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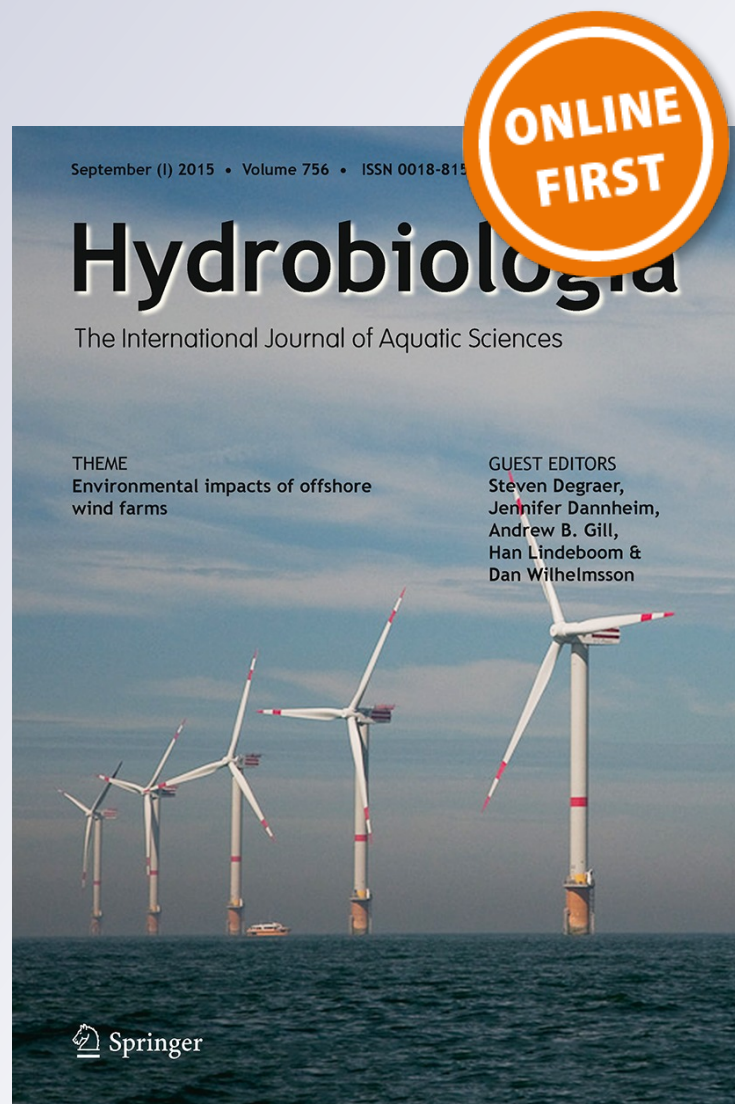
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# Unravelling the role of determinism and stochasticity in structuring the phytoplanktonic metacommunity of the Paraná River floodplain

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**Abstract** One of the ongoing debates around meta-community ecology is to what extent stochastic and deterministic processes act on community assembly. We explored the influence of both determinism, mediated by environmental filters, and stochasticity, mediated by dispersal and ecological drift, on phytoplankton assembly in a floodplain river. A probabilistic co-occurrence model revealed the presence of 94.1% random and 5.9% non-random species pairwise associations. The latter were higher at both hydrologically isolated (4.42%) and connected environments (2.2%). Variation partitioning analysis showed similar significant explanations by the unique environmental

(7.7%, Secchi, conductivity, vegetation, phosphorous) and spatial (7.2%, watercourse distance, longitude) components. Temporal variability was poorly represented (2.4%) because we only considered two low-water periods. Species co-occurrence patterns showed that most taxa coexist randomly. The environmental explanation is in line with niche-assembly models (species sorting), but the similar proportion explained by spatial organisation related to random dispersal guides the evidence to both deterministic and stochastic processes. The higher percentage of random co-occurrence and the larger assemblage variability observed in isolated environments suggests that random dispersal, ecological drift, and priority effects could promote stochasticity. We concluded that both processes affect the structure of phytoplankton metacommunities in a floodplain system and suggest the preponderance of stochastic organisation.

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Random associations

## Introduction

Floodplain rivers constitute a network of environments with different connectivity degrees and capability to exchange organisms and matter (Junk et al., 1989; Neiff, 1990). This configuration resembles that assumed by the metacommunity concept (Wilson,

1992) in which a set of local communities are linked by the dispersal of potentially interacting species. The metacommunity framework (Leibold et al., 2004; Heino et al., 2015) appears to be an appropriate theoretical basis to explain the organisational pattern of the biota in these systems, where the dispersal capacity and colonisation of species are mainly mediated by the hydrological fluctuations that connect and isolate with variable strength the main channel and floodplain waterbodies (Amoros & Bornette, 2002). In this context, local communities are not only the result of local factors, but also of other processes that take place at a regional scale (Ricklefs & Schluter, 1993; Cottenie, 2005).

At least four conceptual models were developed within the metacommunity theory, which explain the different mechanisms that shape community structure and organisation patterns (Leibold et al., 2004; Logue et al., 2011). The main difference among the models is the importance given to the deterministic and stochastic processes (Vergnon et al., 2009). The deterministic perspective assumes that the distribution of species depends on the ability of individuals to develop under environmental filtering and species interactions, and hence results in niche differentiation (Chase & Myers, 2011). The “dispersal-assembly perspective” (Hubbell, 2001) arises as a possibility of considering stochasticity in metacommunity framework as the main explanation of species diversity patterns. The ecological equivalence of individuals (neutrality) has been a controversial aspect of this model that proposes similar fitness among competing species. But more than that, it constitutes a simplification strategy that allows us to explore how community patterns arise from more complex processes such as stochastic dispersal and ecological drift (Hubbell, 2006). Stochasticity could be addressed from different views, and we define it as the changes in relative abundance among species that occur at random with respect to species identity due to individual demographic events (Vellend et al., 2014).

The phytoplankton of floodplain rivers has been largely studied through the niche-assembly perspective (van den Brink et al., 1993; Wehr & Descy, 1998; Amoros & Bornette, 2002; Descy et al., 2012), and it was suggested to be assorted with a great degree of determinism (Lewis et al., 2000). In the Paraná River Basin, the hydrosedimentological pulse is known as the macro-factor that steers phytoplankton composition

and abundance. Water discharge, water transparency, and current velocity that depend on this macro-factor are considered the main controlling factors in the main channel (O'Farrell et al., 1996; Train & Rodrigues, 1998; Devercelli, 2010; Cardoso et al., 2012). According to the lotic influence decrease during low-water periods and in the spatial gradient of connectivity, chemical factors, trophic interactions, and aquatic plant coverage gain importance as phytoplankton structuring factors, especially in the more isolated lakes and ponds (Izaguirre et al., 2001; O'Farrell et al., 2007; Zalocar de Domitrovic et al., 2007; Sinistro, 2010; Devercelli et al., 2014; Frau et al., 2015).

Contrarily to the deterministic perspective of most studies, Thorp et al. (2006) highlighted the potential of floodplain rivers to be dominated by stochastic processes and encouraged future researches in this area. In this sense, this paper contributes to the hypothesis that both determinism, mediated by environmental filters, and stochasticity, mediated by random dispersal and ecological drift, are overlapping forces acting on phytoplankton assembly in floodplain systems. We predict that stochastic process will predominate in rivers and connected lakes because high dispersal rate in these environments mediated by connectivity will promote random co-occurrence and lower species environmental matching, whereas deterministic processes will predominate in isolated environments where we expect strong constraint of species interactions and environmental filters.

