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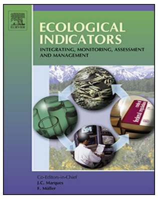

Original Articles

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.

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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 × 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

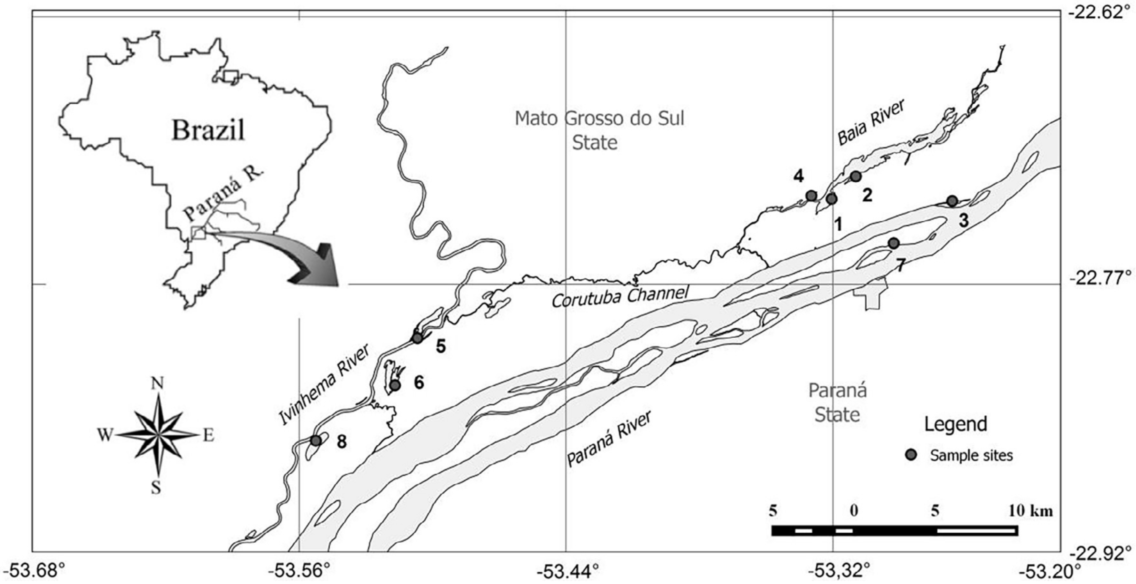

Fig. 1. Sampling sites monitored in the long-term ecological research program in the Upper Paraná River floodplain, Paraná, Brazil.

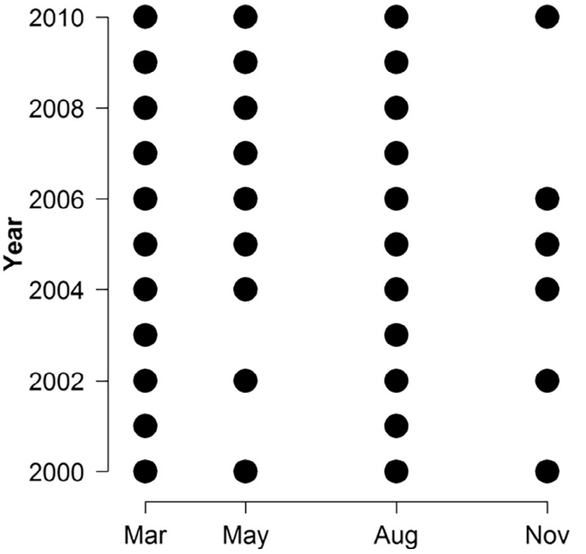

Fig. 2. Sampling schedule of the study in the Upper Paraná River floodplain. Eight sites were studied (see Fig. 1).

according to the Akaike information criterion (AIC) (Akaike, 1974). We used the *nlme* package (Pinheiro et al., 2015) in R (R Core Team, 2013) for these analyses.

