be more important in the case of low levels of temporal coherence.

Epiphytic biomass has been found to respond predictably to different types of environmental variation, either natural or human-induced (e.g., Gaiser, 2009; DeNicola & Kelly, 2014). For example, epiphytic biomass has been shown to correlate significantly with nutrient concentrations (mainly total phosphorus and total nitrogen), flood frequency, land use, temperature, light availability and flow (Horner et al., 1990; Jacoby et al., 1991; Lohman et al., 1992; Dodds et al., 2002; McNair and Chow-Fraser, 2003; Carr et al., 2005; Mahdy et al., 2015; Huang et al., in press; McCall et al., 2017). Gaiser (2009) summarized, inter alia, the following key features that make epiphytic biomass a reliable ecological indicator: (i) wide spatial distribution and (ii) rapid response to environmental change. Because of its spatial distribution within aquatic ecosystems (land-water interface), epiphyton may be among the first to respond to external nutrient loading.

Thus, epiphyton may potentially be a useful early warning of eutrophication processes (Lambert et al., 2008; Rosenberger et al., 2008). In this context, epiphytic biomass in floodplains may provide an ideal model system to study synchrony. For example, in addition to the factors mentioned above, epiphytic biomass may respond to several regional factors, including altitudinal variations (He et al., 2015) and temperature (Ren et al., 2013). Also, floodplains are characterized by high landscape heterogeneity (Tockner, 2010) and the strong environmental changes caused by floods (Junk et al., 1989; Tockner et al., 2000). One may hypothesize, for example, that seasonal floods synchronize the population dynamics of several species and different ecosystem processes as they operate at regional scales (Bozelli et al., 2015; Thomaz et al., 2007).

The main objective of this study was to quantify the strength of synchrony in epiphytic biomass among different habitats in the Upper Paraná River floodplain (Brazil). First, we hypothesized that high levels of synchrony would be consistent with the strong impacts of floods, affecting different habitats simultaneously. In contrast, low levels of synchrony would be consistent with the hypothesis of a higher importance of environmental heterogeneity (across space), since floodplains are considered a mosaic of habitat patches (Ward and Stanford, 1995a,b). In other words, floods would not be sufficient to homogenize the environmental conditions at the floodplain scale and, consequently, synchronize epiphytic biomass dynamics. Second, we also modeled synchrony to explore the possible mechanisms underlying its variation. We predicted a negative relationship between biomass synchrony and the following two predictors: geographic distance and environmental distance. We also predicted a positive relationship between biomass synchrony and environmental synchrony. Third, we conducted a meta-analysis of studies on algal biomass synchrony to place our study in a broader context. Fourth, we investigated the influence of local and regional factors (nutrients, light availability and water level) on the site-specific dynamics of epiphytic biomass. If low synchrony is observed, we expect high predictive values of local environmental variables.

2. Methods

2.1. Study area

We carried out this study in the Upper Paraná River floodplain, located at the border of the states of Mato Grosso do Sul and Paraná, Brazil. In addition to the region under the influence of the main channel (Paraná River), the Ivinhema and Baia Rivers are two tributaries that contribute to the landscape heterogeneity of the Upper Paraná River floodplain (Padial et al., 2012). The spatial extent of our study was approximately 60 km long, and we sampled eight sites that are under the influence of the hydrological regime of these three rivers (i.e., Paraná, Ivinhema and Baia; Souza-Filho et al., 2004; Fig. 1). We carried out 37 sampling campaigns from 2000 to 2010 during the months of March, May, August and November. Some months were not sampled due to logistical problems (see Fig. 2). Our study is part of a long-term ecological research project, which started in 2000 (see http://www.peld.uem.br/). In general, this sampling frequency was similar to those of previous studies addressing algae biomass synchrony (see references in Table 4).

2.2. Data

Sixteen limnological variables were obtained at the subsurface of the water column (approx. 50 cm). In the field, we used a Secchi disk and YSI equipment to measure water transparency, water temperature and the dissolved oxygen concentration. Also, we measured pH, conductivity (Digimed portable meters) and total alkalinity (Carmouze, 1994). Turbidity values were obtained using a portable turbidimeter (LaMotte). Water samples were analyzed for phytoplankton biomass (chlorophyll-a), total nitrogen, nitrate, ammoniacal nitrogen, total

phosphorus, orthophosphate, organic suspended solids, inorganic suspended solids, and total suspended solids according to standard methods (Bergamin et al., 1978; Giné et al., 1980; Golterman et al., 1978; Mackereth et al., 1978; Wetzel and Likens, 2000).

We quantified the epiphyton biomass that adhered to petioles of *Eichhornia azurea* (Sw.) Kunth, which is one of the most ubiquitous aquatic macrophytes in the Upper Paraná River floodplain. In the laboratory, we used a stainless-steel blade and distilled water jets to scrape the epiphyton material from the petioles into a flask. Next, the resultant volume was filtered (using Whatman GF/C filters) and analyzed for chlorophyll-*a* concentration according to Golterman et al. (1978).

2.3. Data analysis

2.3.1. Spatial synchrony

We estimated the synchrony in epiphytic biomass between pairs of sampling sites using the Pearson correlation coefficient. The original dataset used for this analysis was a matrix containing the values of epiphytic biomass for each sampling site (in the columns) across sampling months (in the rows). Thus, a high (positive) Pearson coefficient would indicate that the epiphytic biomass values of a particular pair of sampling sites vary synchronously. Using the mean of the off-diagonal elements of the resultant **R** matrix (8×8), we estimated the floodplain-wide level of synchrony. To estimate a confidence interval (95%) for this mean, we used a bootstrap method described by Bjørnstad et al. (1999). These analyses were carried out using the function *mSynch* of the *ncf* package (Bjørnstad, 2013) in the R software (R Core Team, 2013).

2.3.2. Environmental synchrony

We used the same procedures described above to estimate a matrix of environmental synchrony separately for each environmental variable. The corresponding elements of these matrices were averaged to yield a single matrix of environmental synchrony (**E**). We also calculated an environmental distance matrix (**D**). For this purpose, we used the data of environmental variables over time to calculate the averages per sampling site. This matrix of averages (8 sampling sites $\times$ 16 variables) was then used to calculate the standardized Euclidean distance between sampling sites (8×8). We also calculated a geographic distance matrix (Euclidean) between sites (**G**) based on their geographic coordinates.

We used the Mantel test (Mantel, 1967) to model the relationships between the matrix **R** and matrixes **E**, **D**, and **G**. Therefore, we tested whether the values of epiphytic biomass synchrony (**R**) were more correlated to environmental synchrony (**E**), environmental distance (**D**) or geographical distance (**G**). The Mantel tests were carried out using the *ecodist* package (Goslee and Urban, 2007) in R (R Core Team, 2013), with 999 permutations.

2.3.3. GLS models

We used a generalized least squares (GLS) regression to model the temporal variation of epiphytic biomass for each site as a function of a preselected set of environmental variables (temperature, coefficient of light attenuation, water level, total nitrogen and total phosphorus concentrations). The coefficient of attenuation was estimated as described by Padial and Thomaz (2008). These variables are commonly used to predict variation in epiphytic biomass (Lambert et al., 2008; McNair and Chow-Fraser, 2003). Because our dataset has unequal time intervals, we used a statistical framework adapted from spatial statistical models that allows for irregularly spaced data in time series (see chapter 7 in Zuur et al., 2009). We used five correlation structures: spherical, rational quadratic, exponential, Gaussian and linear. Each of these options implies a specific structure to account for autocorrelation patterns (Zuur et al., 2009). The GLS models were fitted assuming these different correlation structures, and the best model was selected