Several observational approaches have been proposed to evaluate the relative importance of stochastic and deterministic processes regarding metacommunity structure. Among them, methods assessing species co-occurrence patterns and multivariate ordination analysis have been largely used (Gotelli & Graves, 1996; Legendre et al., 2005; Chase & Myers, 2011). Analyses of co-occurrence were particularly applied in the study of ecological interactions, community structure (MacKenzie et al., 2004; Ulrich & Zalewski, 2006; Kuebbing et al., 2013), species dispersal assembly (Driscoll & Lindenmayer, 2010), and environmental filtering (Silva & Batalha, 2010), among others. They were performed using different co-occurrence models as Veech (2014) reviewed (e.g. Patterson & Atmar, 1986; Gotelli, 2000; Sfenthourakis et al., 2006; Carstensen & Olesen, 2009; Arita et al., 2012). Recently, Veech (2013) developed a probabilistic method based on pairwise analysis that applies



probability-based equations to find non-random species pair associations. The frequency of non-random with respect to random associations can be used to estimate the importance of deterministic with respect to stochastic processes in a metacommunity assembly. In this work, the co-occurrence model proposed by Veech (2013) was used, and it was considered that the more the random species associations found in the analyses, the greater the relative importance of stochastic processes in structuring the metacommunity. Then, the more structured the species associations found (non-random co-occurrences), the greater the relative importance of the deterministic process involved.

Furthermore, multivariate ordination analysis initially used the degree of correlation of species matrix with relevant environmental variables to measure the strength of species–environment associations as evidence for deterministic processes. Current approaches utilise variance-partitioning methods to decompose variation of species matrix in unique and shared components of spatially, temporally, and environmentally correlated variation (Anderson & Gribble, 1998; Legendre & Gauthier, 2014). In this work, this method was applied to measure the strength of the association of phytoplankton with the environmental and spatial components of the system. On one hand, a significant correlation between phytoplankton and environmental variables would be indicative of niche selection process due to species-sorting mechanisms determining the turnover in species biovolume. The portion of variance explained by environmental variables is used as an evidence of deterministic processes on phytoplankton assembly. On the other hand, the amount of variance explained by spatial variables but unrelated with environmental variables would suggest a strong effect of random dispersal mediated by the connectivity and exchange of organisms among environments. Hence, it can be inferred that stochastic processes should be influencing metacommunity organisation.

Summarising, we used variance partitioning as a complementary method of the co-occurrence models to find out the contribution of stochastic and deterministic factors acting in phytoplankton assembly in the Paraná River floodplain. We included in the analyses the temporal variability that was due to the two low-water periods that we sampled for this study. Given the high number of environmental variables

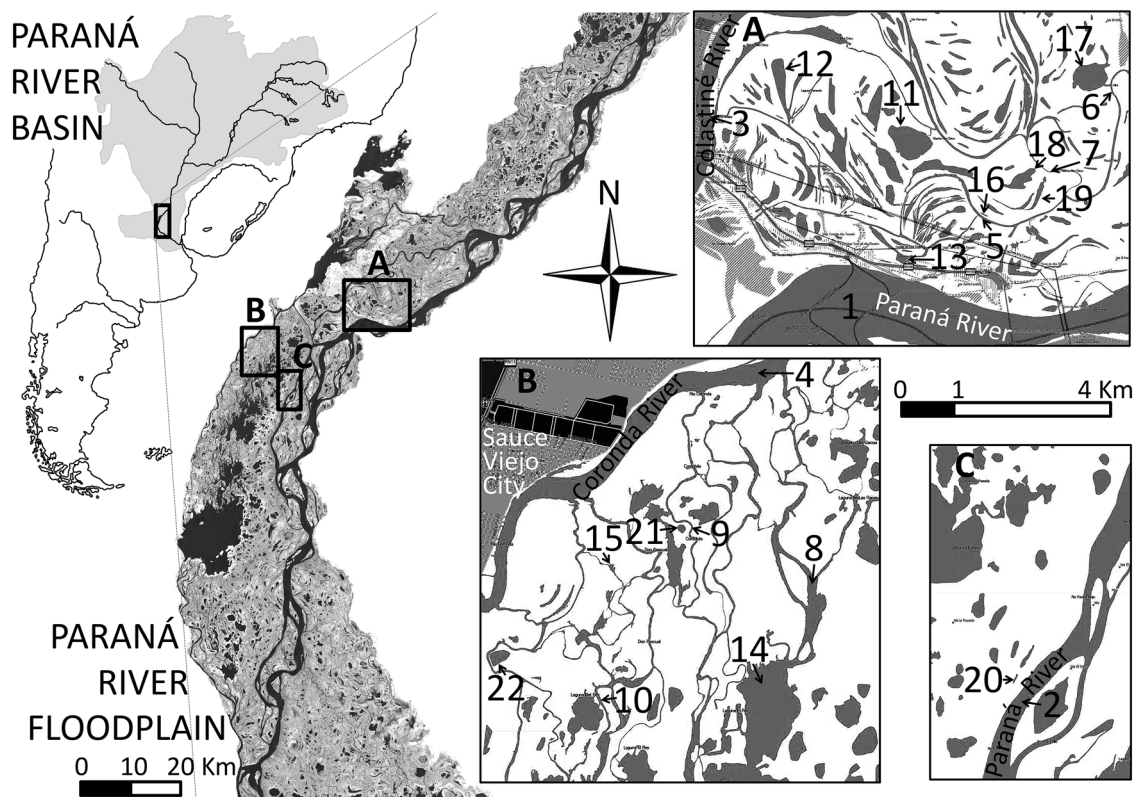
measured (21) and that most of them are known to be relevant for phytoplankton structuring, we assumed that we included in the analyses most of the environmental explicative factors for this assemblage (Vellend et al., 2014).

## Methods

### The Paraná River floodplain and selected sampling sites

The Paraná River flows from North to South along 3800 km, draining an area of  $2.6 \times 10^6 \text{ km}^2$  (Fig. 1). Downstream from the confluence with the Paraguay River, it reduces its general slope and receives a huge amount of sediments coming from the Andean tributaries (mainly Bermejo River). This process determines the development of a large floodplain about 20–30 km wide with a mosaic of geomorphologic units coexisting laterally (Amsler et al., 2007; Marchetti et al., 2013). Historical mean water discharge is about  $17,000 \text{ m}^3 \text{ s}^{-1}$ , and about 50% of the water flows through a well-defined main channel (0.4–8 km width) (Drago, 2007). The remaining percentage flows through large secondary channels (Colastiné River and Coronda River) and minor secondary channels. The geomorphologic units differ in the size, shape, and degree of hydrological connectivity of floodplain lakes and the several lentic waterbodies, as well as in the general topographic level, local relief, and composition of vegetation (Marchetti et al., 2013).