2.3.4. Meta-analysis

To compare our results to those available in the literature, we carried out a random-effects meta-analysis. We searched for primary studies (up to June 2015) in the Web of Knowledge (http://thomsonreuters.com/web-of-knowledge) and Scopus (http://www.scopus.com) databases. We used the following search string: "spatial synchrony" OR "temporal coherence*" AND "ecology" AND "chlorophyll-a*". We identified 1724 studies with this search. We excluded articles that (i) did not investigate patterns of spatial synchrony (or temporal coherence); (ii) did not present results based on chlorophyll-a data; and (iii) were carried out in marine environments. After applying these criteria, we selected 16 studies showing region-wide levels of synchrony (i.e., average correlation) for chlorophyll-a. For eight studies, we were also able to extract the correlation values between pairs of sampling sites along with the respective geographic distances between these sites. Correlation coefficients were extracted from the main text, tables and figures (*WebPlotDigitizer v. 3.8:* Rohatgi, 2015) of the articles.

As usual in a meta-analysis, we converted the correlation coefficients (r) to Fisher's z scale ($z = 0.5 \times \ln(1 + r/1 - r)$). The variance of z was estimated by $V_z = 1/n - 3$ (Borenstein et al., 2009), where n is the number of temporal samples used to estimate the level of synchrony (as given by the correlation coefficient). Subsequently, we calculated a correlation coefficient (Pearson) between pairwise synchrony and geographic distance for the 8 datasets (plus our dataset).

3. Results

All of the variables studied, except nitrate, organic suspended solids, ammoniacal nitrogen, and phytoplankton biomass, showed significant levels of synchrony. Levels of synchrony were also highly variable (Table 1). Epiphytic biomass (Fig. 3) showed low synchrony ($r_s = 0.21$, CI = 0.06–0.35), whereas water temperature and inorganic suspended solids were the variables with the highest and lowest mean levels of synchrony, respectively. Water temperature, orthophosphate, pH, total phosphorus, conductivity, and nitrate synchronies were significantly related to geographic distances (Table 1). We did not detect significant relationships between the epiphytic biomass synchrony and the explanatory matrices **E**, **D**, and **G** (Table 2).

The explanatory variables used to model the temporal variation of epiphytic biomass in each site ranged widely (see Fig. 4). For example, the total phosphorus and total nitrogen concentrations ranged from 13.5 to 313.6 μg/L (e.g., at site 4) and from 85.7 to 1000.9 μg/L (e.g., at site 7), respectively. The water temperature varied seasonally (and synchronously; see Table 1), between 16.8 and 32.3 °C (e.g., at site 8). The maximum variation in the light attenuation coefficient was recorded at site 8 ($0.2–3.4\,m^{-1}$). The water level also ranged widely, from 1.6 to 6.4 m. The model without a correlation structure was the best model according to the AIC values (Table 3). Thus, the use of a residual correlation structure did not improve our models. According to the best models, the temporal variation in epiphytic biomass was significantly related to total nitrogen at site 2 and to total phosphorous at sampling sites 5 and 6. No explanatory variable was significantly related to the temporal variation in epiphytic biomass for the other sites (1, 3, 4, 7 and 8; Table 3).

Region-wide levels of synchrony in algae biomass (from epiphyton

Table 1
Average synchrony and confidence intervals ($CI_{95\%}$) for each limnological variable monitored in the Upper Paraná River floodplain, Brazil. Mantel correlation tests evaluating the relationship between environmental synchrony and geographic distance are also shown (significant values are shown in bold).

Variable	Synchrony			Mantel	
	Average	Lower $CI_{95\%}$	Upper $CI_{95\%}$	r	P
Water temperature	**0.69**	0.27	0.97	**−0.56**	0.009
Total nitrogen	**0.52**	0.31	0.74	−0.41	0.066
Ortho-P	**0.38**	0.16	0.59	**−0.55**	0.015
Dissolved oxygen	**0.29**	0.08	0.62	−0.37	0.092
Alkalinity	**0.38**	0.28	0.51	−0.15	0.421
pH	**0.32**	0.2	0.5	**−0.35**	0.046
Total phosphorous	**0.20**	0.01	0.36	**−0.47**	0.02
Turbidity	**0.23**	0.04	0.48	−0.3	0.152
Secchi	**0.23**	0.13	0.36	−0.12	0.558
Conductivity	**0.25**	0.15	0.37	**−0.4**	0.035
Total Suspended Solids	**0.17**	0.05	0.35	−0.22	0.29
Inorganic Suspended Solids	**0.14**	0.01	0.29	−0.25	0.236
Organic Suspended Solids	0.11	−0.03	0.3	−0.17	0.437
N ammoniacal	0.06	−0.06	0.21	−0.27	0.194
Phytoplankton Chlorophyll-*a*	0.05	−0.05	0.15	−0.06	0.775
Nitrate	0.06	−0.04	0.22	**−0.49**	0.011