Two samplings that lasted 10 days each (November–December 2013, and March–April 2014) were performed during an early (3 months after isolation) and a late (7 months after isolation) low-water period. The hydrometric level information was obtained from the nearest Paraná Harbour gauge (Centro de Informaciones Meteorológicas, UNL). We selected twenty-two environments (Table 1; Fig. 1) with different hydrological connectivity and morphological features, as representative of the aquatic waterbodies of the sampled area. The spatial extent measured by the convex polygon, including all sampling sites, spanned  $344 \text{ km}^2$ . In a decreasing connectivity degree, we sampled four environment types: the main channel and large secondary channels (MC), minor secondary channels (SC), connected lakes (CL), and isolated lakes and swamps (ISL).



**Fig. 1** Map of a section of the Paraná River floodplain showing the placement of the study area. Numbers and arrows indicate the sampling sites (see Table 1 for references)

## Environmental variables

### Physical and chemical variables

Depth, subsurface water velocity (current metre), temperature, pH, dissolved oxygen (DO), total dissolved solids (TDS), conductivity (water quality checkers), and water transparency (Secchi disc depth) were measured in situ. Subsurface water samples for physical and chemical analyses were collected in duplicates, and transported on ice and in darkness to the laboratory. Turbidity (formazin turbidity units) was measured from unfiltered water at 450 nm with a spectrophotometer. Total phosphorous (TP) was estimated by digestion with nitric and hydrochloric acids followed by determination of soluble reactive phosphorous (SRP), and total nitrogen (TN) by digestion with potassium persulfate in alkaline medium followed by determination of nitrate + nitrite ( $\text{N-NO}_3^- + \text{N-NO}_2^-$ ). Water samples were filtered through membrane filters (0.45  $\mu\text{m}$  pore size) for determination of

dissolved components.  $\text{N-NO}_3^- + \text{N-NO}_2^-$  was estimated by reduction of  $\text{N-NO}_3^-$  with hydrazine sulphate and subsequent colorimetric determination of  $\text{N-NO}_2^-$  (Hilton & Rigg, 1983), ammonium ( $\text{N-NH}_4^+$ ) by the indophenol blue method, SRP by the ascorbic acid method, and silica ( $\text{SiO}_2$ ) by the molybdsilicate method. In all cases, the methods proposed in APHA (2005) were followed.

Chromophoric dissolved organic matter (CDOM) was analysed by UV-Vis spectroscopy (spectrophotometer HACH DR5000). Water colour (platinum-cobalt (Pt-Co),  $\text{mg l}^{-1}$ ) was measured at 455 nm. Optical density at 250, 365, 440, and 700 nm was determined using quartz cuvettes with 1 cm path length. Filtered Milli-Q water was used as a baseline. As the absorbance of the CDOM was assumed to be equal to zero above 700 nm, the absorbance at this wavelength was subtracted from all the rest to correct offsets. Absorption coefficients ( $\text{m}^{-1}$ ) were determined from the corrected optical density at 250, 365, and 440 nm according to Kirk (1994):  $A_\lambda = 2.300 D_\lambda/r$ ,

**Table 1** Mean values and standard deviations of environmental variables and ranges of variation for aquatic vegetation coverage, measured at each sampling site in the Paraná River floodplain. For the area of rivers and streams an arbitrary value was estimated equivalent to 10 times the channel width

Environments	Type	Code	Area (m <sup>2</sup> )	Depth (m)	Veg (%)	Cond ( $\mu\text{S cm}^{-1}$ )	DO (%)	Secchi (cm)
Paraná River	MC	1	5822.57	8.6 ± 0.3	0	78 ± 8	101.3 ± 23.6	21 ± 15
Paraná River	MC	2	109.56	4.0 ± 0.1	0	74 ± 2	88.3 ± 4.5	23 ± 16
Colastiné River	MC	3	134.93	7.1 ± 1.2	0	78 ± 1	93.9 ± 5.1	23 ± 17
Coronda River	MC	4	114.47	12.0 ± 0.1	0	332 ± 64	85.5 ± 1.4	23 ± 9
Correntoso Stream	SC	5	3.43	3.1 ± 0.3	21–60	87 ± 13	74.4 ± 2.9	25 ± 9
Correntoso Stream	SC	6	2.50	3.7 ± 0.1	21–40	82 ± 5	81.9 ± 20.0	27 ± 10
Colastiné de las Cruces Stream	SC	7	0.65	3.5 ± 0.2	21–60	82 ± 5	92.3 ± 37.3	23 ± 11
Cataratas Stream	SC	8	16.38	1.9 ± 0.5	1–40	157 ± 38	88.2 ± 2.8	25 ± 9
Cordobés Stream	SC	9	6.24	6.1 ± 0.6	1–40	255 ± 8	92.4 ± 13.5	22 ± 7
Pascual Stream	SC	10	2.33	4.4 ± 0.8	1–20	320 ± 46	93.8 ± 11.7	24 ± 13
Perla Lake	CL	11	86.00	0.9 ± 0.2	41–80	90 ± 9	29.5 ± 23.1	23 ± 12
Fernanda Lake	CL	12	57.16	2.0 ± 0.4	41–80	96 ± 19	69.1 ± 5.7	75 ± 4
Mimí Lake	CL	13	6.41	1.6	0	85	108.9	12
Blanca Lake	CL	14	262.00	0.9 ± 0.0	1–20	167 ± 44	66.4 ± 1.7	23 ± 9
Pascualito Lake	CL	15	1.78	0.9 ± 0.3	41–60	323 ± 36	82.9 ± 3.6	15 ± 7
Correntoso Swamp	ISL	16	0.42	0.3 ± 0.1	81–100	101 ± 27	11.2 ± 14.2	30 ± 7
Del Medio Lake	ISL	17	64.90	1.1 ± 0.3	21–40	70 ± 20	111.2 ± 11.1	54 ± 36
Chajá Lake	ISL	18	42.70	1.1 ± 0.0	41–100	70 ± 16	142.9 ± 21.4	110 ± 0
Chajacito Lake	ISL	19	22.20	0.8 ± 0.4	41–100	80 ± 26	75.5 ± 95.8	65 ± 57
Escondido Swamp	ISL	20	2.63	0.6 ± 0.1	61–100	72 ± 14	43.7 ± 58.9	53 ± 20
Chicana Lake	ISL	21	4.88	0.9 ± 0.1	61–100	290 ± 41	49.7 ± 4.5	66 ± 30
Curva Lake	ISL	22	7.31	0.8 ± 0.4	21–40	212 ± 42	88.6 ± 31.5	58 ± 59