Table 2
Mantel correlations (rM) between synchrony in epiphytic biomass (**R**) and matrices **G** (geographic distances), **E** (environmental synchrony), and **D** (environmental distances).

Relationship	r_M	P
R ~ G	−0.14	0.520
R ~ E	0.30	0.236
R ~ D	−0.23	0.309

or phytoplankton samples) varied strongly among studies (Table 4). The weighted mean effect size was positive and significant ($z = 0.382 \pm 0.060$ SE; $CI_{95\%} = 0.26$ to 0.50, total $Q = 29.58$ $P = 0.01$; $k = 17$ studies) (Fig. 5). According to the I^2 statistic (see Borenstein et al., 2009), 46% of the observed variance among effect sizes is due to real differences between studies. In addition, correlation results based on the 242 pairwise correlations ($k = 9$ studies) revealed a negative relationship ($r = -0.54$; $CI_{95\%} = -0.44$ to -0.62) between correlation coefficients (synchrony) and geographic distances (Fig. 6).

4. Discussion

The mechanisms underlying synchrony can be extrinsic, such as regional processes (e.g., flooding) or intrinsic (different processes occurring with different intensities at different sites: herbivory, nutrient pulses, light limitation). The epiphytic biomass in the Upper Paraná River floodplain exhibited low spatial synchrony. This result is consistent with the view that the high spatial heterogeneity of floodplain environments (Tockner, 2010; Ward et al., 2002) softens the synchronization effects caused by floods. For instance, floodplains are characterized by high environmental heterogeneity resulting from aquatic systems with different hydrological behaviors that vary from stagnant waters to those with strong unidirectional flows. Also, there is evidence that the homogenizing effects of flood pulses are not always noticeable (Mayora et al., 2013). Thus, the low spatial synchrony in the Upper Paraná River floodplain implies considerable spatial differences in the patterns of temporal variation, indicating a strong effect of local conditions and, consequently, the low influence of regional factors. This

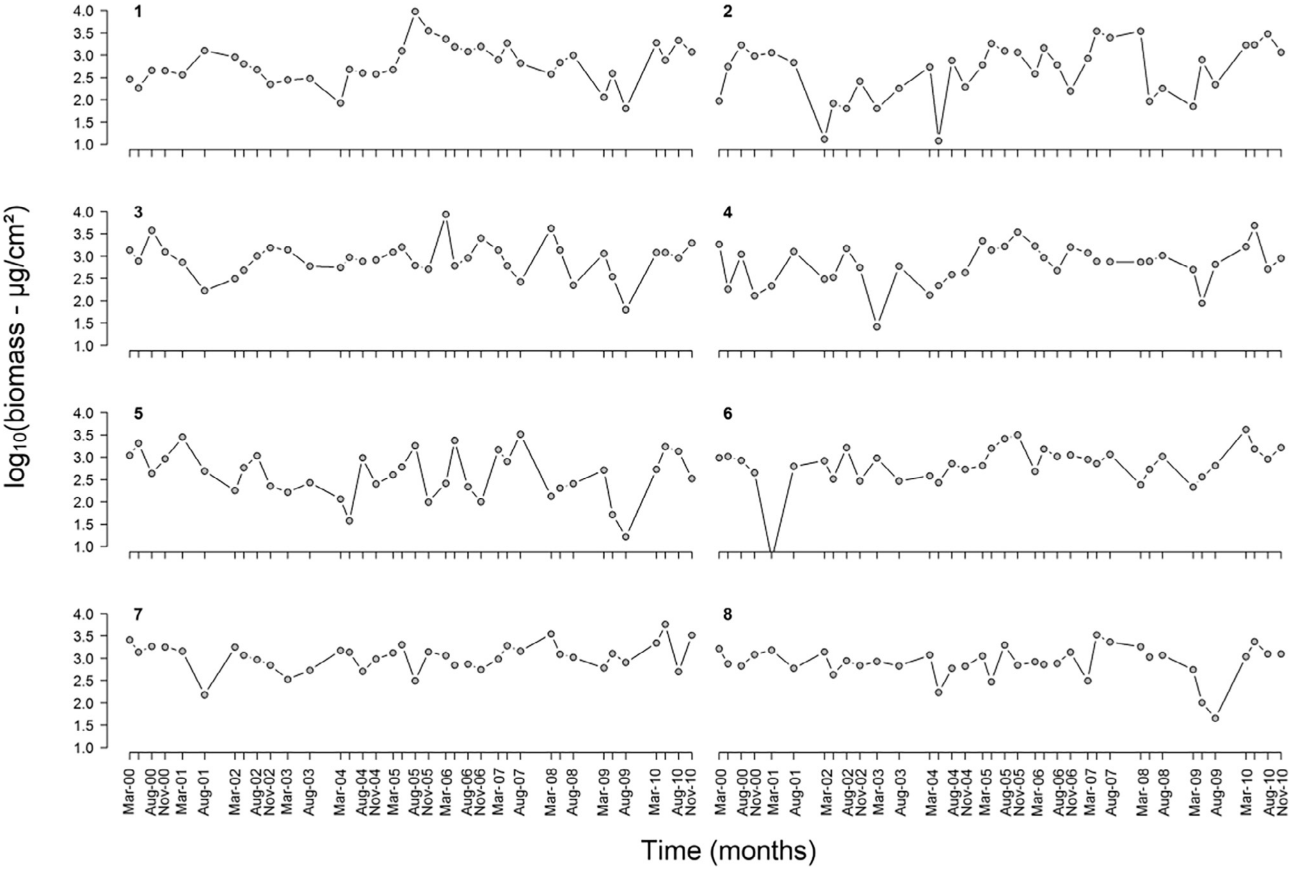

Fig. 3. Temporal variation (2000–2010) in the epiphytic biomass for different sites (1–8) in the Upper Paraná River floodplain, Paraná, Brazil.