Table 1 continued

Environments	Type	Code	Color (mg l <sup>-1</sup> ) Pt-Co	pH	SRP (μg l <sup>-1</sup> )	N-NO <sub>3</sub> <sup>-</sup> (μg l <sup>-1</sup> )	TN (μg l <sup>-1</sup> )	TP (μg l <sup>-1</sup> )	Total Phytoplankton (mm <sup>3</sup> l <sup>-1</sup> )
Paraná River	MC	1	34 ± 15	7.2 ± 0.4	27 ± 18	380 ± 112	1003 ± 275	107 ± 92	0.3112 ± 0.4127
Paraná River	MC	2	37 ± 13	7.5 ± 0.8	19 ± 9	399 ± 126	2829 ± 2578	171 ± 13	0.1497 ± 0.1213
Colastiné River	MC	3	22 ± 7	7.6 ± 0.3	23 ± 1	383 ± 90	434 ± 142	151 ± 126	0.3162 ± 0.4124
Coronda River	MC	4	53 ± 9	7.4 ± 0.1	84 ± 38	284 ± 109	652 ± 10	188 ± 16	0.2773
Correntoso Stream	SC	5	30 ± 1	6.8 ± 0.5	13 ± 7	296 ± 120	1255 ± 488	82 ± 53	1.5510 ± 1.9118
Correntoso Stream	SC	6	19 ± 9	7.0 ± 0.6	22 ± 13	357 ± 61	742 ± 300	61 ± 58	0.2169 ± 0.1670
Colastiné de las Cruces Stream	SC	7	25 ± 0	7.3 ± 0.1	19 ± 23	341 ± 129	595 ± 374	73 ± 32	3.2099 ± 3.3027
Cataratas Stream	SC	8	42 ± 10	7.2 ± 0.3	42 ± 25	254 ± 73	651 ± 148	156 ± 10	0.3706 ± 0.2155
Cordobés Stream	SC	9	57 ± 17	7.5 ± 0.4	66 ± 32	291 ± 31	638 ± 10	214 ± 16	0.5761 ± 0.4988
Pascual Stream	SC	10	60 ± 24	7.0 ± 0.3	95 ± 61	194 ± 81	1293 ± 963	156 ± 53	0.5804 ± 0.2110
Perla Lake	CL	11	24 ± 6	7.2 ± 0.5	12 ± 14	138 ± 60	838 ± 344	135 ± 68	5.2133 ± 0.0106
Fernanda Lake	CL	12	22 ± 8	7.4 ± 0.3	2 ± 3	64 ± 89	633 ± 269	43 ± 2	1.5059 ± 0.8807
Mini Lake	CL	13	12	7.4	45	366	548	129	0.0283
Blanca Lake	CL	14	45 ± 17	7.1 ± 0.1	47 ± 30	278 ± 135	563 ± 27	148 ± 8	0.2652 ± 0.0128
Pascualito Lake	CL	15	61 ± 33	7.2 ± 0.4	91 ± 57	207 ± 48	1350 ± 990	153 ± 51	0.9315 ± 0.8496
Correntoso Swamp	ISL	16	112 ± 37	6.5 ± 0.4	196 ± 14	96 ± 103	3268 ± 1461	894 ± 497	3.0043 ± 0.0861
Del Medio Lake	ISL	17	27 ± 13	7.1 ± 0.6	26 ± 1	127 ± 31	1279 ± 165	81 ± 7	0.9034 ± 0.5137
Chajá Lake	ISL	18	28 ± 2	7.1 ± 0.1	11 ± 16	89 ± 66	915 ± 30	65 ± 12	4.3250 ± 2.3054
Chajacito Lake	ISL	19	41 ± 11	7.1 ± 1.1	15 ± 1	54 ± 76	1484 ± 932	110 ± 80	1.7283 ± 1.0023
Escondido Swamp	ISL	20	43 ± 2	7.0 ± 0.4	7 ± 8	45 ± 48	778 ± 196	130 ± 105	17.4937 ± 13.6525
Chicana Lake	ISL	21	36 ± 3	7.4 ± 0.5	24 ± 8	4 ± 3	690 ± 10	144 ± 77	10.3530 ± 0.0824
Curva Lake	ISL	22	40 ± 13	7.1 ± 0.3	57 ± 38	0 ± 0	2150 ± 1553	3664 ± 5016	15.7713 ± 17.9660

Veg vegetation coverage, Cond conductivity



where  $A_\lambda$  is the CDOM absorption coefficient at wavelength  $\lambda$ ,  $D_\lambda$  is the corrected optical density at wavelength  $\lambda$ , and  $r$  is the cuvette path length in m.

The area and the perimeter of each aquatic environment on georeferenced satellite images were measured using Google Earth Pro (Trial version). For channels, the area and perimeter of a reach were measured with a length equivalent to 10 times the channel width. This factor was applied to represent the dominance of the longitudinal dimension of lotic environments to estimate habitat size. Additionally, the index of shoreline development (the ratio of the waterbody perimeter to the perimeter of a circle of equivalent area) was calculated as a measure of shoreline complexity.

#### *Aquatic vegetation*

The aquatic vegetation of each waterbody was surveyed by foot or from a boat moving at low velocity. The main stands of macrophytes were explored, and plants were recorded or collected for subsequent identification. Rakes were used when necessary to sample submerged taxa. Additionally, the total percentage cover of macrophytes was visually estimated in each waterbody, and a value was assigned according to the following scale: 0 (0% cover); 1 (1–20%); 2 (21–40%); 3 (41–60%); 4 (61–80%); and 5 (81–100%). Species were identified to the possible lowest taxonomic level according to Pott & Pott (2000).

#### *Spatial variables*

The spatial pattern was modelled by the method of trend surface analysis (Legendre & Legendre, 1998). This method uses the residuals of geographical coordinates of longitude ( $x$ ) and latitude ( $y$ ) to calculate the terms of a cubic polynomial function ( $x$ ,  $y$ ,  $x^2$ ,  $y^2$ ,  $xy^2$ ,  $yx^2$ ,  $x^3$ ,  $y^3$ ). This regression method is commonly used in spatial analysis to predict coarse non-linear patterns in a species matrix. As an estimator of connectivity, the watercourse distance was calculated as the minimal distance from the lake margin to the main channel or nearest secondary channel, and the overland distance was considered as the nearest distance on a straight line. It was expected that water course distance should capture the effect of water dispersal during low waters in permanent connected environments, whereas overland distance should

capture variation associated with water dispersal among all types of environments during high waters or dispersal by other ways (e.g. wind, birds) during low waters. All variables were measured by georeferenced satellite images, using Google Earth Pro.

#### *Phytoplankton*

Subsurface phytoplankton samples were collected, fixed in situ with Lugol's acidified solution (1% final concentration), and stored in bottles of 125 ml. Individuals were counted with an inverted microscope using settling chambers in which a known volume of water sample was sedimented (Utermöhl, 1958). Biovolume ( $\text{mm}^3 \text{ l}^{-1}$ ) was calculated multiplying density ( $\text{ind. ml}^{-1}$ ) by mean volume of each species based on geometric formulae and measures of individual dimensions (Hillebrand et al., 1999). 35 and 65% of the biovolume of pennate and centric diatoms, respectively, were extracted in order to consider the intracellular vacuoles (Round et al., 1990). Species occurring in less than 5% of the samples and representing less than 1% of total biovolume were excluded from phytoplankton matrices. Samples for taxonomic purposes were obtained with a 25  $\mu\text{m}$  pore net filtering at least 200 l, and fixed with formalin (2% final concentration).

#### *Statistical analyses*

PERMANOVA (9999 permutations,  $P$  value Bonferroni adjusted) was performed on Jaccard and Bray–Curtis triangular matrices to examine differences in the composition and biovolume, respectively, of phytoplankton species among the different types of environments (MC, SC, CL, ISL). The similarity percentage analysis (SIMPER) was used to identify which species contributed to the dissimilarities on phytoplankton structure. Past Software (version 3) was used to run the analyses mentioned. Non-metric multidimensional scaling (NMDS) was used to ordinate phytoplankton samples on the basis of species biovolume, using Chord distance measure to give low weight to rare species (Legendre & Gallagher, 2001). The stress value was used to represent the discrepancy between the distances on a two-dimensional graph and actual distances measured. This index varies from 0 to 100% indicating perfect matching to no-correspondence, respectively (Legendre & Legendre, 1998). We used  $<20\%$  as a

threshold value to determine if two dimensions were sufficient to represent the main data structure.

Compositional data were used to obtain the probability of pairwise species co-occurrence for finding evidence of whether the organising processes of the metacommunity were due to random or structured patterns. The probabilistic method proposed by Veech (2013) was used for testing co-occurrence, that is, distribution and metric free, and it has lower Type I and II errors than null models. It is useful for analysing large matrices of hundreds of species because it does not have the weakness of a randomisation algorithm producing partial sets of possible matrices (Griffith et al., 2014). The model obtains the probability that two species co-occur in a frequency, lower and/or greater than the co-occurrence frequency observed, and the total number that the two species could be distributed among the total studied sites. The probabilistic model classifies the species co-occurrence into positive, negative, and random. Positive associations are those species pairs that occur in the same site more often than expected by chance. Negative associations are those species that occur at the same site less often than expected by chance. Random associations are those pairs of species that do not deviate from their expected co-occurrences by more than  $0.1 \times$  the total number of sites (Pitta et al., 2012; Griffith et al., 2014). For the co-occurrence analysis, we used only the pairs of species with expected co-occurrence greater than 1. The species co-occurrence was evaluated for the whole system (42 sites), for all connected environment (MC + SC + CL = 28 sites), and for each type of environment (MC = 7; SC = 12; CL = 9; ISL = 14 sites). The analyses were done with the 'cooccur' package (R Development Core Team, 2008) developed by Griffith et al. (2014).

Variation partitioning analysis was used to determine the relative contribution of environmental and spatial factors to the variation in phytoplankton structure considering species biovolume. A third group of temporal variables was considered in order to include the variability that was due to the 2 samplings performed. First, a series of canonical correspondence analyses (CCA) were run to obtain the groups of environmental and spatial explanatory variables. Forward selection was performed to include in the CCA only those variables with a significant ( $P < 0.05$ ) association to the species matrix, reducing the degree of multicollinearity within each group.

Variance inflation factor (VIF) was used for testing collinearity among the predictors. For the temporal group, a dichotomous variable (dummy binary variable) was created to differentiate between both samplings and to consider the temporal variability (Anderson & Gribble, 1998). Then, a partial CCA (pCCA) was performed with the obtained environmental, spatial, and temporal groups of variables to partition the variation of the phytoplankton assemblage explained by independent variables into different components. We used the percentage of total explained variation (TVE) which is the variation explained by each component calculated as the ratio between the sum of all canonical eigenvalues and total inertia (Økland, 1999). Significance values in forward selection were adjusted using Bonferroni's correction as well as significance values in terms evaluation. Then AIC with finite sample correction was applied (Akaike, 1973). CCA and pCCA were run with the software CANOCO version 5 (ter Braak & Šmilauer, 2012).

## Results

### Environment

A wide range of physical and chemical conditions was observed between the sampling sites representing a wide environmental gradient for phytoplankton (Table 1). Water temperature varied among 20.6 and 30.0°C during the sampling periods. Noticeable changes along the connectivity gradient from MC to ISL were observed for mean values of  $\text{N-NO}_3^- + \text{N-NO}_2^-$  ( $383 \mu\text{g l}^{-1}$  in MC to  $59 \mu\text{g l}^{-1}$  in ISL),  $\text{SiO}_2$  (from 13.5 to  $9.2 \text{ mg l}^{-1}$ ), and Secchi disc (from 21 to 62 cm). The lowest conductivity values were observed in the MC. In most sites, water was moderately coloured ( $20\text{--}50 \text{ mg l}^{-1}$  Pt-Co) and well oxygenated. However, the swamps and some highly coloured lakes and streams (up to  $138 \text{ mg l}^{-1}$  Pt-Co) showed low values of DO (minimum value: 1.1%) and high SRP concentrations (up to  $206 \mu\text{g l}^{-1}$ ). In other sites, SRP varied from undetectable to  $60 \mu\text{g l}^{-1}$ . As regards TP and TN, the lowest average values were observed at SC ( $124$  and  $862 \mu\text{g l}^{-1}$ , respectively) and CL ( $121$  and  $813 \mu\text{g l}^{-1}$ , respectively), and the highest average value at ISL ( $727$  and  $1509 \mu\text{g l}^{-1}$ , respectively).

**Table 2** Differences in phytoplankton assemblage among environmental types of the Paraná River floodplain, performed with PERMANOVA, and based on species composition (a:

a:	Jaccard <i>P</i> values			
	MC	SC	CL	ISL
MC		1	0.5298	<b>0.0006</b>
SC			1	<b>0.0006</b>
CL				<b>0.0396</b>
ISL				

Jaccard *P* values) and species biovolume (b: Bray–Curtis *P* values, and SIMPER percentage of overall average dissimilarities)

b:	Bray–Curtis dissimilarity \ <i>P</i> values			
	MC (%)	SC (%)	CL (%)	ISL
		1	1	<b>0.0012</b>
	87.2		1	<b>0.0006</b>
	91.11	88.55		<b>0.0174</b>
	97.25	94.57	94.21%	

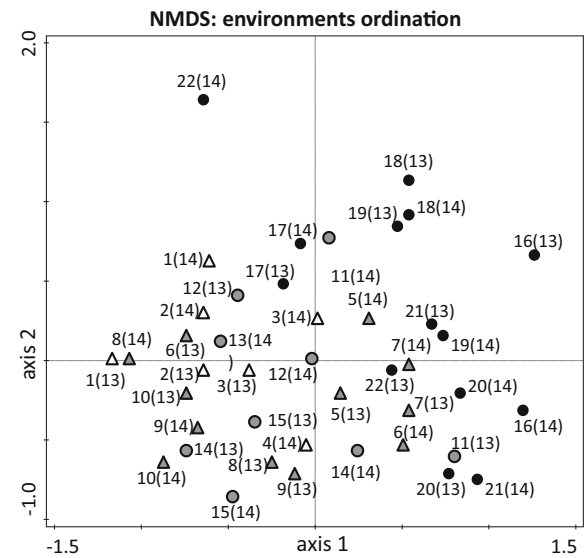
Significant values are indicated with bold letter

The aquatic vegetation was mainly represented by emergent species that predominated both in lakes and channels. Free-floating and rooted-floating species decreased from SC to CL and from ISL to MC, respectively. Submerged macrophytes were the poorest represented life form, which were more frequent in transparent ISL. The most common species was the free-floating *Eichhornia crassipes* (Mart.) Solms, followed by the rooted emergent *Paspalum repens* Bergius and *Ludwigia peploides* (Kunth) Raven, and the free-floating *Salvinia biloba* Raddi and *Azolla* sp.

Phytoplankton

We found a total of 308 algal species for the whole system and a local richness between 8 and 98 species. Phytoplankton biovolume ranged between 0.02 and 28.48 mm<sup>3</sup> l<sup>-1</sup> for the whole system. PERMANOVA showed that species composition differed significantly among the four environment types (Jaccard Index: *F* = 1.567; *P* = 0.0001), as well as phytoplankton structure considering species biovolume (Bray–Curtis index: *F* = 1.685; *P* = 0.0001). For both, differences were found among the isolated lakes and swamps (ISL) and the connected environments (MC, SC, CL) (Table 2). SIMPER showed that the dissimilarity among overall environment types was of 92%, and 42 species (Table 4) were responsible of the 70% of the dissimilarity.