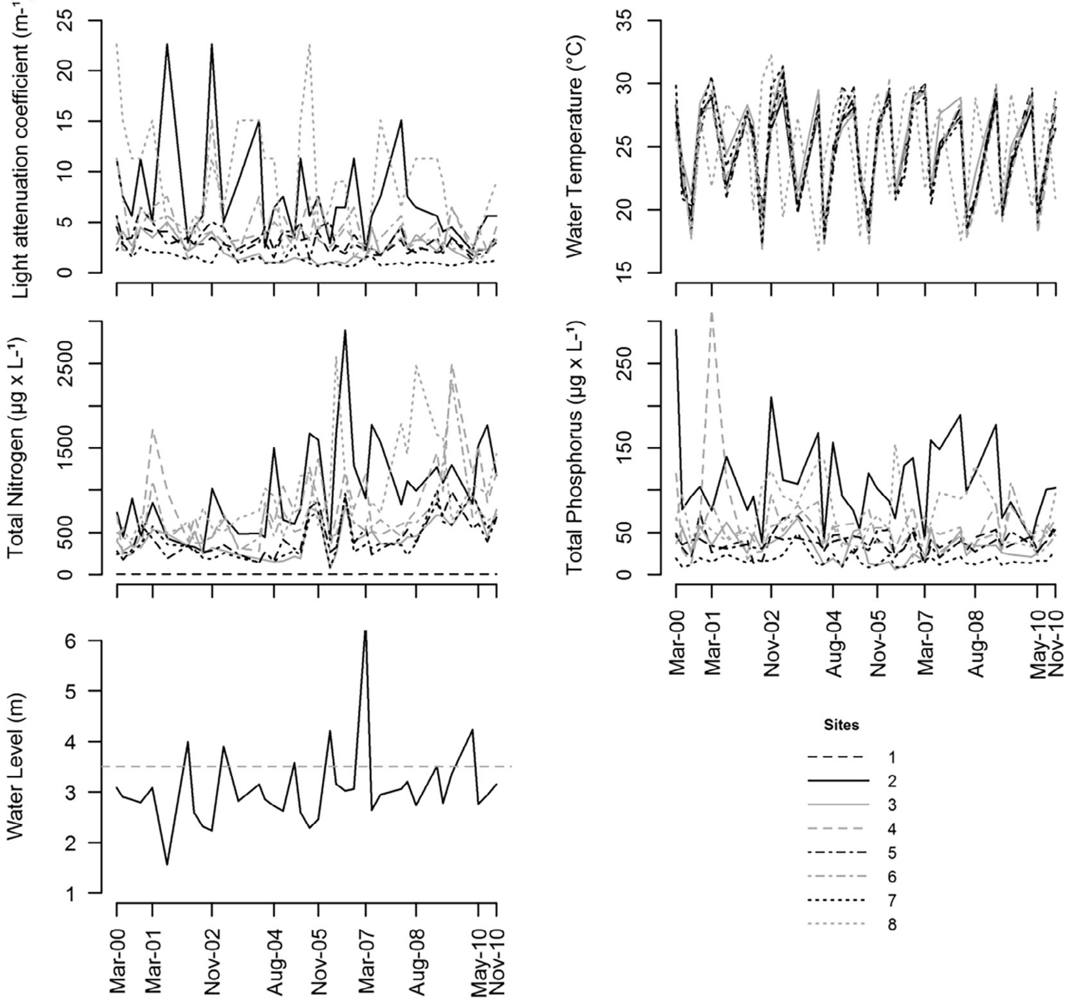

Fig. 4. Temporal variation of a selected set of environmental variables in the Upper Paraná River floodplain.

Table 3
Regression coefficients and AIC values for the GLS models (one model per sampling site: 1–8) explaining epiphytic biomass variation as a function of limnological variables in the Upper Paraná River floodplain. Correlation structures (CS); without correlation structure (WCS); spherical correlation (corSpher); linear correlation (corLin); rational quadratic correlation (corRatio); Gaussian correlation (corGau); and exponential correlation (corExp). Values in bold indicate statistically significant partial regression coefficients.

	Sites							
WCS	1	2	3	4	5	6	7	8
(Intercept)	2.803	2.640	2.939	2.807	2.611	2.831	3.043	2.903
Water temperature	0.004	0.102	0.022	−0.080	0.155	−0.097	−0.019	0.017
Attenuation coefficient	−0.061	0.253	−0.006	0.058	−0.007	0.177	0.014	0.058
Total nitrogen	0.039	**0.371**	−0.079	0.075	−0.086	0.047	0.024	−0.004
Total phosphorus	−0.081	−0.237	0.020	−0.085	**−0.305**	**−0.255**	−0.034	0.009
Water level	−0.068	−0.006	0.098	0.036	−0.118	0.079	0.057	−0.013

	AIC							
CS	1	2	3	4	5	6	7	8
WCS	75.01	87.71	66.04	76.37	78.16	73.68	53.99	64.69
corSpher	79.01	91.71	69.98	79.59	82.16	82.15	57.99	68.69
corLin	79.01	91.71	69.98	79.59	82.16	82.15	57.99	68.69
corRatio	79.01	91.71	69.46	79.52	82.15	82.15	57.99	68.69
corGaus	79.01	91.71	69.98	79.26	82.16	82.16	57.99	68.69
corExp	79.01	91.71	69.47	79.41	82.10	82.10	57.99	68.69

Table 4
Studies used to obtain the global effect size for chlorophyll-*a*. (r = mean synchrony; n = number of temporal samples in each study). * studies on epiphytic biomass; ** studies on benthic biomass.