Accordingly, the samples of ISL environments were arranged on the right side of the NMDS graph (Fig. 2), whereas the connected environments were plotted on the left side. The second axis accounted for the variation in the phytoplankton structure of sites and samplings within each type of environments. ISL lakes exhibited more dispersion along the second axis



**Fig. 2** First two axes of NMDS based on phytoplankton biovolume, showing the ordination of sampling sites (see Table 1 for references), sampling periods (indicated between brackets (13: November–December 2013; 14: March–April 2014), and different environmental types (MC: open triangles; SC: grey triangles; LC: grey circles; ISL: black circles)

in comparison with the other types of environment. Stress value was 13.88%, indicating that the two axes were sufficient to represent assemblage variations.

Species co-occurrence revealed a high percentage of random association for the whole data set, and 5.9% of non-random significant associations (Table 3). Regarding the connected and ISL environments, a slightly higher percentage of non-random associations was found in the former (4.42 vs. 2.2%, respectively). The unclassified number of co-occurrences was higher in ISL. They represent pairs of species with low statistical power to classify, being the cutoff 10%. The

**Table 3** Co-occurrence results from the probabilistic model based on phytoplankton species (presence–absence), considering different types of environments in the Paraná River floodplain

Environments	Spp. no	Total combination pairs Pairs removed Pairs analysed	No of associations				%	
			Pos	Neg	Rand	Unclass	Non-rand	Rand
All ( $n = 42$ )	284	30,628 24,047 (79%) 6581	308	83	6058	132	5.9	94.1
Connected ( $n = 28$ )	230	26,335 21,747 (83%) 4588	178	26	4384	0	4.42	95.55
MC ( $n = 7$ )	93	4278 3821 (89%) 457	8	0	341	108	1.8	98.2
SC ( $n = 12$ )	161	12,880 10,617 (82%) 2263	38	22	2021	182	2.7	97.3
CL ( $n = 9$ )	181	16,290 14,092 (87%) 2198	50	8	1672	468	2.6	97.4
ISL ( $n = 14$ )	237	27,966 23,130 (83%) 4836	78	30	4506	222	2.2	97.76

*Pos* positive; *Neg* negative; *Rand* random; *Unclass* unclassified

frequency of non-random positive co-occurrences increased with decreasing connectivity among environment types, with the highest frequency observed in ISL and the lowest in MC (Table 4). This pattern agreed with the species richness of these environments (Table 3).

From a matrix of 21 environmental variables (waterbody area, index of shore line, depth, vegetation coverage, water temperature, Secchi disc depth, turbidity, conductivity, pH, DO, TDS, SRP,  $\text{N-NO}_3^- + \text{N-NO}_2^-$ ,  $\text{N-NH}_4^+$ , TP, TN,  $\text{SiO}_2$ , colour,  $A_{440}$ ,  $A_{365}$ ,  $A_{250}$ ), forward selection included Secchi disc depth, conductivity, and vegetation coverage in the CCA model that best explained phytoplankton structure ( $P = 0.008$ ) (Online Resource 1). TP was also retained in the analysis but with less significance ( $P = 0.048$ ). Among the available spatial variables, longitude ( $x$ ,  $x^3$ ) and watercourse distance were retained by forward selection with significant explanation power ( $P = 0.01$ ) (Online Resource 2).

The pCCA including environmental, spatial, and temporal variables explained 17.8% of the adjusted total variation of species-by-site matrix. Variation

partitioning showed a similar amount of variation explained by the unique (non-overlap) components of environmental (7.7%) and spatial variables (7.2%), whereas temporal variables explained a low fraction of phytoplankton variability (Table 5). Environmental and spatial variables showed a small significant shared component, indicating that a portion of the environmental variation relevant to phytoplankton was spatially structured (1%). All the tested fractions were significant at  $P < 0.001$ , except the temporal fraction in combination with the shared environmental fraction that was significant at  $P < 0.002$ . The unexplained variation was 82.2%.

## Discussion

Metacommunity theoretical framework enables us to empirically find out the different processes acting at different spatial scales in the organisms assembly of floodplain rivers and captures the emergent biocomplexity. We found evidence for both stochastic and deterministic mechanisms that affect the structure of

**Table 4** Phytoplankton species contributing to 70% dissimilarity among the types of environments of the Paraná River floodplain, performed with SIMPER analysis (Bray–Curtis index)

	Contribution (%)	Mean biovolume (mm <sup>3</sup> l <sup>-1</sup> )			
		MC	SC	CL	ISL
<i>Peridinium</i> sp.	6.187	0.0096	0.0323	0.0930	0.8260
<i>Pinnularia major</i> (Kützing) Rabenhorst	5.024	0.0027	0.0692	0.0201	0.2510
<i>Aulacoseira granulata</i> (Ehrenberg) Simonsen	3.455	0.0124	0.0720	0.0602	0.0000
<i>Trachelomonas curta</i> Da Cunha	3.421	0.0027	0.0185	0.0139	0.2900
<i>Ceratium furcoides</i> (Levander) Langhans	3.375	0.0000	0.0000	0.0000	0.1920
<i>Synura uvella</i> Ehrenberg	3.341	0.0003	0.1120	0.0291	0.2700
<i>Cyclotella meneghiniana</i> Kützing	3.178	0.0183	0.0428	0.0369	0.0091
<i>Spirogyra</i> sp.	3.042	0.0000	0.0000	0.0000	0.5210
<i>Strombomonas gibberosa</i> (Playfair) Deflandre	2.928	0.0360	0.0168	0.0355	0.0155
<i>Woronichinia</i> cf. <i>delicatula</i> (Skuja) Komárek et Hindák	2.718	0.0000	0.0000	0.0332	0.1340
<i>Oedogonium</i> sp.	2.521	0.0000	0.0000	0.1050	0.2640
<i>Cryptomonas</i> sp.	2.355	0.0160	0.0312	0.0564	0.1980
<i>Ulnaria ulna</i> (Nitzsch) Compère	1.611	0.0000	0.0000	0.1930	0.0229
<i>Trachelomonas volvocina</i> Ehrenberg	1.564	0.0000	0.0000	0.1380	0.0248
<i>Aulacoseira italica</i> (Ehrenberg) Simonsen	1.424	0.0145	0.0048	0.0484	0.0119
<i>Amphora</i> sp.	1.402	0.0000	0.0000	0.0552	0.1430
<i>Coelastrum pseudomicroporum</i> Korshikov	1.396	0.0000	0.0000	0.0000	0.5080
<i>Staurastrum leptocladum</i> Nordstedt	1.293	0.0000	0.0000	0.0000	0.0797
Chroococcal n.i.	1.277	0.0000	0.0000	0.0000	0.1160
<i>Euglena polymorpha</i> Dangeard	1.247	0.0000	0.0176	0.0000	0.0902
<i>Microcystis aeruginosa</i> Kützing	1.243	0.0121	0.0282	0.0000	0.0000
<i>Protoperidinium achromaticum</i> (Levander) Balech	1.097	0.0000	0.0000	0.0000	0.0912
<i>Scenedesmus opoliensis</i> Richter	1.002	0.0000	0.0003	0.0000	0.4390
Pennate diatom sp.1	0.9614	0.0005	0.0063	0.0017	0.0403
<i>Trachelomonas intermedia</i> Dangeard	0.9363	0.0000	0.0108	0.0006	0.0498
<i>Staurodesmus glaber</i> (Ralfs) Teiling	0.9011	0.0000	0.0000	0.0000	0.0460
<i>Lepocinclis</i> sp.	0.8728	0.0000	0.0026	0.0062	0.1100
<i>Eudorina elegans</i> Ehrenberg	0.8506	0.0000	0.0000	0.0000	0.0257
<i>Trachelomonas oblonga</i> Lemmermann	0.8163	0.0021	0.0085	0.0072	0.0310
<i>Cryptomonas</i> cf. <i>erosa</i> Ehrenberg	0.809	0.0066	0.0095	0.0010	0.1100
<i>Pteromonas angulosa</i> Lemmermann	0.7983	0.0013	0.0087	0.0019	0.0098
<i>Nitzschia</i> sp.	0.7788	0.0307	0.0000	0.0000	0.0000
<i>Trachelomonas</i> cf. <i>rotunda</i> Svirenko	0.7685	0.0000	0.0061	0.0000	0.1350
<i>Oscillatoria</i> n.i.	0.7657	0.0003	0.0024	0.0421	0.0077
<i>Euglena</i> cf. <i>gaumei</i> Allorge et Lefèvre	0.7237	0.0028	0.0069	0.0168	0.0190
<i>Dolichospermum</i> sp.	0.7221	0.0000	0.0000	0.0321	0.0511
<i>Skeletonema potamos</i> (Weber) Hasle	0.696	0.0151	0.0122	0.0007	0.0003
<i>Scenedesmus disciformis</i> (Chodat) Fott et Komárek	0.6682	0.0002	0.0000	0.0000	0.2870
<i>Eunotia</i> sp.	0.5743	0.0005	0.0099	0.0137	0.0028
<i>Oocystis</i> sp.	0.529	0.0012	0.0021	0.0048	0.0831
<i>Aphanocapsa planctonica</i> (Smith) Komárek et Anagnostidis	0.5013	0.0000	0.0000	0.0249	0.0097
<i>Anabaenopsis elenkinii</i> Miller	0.4972	0.0000	0.0000	0.0519	0.0000



**Table 5** Variation partitioning of phytoplankton species biovolume based on pCCA, according to environmental (env), spatial (space), and temporal (time) components. All fractions were significant at  $P = 0.002$

Permutation test: on all axes, pseudo- $F = 2.3$ ,  $P = 0.001$

Fractions	Explained variation		
	Adjusted	%	% of all
Env	0.7357	43.1	7.7
Space	0.6860	40.2	7.2
Time	0.2258	13.2	2.4
Env   space	0.0949	5.6	1.0
Space   time	-0.0169	-1.0	-0.2
Env   time	-0.0222	-1.3	-0.2
Env   space   time	0.0040	0.2	<0.1
Total explained	1.7072	100	17.8
All variation	9.5802		100

the phytoplankton metacommunity at the Paraná system. Even when this is a well-known fact, few phytoplankton studies support this idea in floodplains or complex river networks (Liu et al., 2013; Padial et al., 2014), probably due to less evidence looked for to verify stochastic processes in comparison with niche-related processes. Evidences obtained by our study showed a strong stochasticity according to the metacommunity species structure, probably due to dispersal mechanisms, priority effects, and demographic stochasticity (Vellend et al., 2014). Vanormelingen et al. (2008) and Angeler et al. (2010) found stronger environmental influence, whereas Nabout et al. (2009) prompt a degree of unpredictability in phytoplankton organisation. In agreement with our findings, Thorp et al. (2006) held a series of model tenets in the “Riverine Ecosystem Synthesis” in which it is stated that deterministic and stochastic factors contribute significantly to community regulation. Evidences for both factors structuring phytoplankton were found in many other ecosystems (e.g. Beisner et al., 2006; Gravel et al., 2006; Soininen et al., 2007, 2013; Chust et al., 2013; Heino et al., 2014), and the degree to which community variation consents with deterministic ones and stochasticity may be related to specific habitats. In this respect, Thorp et al. (2006) argued that stochastic factors are more important than deterministic throughout floodplain rivers.

The co-occurrence probabilistic model (Veech, 2013) applied in this study to find evidence of random and non-random phytoplankton associations was for the first time empirically applied to a large species data set. Species co-occurrence showed that most of the species coexist randomly; hence, phytoplankton

assembly could be explained by a high level of stochastic organisation at the metacommunity level. When comparing connected and isolated environments, we expected stochastic mechanisms to act with less strength at isolated environments due to dispersal limitation and higher constraint of environmental factors in the absence of hydrological influence. Nevertheless, the percentages of randomness were both high. At these isolated lakes and swamps, the progress of the ecological succession could take different directions after the disconnection from the drainage network. Differences in the initial conditions (e.g. magnitude and duration of the lotic influence, the amount of inoculum, the time of disconnection, initial habitat conditions) may be crucial for the successional stage reached by the species assemblages (Amoros & Bornette, 2002). A possible role of priority effects (Chase, 2007; Vellend et al., 2014), understood as variations in the order that species colonise habitats, amplifies initial differences and creates variations in the structure that lead to more stochasticity. This is related to chaotic systems property of sensitive dependence on initial conditions. Initial differences blow up with time (Lewin, 2000) leading to differences in assemblage configuration at each environment and consequently, driving the evolution of the community. The high level of stochasticity found in our system with the co-occurrence model could be related to the fact that the analysis works at fine resolution level (pairs of species associations). In stochastic systems, when patterns are analysed at a low aggregation level (such as the presence-absence species resolution, or trajectories of individual particles in mathematical models), things seem to be more erratic and less predictable than if we look at more

aggregated level such as total phytoplankton biomass or certain groups of algae (e.g. diatoms or cyanobacteria) for which the systems turn more predictable (Hastings et al., 1993; Smale, 1998; Scheffer, 1999).

The non-random co-occurrence patterns suggest species interactions both positive and negative (Pitta et al., 2012), or of environmental conditions that favour or inhibit species coexistence. Our results indicated that the weaker pattern of non-random co-occurrence found at the main channels was due to the fact that the mechanisms of species selection are stronger than in the other sites. Then, the low positive and absence of negative co-occurrences may be a result of the environmental filtering at large rivers, where conditions of turbulence, flow velocity, and turbidity determine the presence of a pauperised assemblage of few specialised functional groups (Zalocar de Domitrovic et al., 2007; Devercelli et al., 2014). The connected lakes and isolated environments were the sites with the highest number of positive associations. The phytoplankton of lentic environments undergoes less frequent hydrological fluctuations (Devercelli et al., 2014), allowing the development of pairs of species associations more often than the expected by chance. The number of negative associations was higher in isolated sites and secondary channels indicating higher frequency of interspecific competition or 'mutual exclusions'. Particularly, in ISL negative co-occurrence, patterns may result from species turnover along a heterogeneous environmental gradient (high variability in the NMDS) in which species preferring one of both extremes rarely coexist.