Study	Year	r	Number of sites	n
This study*	2015	0.21	8	37
(Godwin and Carrick, 2008)*	2008	0.51	5	17
(Steinman et al., 2011)*	2011	0.00	3	16
(van der Wal et al., 2010)*	2010	0.07	7	72
(Magnuson et al., 1990)	1990	0.25	7	21
(Baines et al., 2000)	2000	0.29	7	58
(Anneville et al., 2005)	2005	0.31	4	27
(Vogt et al., 2011)	2011	0.57	6	120
(George et al., 2000)	2000	0.12	5	25
(McGowan et al., 2005)	2005	0.40	6	48
(Knowlton and Jones, 2007)	2007	0.13	4	17
(Patoine and Leavitt, 2006)**	2006	0.53	7	43
(Kling et al., 2000)	2000	0.70	10	20
(Webster et al., 2000)	2000	0.41	4	26
(Xu et al., 2010)	2010	0.54	26	36
(Xu et al., 2011)	2011	0.45	2	33
(Östman and Langenheder, 2013)	2013	0.04	16	8

result is similar to those obtained in other studies, such as Steinman et al. (2011) and Godwin and Carrick (2008), who also verified low epiphytic synchrony, suggesting the importance of local factors. In the same vein, Graba et al. (2013) demonstrated strong control of the local hydrological factors in epiphytic accrual.

In addition to the strong local component (low synchrony), we did not observe a significant relationship between synchrony and geographic distance, indicating that the synchrony may be lower or higher regardless of the distance between sampling sites. Although a negative relationship is commonly expected to occur between synchrony and distance (Koenig, 2002), there is evidence that this relationship is not universal (Fölster et al., 2005). Xu et al. (2012) on the other hand, found strong and weak patterns of synchrony for abundance and taxonomic composition of phytoplankton in two regions (mainstream and a tributary bay, respectively) of the Three Gorges Reservoir. However, when our data were merged with other data from the literature, we found a significant negative relationship between synchrony and geographic distance. Although not sufficient, this result suggests the importance of Moran's effect.

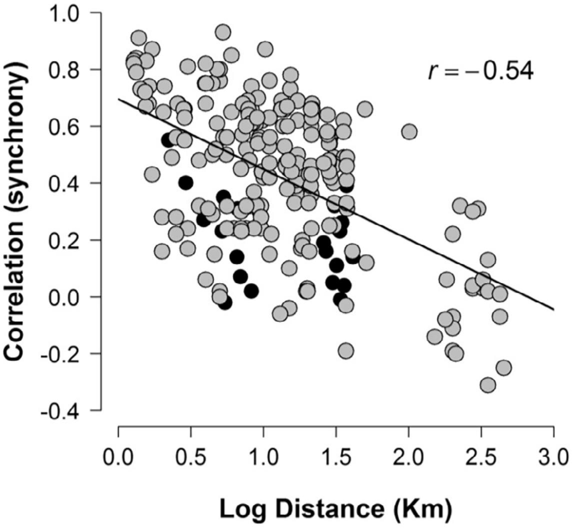

Fig. 6. Pairwise correlations (synchrony) against geographic distances for the 8 datasets from the literature (gray dots) plus the dataset obtained in this study (black dots).

The temporal dynamics of epiphytic biomass at the different sampling sites were not consistently predicted by our set of environmental variables. This result occurred despite the large variation in these variables, which would provide a large scope for changes in epiphytic biomass. This result probably occurs because epiphytic biomass has a fast response to local environmental variations. Also, because of its spatial distribution, epiphytic biomass may be strongly dependent on patchy processes occurring in adjacent terrestrial ecosystems (e.g., runoff and shading; Jacoby et al., 1991; Lambert et al., 2008), increasing the idiosyncrasy of epiphytic biomass dynamics. We also found low temporal autocorrelation (as indicated by the results of our GLS models, where the inclusion of residual autocorrelation structures was inconsequential; see Table 3). Thus, epiphytic biomass may be hard to predict even with the use of the variable itself as a lagged explanatory variable. Epiphytic biomass may exhibit low temporal autocorrelation for various reasons (e.g., short life cycle and fast response to environmental variations). The predictive power of models that include environmental explanatory variables is therefore likely to increase when

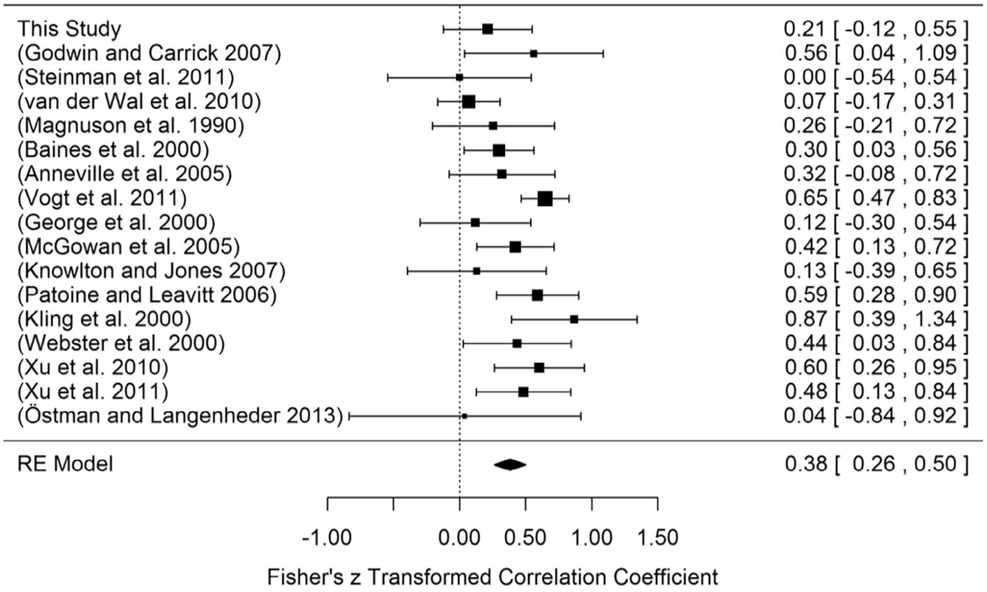

Fig. 5. Variation in the level of spatial synchrony of chlorophyll-a among different studies and the random effects estimate (filled diamond). The first four studies refer to epiphytic biomass, and the remaining studies correspond to phytoplankton biomass.

data are gathered in timescales equivalent to the epiphyton generation time.

Some of the aforementioned results, especially low synchrony levels (despite being significant) and the low relationship with geographic distance, are consistent with the available literature (see meta-analysis results). The low magnitude of synchrony has implications for biomonitoring programs since the biomass values observed in a single site would not reliably represent the dynamics of this variable in the floodplain as a whole. In other words, the results obtained in a single site could not be spatially extrapolated (or regionalized) due to low synchrony (Urquhart et al., 1998).

Epiphytic biomass responds quickly to local changes in light (Hill, 1996; Schiller et al., 2007; Fanta et al., 2010), nutrients (Hill et al., 2000; Hoyle et al., 2015), water level (Bondar-Kunze et al., 2015), substrate (Vadeboncoeur et al., 2006), herbivory (Hillebrand, 2009), and aquatic macrophyte composition (Souza et al., 2015). Accordingly, we found that epiphytic biomass was very hard to predict independently of the type of analysis. For instance, low synchrony values indicate that the temporal dynamics of epiphytic biomass at a given site were poorly predicted by those dynamics at other sites. Also, despite the wide variation in local environmental factors, we did not find strong correlates of epiphytic biomass dynamics (GLS models). Finally, the low levels of autocorrelation suggest a low capacity of past observations to predict future observations. These results challenge the efficiency of epiphytic biomass as an ecological indicator, at least in floodplain systems.

5. Conclusion

In conclusion, the low levels of synchrony in epiphytic biomass suggest that multiple sites should be monitored in Upper Paraná River floodplain. Environmental effects on epiphytic biomass variation are probably more likely to be detected in studies considering short time intervals between samples.

Author contributions

JEZ and LMB designed the study. LR and JEZ performed the field work and laboratory determinations. All authors contributed to the writing of the manuscript.

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