The total phytoplankton variation explained by the variation partitioning analysis (pCCA) was only 17.3%. Low explanation percentage is a common feature in ecological studies (ter Braak & Šmilauer, 2012; Soininen, 2014). Explanation power diminishes in unimodal (CCA) with respect to linear methods (RDA) and with increments in species variability and multiple gradients of explanatory variables, all characteristics that present our analysis. The unexplained variation is not only due to methodological characteristics, but it is also the impossibility to represent all the existent variables (environmental, spatial, etc.). For these reasons, the interpretation of the unexplained percentage exclusively as a measure of stochasticity is inappropriate as it is part of the correlative nature of variance-partitioning analyses and of our fail in sampling (Soininen, 2014). As a

consequence, in our study, the residual variation (82.2%) may result from stochastic and historical processes, high temporal variation due to phytoplankton succession and different hydrological phases that cannot be caught in the two periods sampled (further explanation below), and also from environmental variables and stochastic processes that have not been recorded. The inclusion of temporal variation and of other predictors indicative of trophic interactions such as the abundance of certain zooplankton groups will help to improve the explanation of these analyses. Zooplankton interactions could be especially important to explain phytoplankton variations in isolated environments where a higher density of zooplanktonic species able to predate on phytoplankton could be found (José de Paggi & Paggi, 2007; Frau et al., 2015).

Variation partitioning analysis also provided evidence for the importance of stochastic and deterministic factors for the metacommunity. The total variation in phytoplankton structure (17.3%) was decomposed in 7.7% purely environmental, 7.2% purely spatial, 2.4% purely temporal (significant fractions at  $P < 0.001$ ), and 1% shared by environmental and spatial variables (significant fraction at  $P < 0.005$ ). The pure environmental variation was represented by the relation of species biovolume to water transparency, vegetation coverage, conductivity, and TP (CCA) which is a suggestive observation in line with niche-assembly processes. Species turnover from one extreme to the other of environmental gradients depends on their functional traits and mechanisms of trade-off to tolerate or exploit the prevalent conditions (Reynolds et al., 2002). Depletion in the aquatic light climate is compensated with the development of species posing physiological and morphological strategies to capture light under restricted conditions (Izaguirre et al., 2004). The structuring effect of macrophytes on microalgae is undeniable. On one hand, they increase the environmental heterogeneity resulting in new microhabitats for species colonisation; on the other hand, they offer refuge to algal predators, diminish light incidence, and produce allelochemical compounds that inhibit growth in some species, among others (reviewed in: de Tezanos Pinto & O'Farrell, 2014). As regards conductivity, it is a measure of the ion concentration that positively affects photosynthesis (Rocha et al., 2009). In this system, it also responds to dilution-

concentration processes constituting an indicator of the hydrological connectivity degree (Mayora et al., 2013). As regards TP, even the relation with phytoplankton was weaker than with the other variables. It may also be an evidence of a niche effect, in line with Sommer's (1984) early experiments in which it was stated that the oscillations of a single nutrient may increase species diversity.

The environmental factors were almost not spatially structured since the pCCA showed a low overlap (1%) of the environment-space components. This percentage could represent the proportion of conductivity variation (due to its higher VIF with spatial variables) related to the hydrological gradient, therefore spatially structured, as mentioned above. Nevertheless, the proportion explained by the pure spatial component was as large as the environmental fraction (7.2 vs. 7.7%). As regards the pure spatial variation, it has been repeatedly associated with the stochastic processes of random dispersal (Legendre et al., 2005). Nevertheless, there are some caveats with this interpretation (Vellend et al., 2014). Soininen (2015) pointed out that assemblages spatially structured mean that nearer sites are compositionally more similar than the more distant, and this could be due to either stochastic or deterministic processes. In our study, the waterbodies located in close proximity according to geographical coordinates ( $x$  and  $x^2$ ) and watercourse distance to the lotic environment showed a more similar structure than the more distant ones. Watercourse distance was a better predictor than overland distance awarding more importance to passive dispersal via water connections (Soininen et al., 2007; Chisholm et al., 2011; Liu et al., 2013). This means that stochastic processes mediated by random dispersion among waterbodies are an important structuring factor for phytoplankton metacommunities, or at least as important as the environmental component. Other authors found that organisms with high dispersal capacity were more limited by environmental filtering than spatial components, at least in comparison with organisms with low dispersal capacity (Heino, 2011; Padial et al., 2014), but in our case, similar relevance was found.

The remaining explanation percentage (2.4%) in the pCCA corresponded to the temporal component. In floodplain rivers, temporal changes are mostly due to hydrological fluctuations that exert an important influence on the environmental conditions and the

connectivity network (Junk et al., 1989; Amoros & Bornette, 2002; Thorp et al., 2006), besides differences among seasons and interannual variability. The poor temporal explanation found in the analysis is due to the small variability considered that was just attributed to differences between two low-water periods. Therefore, the temporal scale should be increased in future studies including different hydrological phases to fully assess the conditions that shape phytoplankton (Liu et al., 2013; Padial et al., 2014).

Considering the patterns of random and non-random co-occurrences and the data of species distributions along environmental and spatial gradients in the phytoplankton metacommunity, we can guess that several ecological processes both stochastic and deterministic are acting (Vergnon et al., 2009; Soininen et al., 2013). Different combinations of environmental filtering, species interactions, dispersal limitation, and random dispersal, could give place to different metacommunity models. The presence of positive and negative non-random species co-occurrence stands with the species association to certain environmental conditions like in the species sorting model (Leibold et al., 2004). Higher importance to dispersal between environments generates high rates of random co-occurrences in line with the mass effect model that could be interpreted as a special case of species sorting (Heino et al., 2014). Finally, the high frequency of random co-occurrences (both in connected and isolated habitats) and the dependence of community similarities on the spatial scale suggest that local assemblages show less-species structured patterns, as a consequence of random dispersal stimulated by the connectivity among environments (Leibold et al., 2004; Logue et al., 2011). Therefore, it is hypothesised that an integrative perspective of the current metacommunity models is necessary to explain the phytoplankton metacommunity structure in floodplain systems.

Overall, the occurrence of both stochastic and deterministic forces acting on phytoplankton assembly in floodplain rivers is in concordance with the current consensus in metacommunity ecology (Vellend et al., 2014), and the integrated proposals of unifying neutral and niche perspectives (Gravel et al., 2006; Holt, 2006; Scheffer & van Nes, 2006). In this sense, Padial et al. (2014) pointed out that it would be more an exception than a rule excluding one of the both in structuring metacommunities. Once this consensus is

reached, we should look for the properties that determine the variation of the relative importance of one of both processes in a particular ecosystem (Chase & Mayers, 2011). We suggest that the complexity of floodplain rivers mediated by the high environmental heterogeneity and spatiotemporal scales in combination with the intricate drainage network indicates the preponderance of stochastic processes (Thorp et al., 2006).

There are still gaps between theoretical and empirical approaches within metacommunities (Logue et al., 2011). Mathematical models contributed largely to explain chaotic deterministic systems (Lewin, 2000). Experimental studies have provided evidences that ecosystems also behave like that (Ringelberg & Kersting, 1978; Hastings et al., 1993; Benincà et al., 2008). However, difficulties arise when dealing with ecological systems, and especially with floodplain rivers, because of the multiplicity of simultaneous factors and processes, synergic effects of variables, and the impossibility to measure all relevant information. Finding out the mechanisms throughout which randomness operates is a difficult task, but also building the complexity of niche “has so far been prohibitive” (Vergnon et al., 2009). Trying to find out the underlying mechanisms of diversity assembly in view of such difficulties is a challenging—and a slightly stressing—undertaking. Nevertheless, we can go ahead with the encouragement that it is not necessary to know everything exactly to understand (Smale, 1998).

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